

THE INFLUENCE OF SUCCESSIONAL PROCESSES AND DISTURBANCE ON THE STRUCTURE OF *TSUGA CANADENSIS* FORESTS

ANTHONY W. D'AMATO,^{1,2,3,4} DAVID A. ORWIG,² AND DAVID R. FOSTER²

¹Department of Forest Resources, University of Minnesota, St. Paul, Minnesota 55108 USA

²Department of Natural Resources Conservation, University of Massachusetts, Amherst, Massachusetts 01003 USA

³Harvard Forest, Harvard University, 324 North Main Street, Petersham, Massachusetts 01366 USA

Abstract. Old-growth forests are valuable sources of ecological, conservation, and management information, yet these ecosystems have received little study in New England, due in large part to their regional scarcity. To increase our understanding of the structures and processes common in these rare forests, we studied the abundance of downed coarse woody debris (CWD) and snags and live-tree size-class distributions in 16 old-growth hemlock forests in western Massachusetts. Old-growth stands were compared with eight adjacent second-growth hemlock forests to gain a better understanding of the structural differences between these two classes of forests resulting from contrasting histories. In addition, we used stand-level dendroecological reconstructions to investigate the linkages between disturbance history and old-growth forest structure using an information–theoretic model selection framework.

Old-growth stands exhibit a much higher degree of structural complexity than second-growth forests. In particular, old-growth stands had larger overstory trees and greater volumes of downed coarse woody debris (135.2 vs. 33.2 m³/ha) and snags (21.2 vs. 10.7 m³/ha). Second-growth stands were characterized by either skewed unimodal or reverse-J shaped diameter distributions, while old-growth forests contained bell-shaped, skewed unimodal, rotated sigmoid, and reverse J-shaped distributions. The variation in structural attributes among old-growth stands, particularly the abundance of downed CWD, was closely related to disturbance history. In particular, old-growth stands experiencing moderate levels of canopy disturbance during the last century (1930s and 1980s) had greater accumulations of CWD, highlighting the importance of gap-scale disturbances in shaping the long-term development and structural characteristics of old-growth forests. These findings are important for the development of natural disturbance-based silvicultural systems that may be used to restore important forest characteristics lacking in New England second-growth stands by integrating structural legacies of disturbance (e.g., downed CWD) and resultant tree-size distribution patterns. This silvicultural approach would emulate the often episodic nature of CWD recruitment within old-growth forests.

Key words: coarse woody debris; dendroecology; forest structure; gap dynamics; Massachusetts; natural disturbance-based silviculture; old-growth; size-class distributions; stand development; *Tsuga canadensis*.

INTRODUCTION

In recent decades, the maintenance of native biodiversity through the restoration of late successional forest structure has emerged as an important forest management objective (Hunter 1999, Lindenmayer and Franklin 2002). Suggested approaches for accomplishing this objective include basing the frequency, intensity, and landscape distribution of harvests after natural-disturbance patterns (Seymour and Hunter 1999) and artificially creating old-growth structural attributes, especially large snags and downed logs (e.g., Rose et al. 2001, Maguire and Chambers 2005). Central to these approaches is a detailed understanding of the natural dynamics and structure of remnant old-growth

forest ecosystems (Spies and Franklin 1991, Tappeiner et al. 1997). While such information has been developed for regions supporting large areas of old-growth forest in the United States, such as the Pacific Northwest, upper midwest, and Adirondack region of New York, it is largely lacking in regions where old-growth forests are scarce, such as southern New England (D'Amato et al. 2006). In these areas, there is great need for detailed investigations of the dynamics and structural attributes of the few remnant old-growth stands. Study of these systems will increase our understanding of the structures and function of forests historically dominated by natural processes and will facilitate the development of strategies for restoring late seral structure to second-growth forests across northeastern North America (e.g., Keeton 2006). More specifically, establishing mechanistic linkages between patterns of natural disturbance and resulting old-growth structures will allow for the development of silvicultural systems that not only

Manuscript received 5 June 2007; revised 21 December 2007; accepted 24 January 2008. Corresponding Editor: Y. Luo.

⁴ E-mail: damato@umn.edu

approximate patterns of natural canopy disturbance (cf. Seymour et al. 2002), but also integrate their structural legacies.

Old-growth forests are widely recognized as structurally complex ecosystems characterized by a diversity of tree sizes and ages and abundant coarse woody debris in the form of downed logs and snags (Harmon et al. 1986, Spies et al. 1988, Peterken 1996). Natural disturbances, including fire, wind, insects, and diseases, often play a central role in the development of these structures by initiating episodic inputs of dead wood (Schoonmaker 1992, Sturtevant et al. 1997, Palik and Robl 1999, Chokkalingam and White 2002, Muller 2003) and creating canopy gaps that promote the development of complex tree size distributions (Runkle 1982, Veblen 1986, Lorimer 1989, Spies et al. 1990, Winter et al. 2002, Zenner 2005). Similarly, within-stand processes, including competition and mortality, strongly influence the development of old-growth structural features, including snags (Lee et al. 1997, Busing 2005) and rotated sigmoid and reverse-J shaped live-tree diameter distributions (Meyer 1952, Goff and West 1975, Robertson et al. 1978, Leak 1996, Lorimer et al. 2001).

Despite the recognized importance of natural-disturbance processes in the development of forest structure (e.g., Harmon et al. 1986, McComb et al. 1993, Spies 1998, Hennon and McClellan 2003), most studies examining old-growth structural attributes have focused on successional dynamics. For example, the dynamics of coarse woody debris (CWD) are commonly examined with chronosequences of different ages following stand-replacing disturbances (e.g., Spies et al. 1988, Sturtevant et al. 1997, Clark et al. 1998, Hély et al. 2000, Tinker and Knight 2000, Boulanger and Sirois 2006). This approach underscores the role of large, intense disturbances in generating long-lasting biological legacies such as logs, snags, and surviving trees (e.g., Spies et al. 1988, Tinker and Knight 2000), but potentially ignores the importance of more local, gap-scale disturbance in promoting these structures through the course of stand development. Interestingly, the few chronosequence studies that do evaluate gap processes, such as insect outbreaks (Sturtevant et al. 1997, Hély et al. 2000) and low-intensity fires (Spies and Franklin 1991, Weisburg 2004), indicate that they may generate high levels of structural variation.

In northeastern North America, stand-replacing disturbance is uncommon, whereas localized windthrow and other frequent, gap-scale disturbances strongly influence stand development (Runkle 1982, Seymour et al. 2002). This makes quantifying the impact of disturbance on the structure of old-growth ecosystems challenging because easily measured attributes, such as maximum age of canopy trees, do not capture much of the information on disturbance processes. Information on gap-scale processes commonly comes from repeated measurements on the same old-growth stands or dendroecological reconstructions. Studies using repeated

measurements are generally short term (i.e., two to three decades) relative to the longevity of old-growth trees (e.g., Filip et al. 1960, Foster 1988, Runkle 1992, 2000, Lorimer et al. 2001, Muller 2003, Busing 2005; but see Woods 2000*a, b*). In contrast, dendroecological investigations are capable of capturing long-term changes in forest composition and live-tree structure (e.g., Henry and Swan 1974, Oliver and Stephens 1977, Foster 1988, Fritts and Swetnam 1989, Abrams and Orwig 1996, McLachlan et al. 2000). The limited attention that these long-term studies have given to structural attributes, such as CWD, leads to uncertainty in our understanding of the linkages between disturbance history and structural components (Kulakowski and Veblen 2003, Fraver 2004). Moreover, while there have been several characterizations of the structural attributes of old-growth ecosystems in northeastern North America (e.g., Gore and Patterson 1986, Tyrell and Crow 1994*a*, McGee et al. 1999, Ziegler 2000), little attention has been paid to how variation in disturbance history may affect variation in structural attributes within these systems.

To examine the influence of long-term disturbance dynamics on old-growth forest structure, we utilized tree-ring data to reconstruct the stand dynamics of 16 old-growth eastern hemlock (*Tsuga canadensis* L.) stands in western Massachusetts. In addition, we sought to compare downed CWD and live-tree size distributions in old-growth and adjacent second-growth hemlock stands and interpret the importance of contrasting developmental histories on these structures. We then examined how the information gained can inform ecosystem management efforts aimed at restoring old-growth forest structures to managed forests in the region.

METHODS

Study area and sampling

Sampling was conducted in 24 eastern-hemlock dominated forests in the Berkshire Hills and Taconic Mountains of western Massachusetts (Fig. 1, Table 1). This area has a humid, continental climate with elevations ranging from 360–800 m above sea level and well-drained sandy loam soils formed from weathered gneiss and schist (Zen et al. 1983, Scanu 1988). Sixteen sites were old-growth stands, which were defined as forests lacking any evidence of past land use and containing at least five canopy trees >225 years old per hectare, which indicates establishment prior to European settlement (Field and Dewey 1829) and exceeds 50% of the maximum longevity for species commonly encountered in these forests (Dunwiddie and Leverett 1996, McGee et al. 1999). Extensive analysis of historical documents and the collection of increment core samples were used to ensure that each old-growth study area met these criteria (D'Amato et al. 2006). It is important to note that these areas represent the largest

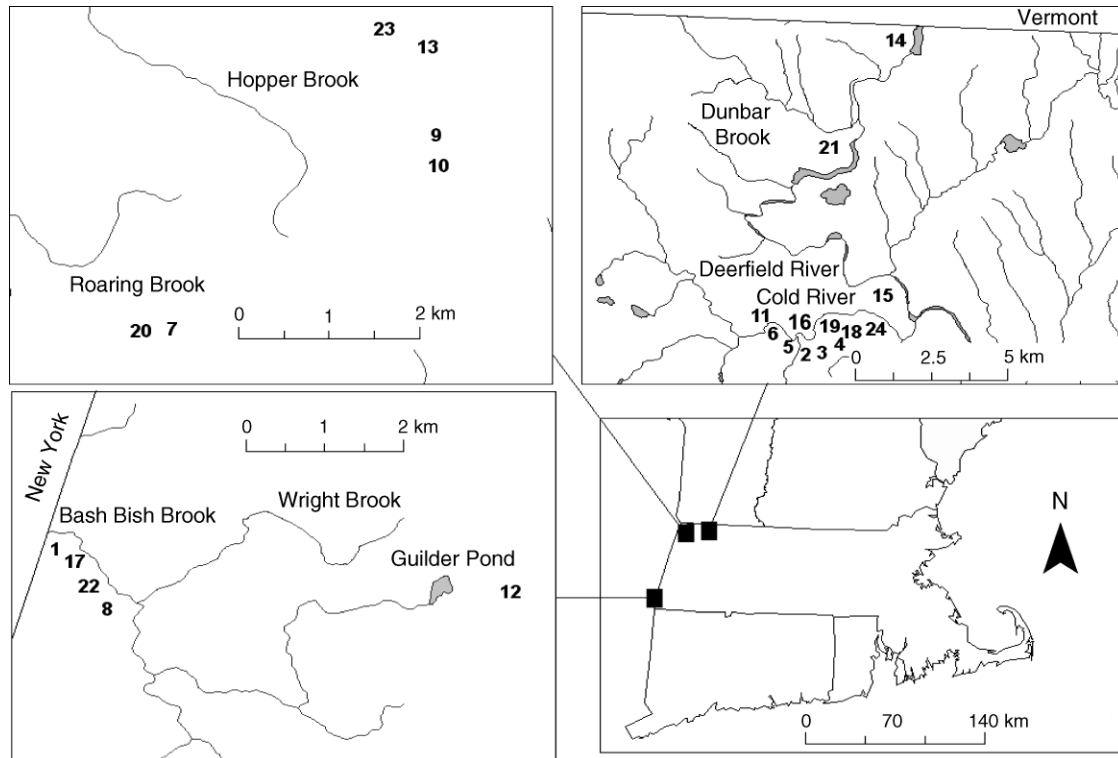


FIG. 1. Location of eastern hemlock-dominated old-growth and second-growth stands in western Massachusetts. See Table 1 for key to stand numbers.

TABLE 1. Physiographic and stand characteristics of old-growth (OG) and second-growth (2G) eastern hemlock study sites in western Massachusetts, USA.

Study site (Fig. 1 map key)	Status	Hemlock (%)†	Density (stems/ha)‡	Basal area (m ² /ha)	Maximum age (yr)§	Mean canopy-tree age (yr)	Elevation (m)	Slope	Aspect
Bash Bish Falls (1)	OG	76.9	525	48.4	277	226	370–450	26°–46°	353°–4°
Black Brook (2)	OG	79.4	627	47.4	328	210	470–520	23°–38°	350°–10°
Cold River A1 (3)	OG	52.7	356	44	374	229	390–480	36°–40°	336°–340°
Cold River A2 (4)	OG	61.6	513	39.5	488	246	400–490	33°–41°	296°–320°
Cold River B (5)	OG	76.5	516	38.6	333	188	330–490	40°–42°	332°–340°
Cold River D (6)	OG	71.2	660	49.1	441	216	350–390	20°–31°	272°–321°
Deer Hill (7)	OG	81.4	325	41.5	282	182	550–580	33°–38°	270°–336°
Grinder Brook (8)	OG	88.1	433	38	333	236	360–450	38°–43°	27°–50°
Hopper A (9)	OG	63.8	606	41.4	414	196	580–700	26°–40°	225°–270°
Hopper B (10)	OG	42.4	549	35.4	329	198	600–680	31°–35°	280°–321°
Manning Brook (11)	OG	75.1	825	57.4	352	219	360–420	29°–35°	45°–77°
Mt. Everett (12)	OG	67.0	399	35.6	325	237	470–530	31°–45°	35°–50°
Money Brook (13)	OG	77.9	588	55.4	302	206	600–660	24°–32°	33°–308°
Tower Brook (14)	OG	50.0	499	48.6	244	177	450–470	33°–42°	70°–88°
Todd Mountain (15)	OG	76.8	551	45	377	209	450–470	28°–35°	315°–358°
Wheeler Brook (16)	OG	73.1	533	52.1	300	206	330–370	19°–28°	107°–143°
Bash Bish Falls (17)	2G	70.0	708	38	171	115	380–430	26°–34°	325°–350°
Cold River A (18)	2G	60.0	992	38.9	182	132	430–510	29°–36°	290°–303°
Cold River B (19)	2G	69.8	1275	39.4	270	108	340–380	31°–35°	255°–290°
Deer Hill (20)	2G	52.5	1217	37.6	216	113	500–540	35°–38°	350°–0°
Dunbar Brook (21)	2G	72.6	875	52.7	204	136	380–410	27°–36°	45°–68°
Grinder Brook (22)	2G	57.3	1042	39.7	151	128	400–460	25°–46°	40°–70°
Money Brook (23)	2G	70.5	825	42.6	201	133	590–620	26°–34°	260°–290°
Trout Brook (24)	2G	63.0	1067	40.4	323	136	320–370	29°–32°	330°–340°

† Importance value calculated as: (Relative basal area + Relative density)/2.

‡ Live trees ≥ 10 cm dbh.

§ Age of oldest tree with complete increment core sample.

known remaining old-growth areas on public land in western Massachusetts.

To facilitate comparisons between successional stages, sampling was also conducted in eight hemlock-dominated second-growth stands in close proximity (i.e., <5 km) to old-growth study sites. Second-growth sites were selected carefully to ensure that the environmental settings (i.e., elevation, topographic position, slope steepness, and aspect) were as similar as possible to those of the old-growth stands (Table 1). Although detailed harvesting records were unavailable for most second-growth areas, early state documents indicated that many of these areas were clear-cut harvested in the late 1800s and early 1900s (Avery and Slack 1926). Dendroecological analyses of these second-growth areas confirmed that they were clear-cut harvested between the 1870s–1900s, as dramatic release and coincident recruitment pulses were observed in each of these stands during these decades.

Stand structure and site disturbance history

Depending on stand size, 3–5 0.04-ha plots were established along transects orientated through the central portion of each study area and permanently marked. Species and diameter at breast height (dbh) was recorded for every tree (stems ≥ 1.37 m tall and ≥ 10 cm dbh) established within these plots. In addition, all saplings (stems ≥ 1.37 m tall and ≤ 10 cm dbh) were tallied by species. Increment cores were taken from all trees at 0.3 m height for radial growth analyses and age determinations. All increment cores were air-dried, sanded, and aged with a dissecting microscope and annual ring widths were measured to the nearest 0.01 mm using a Velmex (East Bloomfield, New York, USA) measuring system. It is important to note that we chose relatively small plot sizes to enable the collection of substantial dendroecological data across multiple old-growth sites. While these plot sizes are appropriate for reconstructing gap-scale disturbances, they may have been inadequate for capturing stand-level heterogeneity in structure (cf. Rubin et al. 2006). Nonetheless, we felt these plot sizes represented a reasonable compromise in levels of accuracy required for dendroecological reconstructions and structural characterizations.

The disturbance history of each study area was reconstructed by examining 56–176 cores per site, for a total of 2577 increment cores. In particular, each core was examined for (1) large, abrupt increases in radial growth indicating the loss of overtopping canopy trees and (2) rapid initial growth rates suggesting establishment in a canopy gap (Lorimer and Frelich 1989). Trees with mean growth rates ≥ 1.2 mm/year over the initial five years of radial growth were considered gap-recruited trees. As such, the date of the innermost ring for these individuals was recorded as the date of canopy accession (i.e., date of recruitment into the forest canopy; Lorimer et al. 1988, Frelich 2002, Ziegler 2002). All cores were evaluated separately for growth releases (i.e., abrupt

increases in radial growth) using the criteria established by Lorimer and Frelich (1989). These analyses determine the date in which understory trees were released into the forest canopy following the loss of overtopping canopy trees. For these analyses, we assumed that the year in which the growth release began represented the date of canopy recruitment for a given individual. Disturbance chronologies for each site characterizing the amount of canopy area disturbed each decade were created using the methodology developed by Lorimer and Frelich (1989; see D'Amato and Orwig [2008] for a detailed description of these methods). Nonmetric multidimensional scaling (NMS) was used to synthesize the dominant gradients in disturbance history among study sites using the approach outlined in D'Amato and Orwig (2008). In brief, a matrix of study sites by decade was constructed and the percentage of canopy area disturbed was entered for each site and decade. NMS was run using this data matrix and the resulting NMS scores from these analyses were utilized to explore relationships between downed CWD and snag volumes, snag density, and disturbance history (see *Methods: Statistical analyses*).

Downed coarse woody debris and snags

The volume of downed coarse woody debris (CWD; downed trees, branch fragments) was measured at each site using the line intercept method (Harmon and Sexton 1996). In each study area, three 50-m transects radiating from a randomly located point were established. To avoid potential bias due to steep slopes, azimuths of 30°, 150°, and 270° were used for the three transects. In addition to the randomly located transects, three 10-m transects originating from the center of each 0.04-ha plot were established along azimuths of 30°, 150°, and 270° to allow for direct comparisons between stand disturbance dynamics and the abundance of downed CWD. Random points resulting in overlap with plot-level transects were not used. It is important to note that the use of relatively short transects (<100 m, sensu Harmon and Sexton 1996) may have limited our ability to fully capture the variation in downed CWD at these sites. Nonetheless, the mean coefficient of variation for within-site downed CWD abundance was 46.5%, which is within acceptable levels of accuracy for sampling coarse woody debris (cf. Woldendorp et al. 2004). As such, we feel our estimates are accurate representations of downed CWD within old-growth and second-growth hemlock systems.

All fallen tree or branch fragments ≥ 10 cm in diameter and ≥ 1.5 m long encountered along each transect line were measured and identified by species. If a determination of species could not be made in the field, samples were taken from the field and examined under a dissecting microscope. In cases in which species could not be determined, samples were broadly classified as either hardwood or conifer. Pieces of downed CWD intersected at their central longitudinal axis by more

TABLE 2. Disturbance history and stand attribute variables used to model coarse woody debris (CWD) and snag abundance in old-growth hemlock stands.

Abbreviation	Definition
DISTDYN90†	scores from nonmetric multidimensional scaling (NMS) ordination utilizing disturbance chronology spanning 1910–1990
DISTDYN40‡	scores from (NMS) ordination utilizing disturbance chronology spanning 1950–1990
CANOPY80	percentage of overstory trees experiencing canopy disturbance from 1980–1994
MEANDIST	mean decadal disturbance rate over length of disturbance chronology utilized in NMS ordinations
MAXAGE	age of oldest canopy tree
AVGDBH	mean diameter at breast height (dbh) of canopy trees

† Variable only utilized in models for CWD volume.

‡ Variable only utilized in models for snag volume and density.

than one transect were tallied for each transect intersection, whereas pieces with a longitudinal axis directly on plot center were only tallied once (FIA 2005).

For each piece of downed CWD encountered, we also recorded orientation, origin (uproot, bole, snap, or unknown event), diameter, and decay class following the four-class system outlined by Fraver et al. (2002). Extent of decay was inspected for each piece using a pointed metal chaining pin. Decay classes were defined according to Fraver et al. (2002) as class I (wood is sound, bark intact, smaller to medium sized branches present), class II (wood is sound to partially rotten, branch stubs firmly attached with only larger stubs present, some bark slippage), class III (wood is substantially rotten, branch stubs easily pulled from softwood species, wood texture is soft and compacts when wet), or class IV (wood is mostly rotten, branch stubs rotted down to log surface, bark no longer attached or absent [except *Betula* spp.], log is oval or flattened in shape). Downed CWD volume was estimated using the following formula:

$$V = (\pi^2 \sum d^2 / 8L) \times 10\,000 \text{ m}^2/\text{ha}$$

where V is the volume (m^3/ha), d is the CWD fragment diameter (m), and L is the transect length in meters (van Wagner 1968). Volume estimates for each transect at the stand- and plot-level were averaged to determine total mean volume for each study site.

The species, height, dbh, decay class (see downed CWD), and fragmentation class (1, crown intact; 2, crown missing but large branches present; 3, bole only; 4, broken bole) were recorded for all snags ≥ 1.5 m tall and ≥ 10 cm dbh within each 0.04-ha plot. Snag volume was calculated from snag basal area and height utilizing volume formulas developed for each fragmentation class (Tyrell and Crow 1994a).

Statistical analyses

Diameter distributions were constructed with 5-cm size-class intervals and converted to relative frequency distributions to allow for comparisons across sites with varying densities. To determine the general trend of each distribution, first-, second-, third-, and fourth-order polynomial functions were fit to the semilogarithmic-transformed diameter distributions of each stand following the methods outlined by Goff and West

(1975) and Zenner (2005). Curve forms with the highest adjusted r^2 were considered the best approximation for a given diameter distribution. Structural attributes, including downed CWD and snag volumes, snag density, and large tree (≥ 50 cm dbh) densities were compared between successional stages using Wilcoxon rank-sum tests. Coarse woody debris decay distributions were analyzed using the Kolmogorov-Smirnov goodness-of-fit test. The directionality of fallen trees within each study area was analyzed using Rayleigh's Uniformity Test (Greenwood and Durand 1955). In cases in which fallen trees displayed uniform directionality, the mean direction of fallen trees was compared to study area aspect using a modified Rayleigh's test (Durand and Greenwood 1958). Tests of directionality were performed using Oriana 2.0 (Kovach 1994), whereas all other statistical analyses were conducted using SAS version 9.1 (SAS Institute 2004). Significance levels were set at $\alpha = 0.05$ for all analyses and experiment-wide probability levels were protected by a sequential Bonferroni procedure (Rice 1989).

Linear regression analyses were used to test specific a priori hypotheses regarding the influence of factors, such as disturbance history and stand age, on the observed downed CWD volume, snag volume, and snag densities in old-growth hemlock stands (Table 2). Scores from NMS ordinations of the disturbance chronologies were used as variables representing the gradients in variation among study sites in terms of disturbance history. For models predicting downed CWD volume, NMS scores were based on NMS ordinations utilizing disturbance chronologies spanning 1910–1990, whereas NMS scores for models predicting snag volume and density were based on chronologies spanning 1950–1990. These chronology lengths were chosen based on log decay rates (McComb 2003) and snag fall rates (Lester 2003) for common species in our study areas and represent an approximation of the disturbance periods during which much of the downed CWD and snags in these stands were likely formed. For detailed analyses of older (i.e., 1720–1909) disturbance dynamics in these study areas, see D'Amato and Orwig (2008).

Based on our understanding of the factors potentially influencing downed CWD and snag abundance, a set of plausible models was constructed and evaluated using

the corrected Akaike Information Criterion, AIC_c (Burnham and Anderson 1998). AIC_c is derived from the maximum log-likelihood estimate and number of parameters in a given model, rewarding models for goodness of fit and imposing penalties for multiple parameters. Smaller AIC_c values indicate better models, and AIC_c values are ranked according to the difference between the AIC_c value for a given model (AIC_{ci}) and the lowest AIC_c value in a given set of models (AIC_{cmin}): $\Delta_i = AIC_{ci} - AIC_{cmin}$. The difference value, Δ_i , allows a strength of evidence comparison among the models, where increasing Δ_i values correspond with decreasing probability of the fitted model being the best approximating model in the set (Anderson et al. 2000). As a rule of thumb, models with $\Delta_i \leq 2$ have considerable support and should be considered when making inferences about the data (Burnham and Anderson 2001). While models with Δ_i between 2 and 4 also have some level of support, we chose to limit our interpretation to those models with the greatest levels of support as the best approximating models in the set (i.e., $\Delta_i \leq 2$). To approximate the probability of a model being the best in a given set, the Δ_i values were used to calculate Akaike weights (w_i) using the following formula (Burnham and Anderson 1998):

$$w_i = \frac{\exp(-\Delta_i/2)}{\sum_{r=1}^R \exp(-\Delta_r/2)}$$

where w_i is the Akaike weight for model i and R is the number of models in the set. For all model comparisons, a null model that only included the intercept term was included in the candidate set of models. Models based on a priori hypotheses were compared to the null model to determine whether the constructed models explained more variation in forest structural attributes. Note, we chose to use the corrected Akaike Information Criterion over the original Akaike Information Criterion due to its superior performance with smaller sample sizes (Burnham and Anderson 2001).

RESULTS

Comparisons between successional stages

Several diameter distribution patterns were observed for the old- and second-growth hemlock stands (Figs. 2 and 3). Size distributions in old-growth stands ranged from bell-shaped and skewed unimodal to rotated sigmoid and reverse J-shaped distributions (Fig. 2), whereas distributions in second-growth stands were either skewed unimodal or reverse-J distributions (Fig. 3). Despite sharing some similar general curve forms, old-growth stands typically had trees distributed over a greater range of diameter classes (Figs. 2 and 3; Plate 1). In addition, rotated sigmoid distributions, which contain distinct plateaus or bumps in the mid-range diameter classes (e.g., Tower Brook; Fig. 2), were not observed in second-growth stands (Fig. 3). Overall,

the density of large trees (≥ 50 cm) and saplings was higher in old-growth stands than in second-growth stands (Fig. 4).

Old-growth stands had approximately four times the volume of downed coarse woody debris (CWD; 135.2 ± 10.5 m³/ha; mean \pm SE) as second-growth (33.2 ± 4.4 m³/ha) stands (Table 3). Downed CWD input size, as measured by line-intercept diameters, was also greater in old-growth stands (mean [\pm SE] intercept diameters of 21.0 ± 0.6 and 16.0 ± 0.7 cm for old-growth and second-growth stands, respectively; $Z = -3.70$, $P < 0.0001$). The majority of downed woody debris in old-growth stands was composed of conifer species (i.e., *Tsuga canadensis* and *Picea rubens*; see Plate 1), whereas most downed wood inputs in second-growth stands were from hardwood species, particularly *Betula papyrifera*, *Fagus grandifolia*, and *Acer rubrum* (Table 3). Downed logs were randomly oriented in all second-growth stands except for the Dunbar Brook study site, which displayed uniform directionality (mean vector = 351° ; Rayleigh's $P < 0.05$) that was consistent with the mean slope aspect in this study area (slope aspect = 352° ; modified Rayleigh's $P < 0.05$). In contrast, downed logs displayed uniform directionality (Rayleigh's $P < 0.05$) in nine out of the 16 study old-growth study areas, with four sites (Cold River A1, Cold River D, Hopper B, Manning Brook) displaying orientations different from mean slope aspects (mean vectors = 43° , 65° , 270° , and 90° , respectively; modified Rayleigh's $P > 0.3$).

There were a greater total number of snags in second-growth stands vs. old-growth stands (Table 3); however, these were composed primarily of small diameter stems. In particular, mean snag diameter and the density of large snags (≥ 35 cm dbh) were both significantly greater in old-growth stands (Table 3). Nearly two-thirds ($64.8 \pm 6.6\%$; mean \pm SE) of the snags in old-growth sites had diameters greater than the mean live-tree diameter, while the majority ($61.4 \pm 8.0\%$) of the snags in second-growth stands had diameters smaller than the mean live-tree diameter. Total snag volumes were significantly greater in old-growth stands despite the higher total number of snags in second-growth stands (Table 3).

The distribution of downed CWD among decay classes did not differ between old-growth and second-growth stands (Fig. 5; Kolmogorov-Smirnov test $P = 0.89$). For both successional stages, the lowest proportion of downed CWD was in decay class IV (highest level of decay). However, downed CWD volume in decay class IV was 89.4% greater in old-growth vs. second-growth stands. Similar to the distributions of downed CWD, there was no difference in the distribution of snag volumes among decay classes between successional stages (Fig. 5; Kolmogorov-Smirnov test $P = 0.98$). Despite the similarities in distributions between successional stages, it is important to note that no second-growth stands had any snags in decay class IV (Fig. 5).

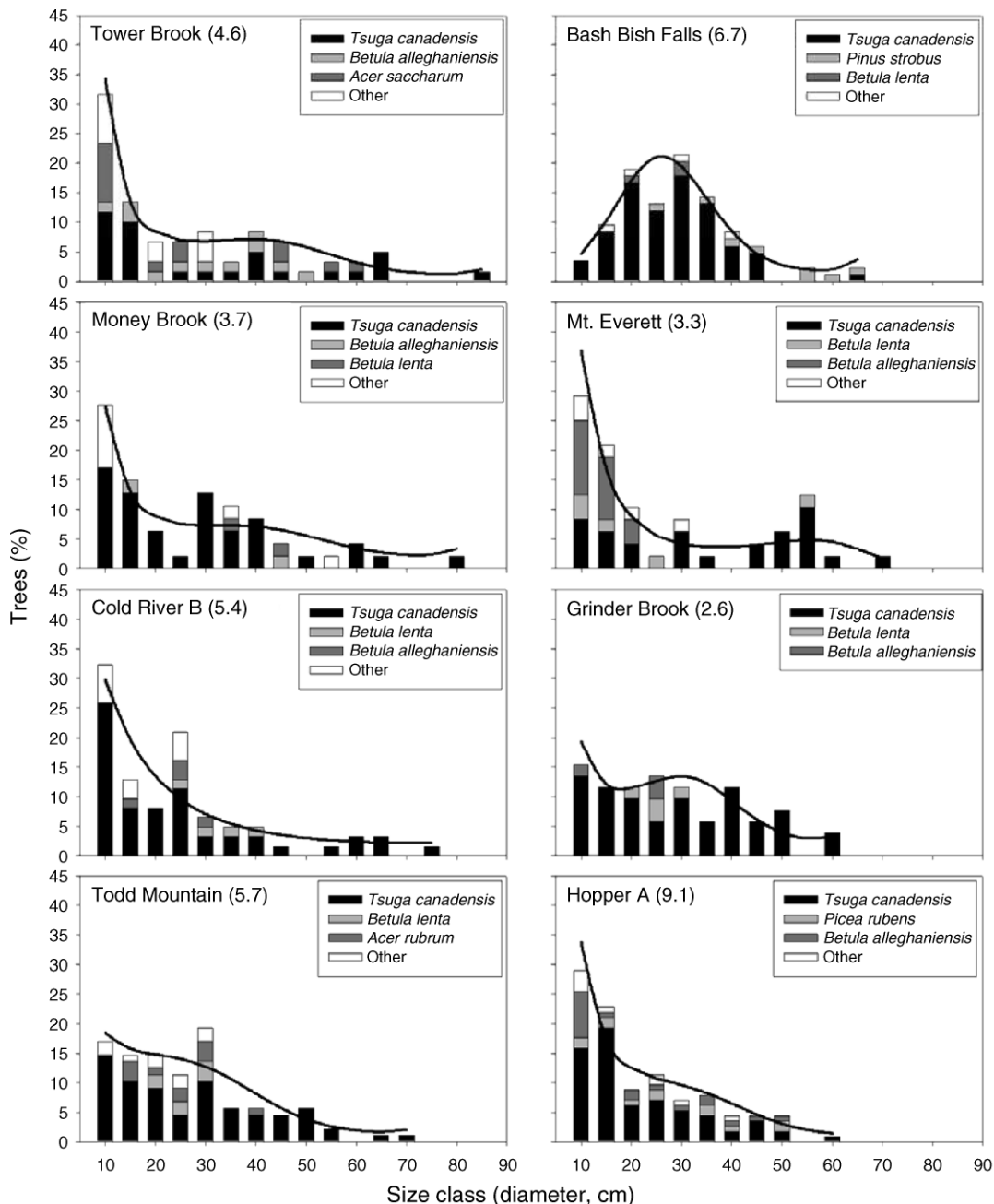


FIG. 2. Size-class distributions (based on relative frequency) for all tree species combined within old-growth eastern hemlock stands. Stands are ordered by maximum age, and regression curves are superimposed on the diameter distribution. Values in parentheses represent mean decadal disturbance rate (percentage of canopy area disturbed) from 1870 to 1989.

Variation in structure among old-growth forests

In addition to the differences in forest structure between successional stages, there was also a great degree of variation in structural attributes, such as size distributions, downed CWD volumes, snag volumes, and snag densities, among old-growth stands (Fig. 2, Table 3). Disturbance rates were also different among old-growth stands with mean decadal disturbance rates

ranging from 2.4% to 9.9% canopy area disturbed. In general, old-growth stands with moderate to high levels of canopy disturbance over the past 130 years (i.e., >3.0% canopy area disturbed per decade) tended to have well-formed reverse-J (e.g., Cold River D and Cold River A2 in Fig. 2) or rotated sigmoid size distributions (e.g., Tower Brook in Fig. 2), whereas stands with low levels of disturbance had bell-shaped (e.g., Deer Hill in

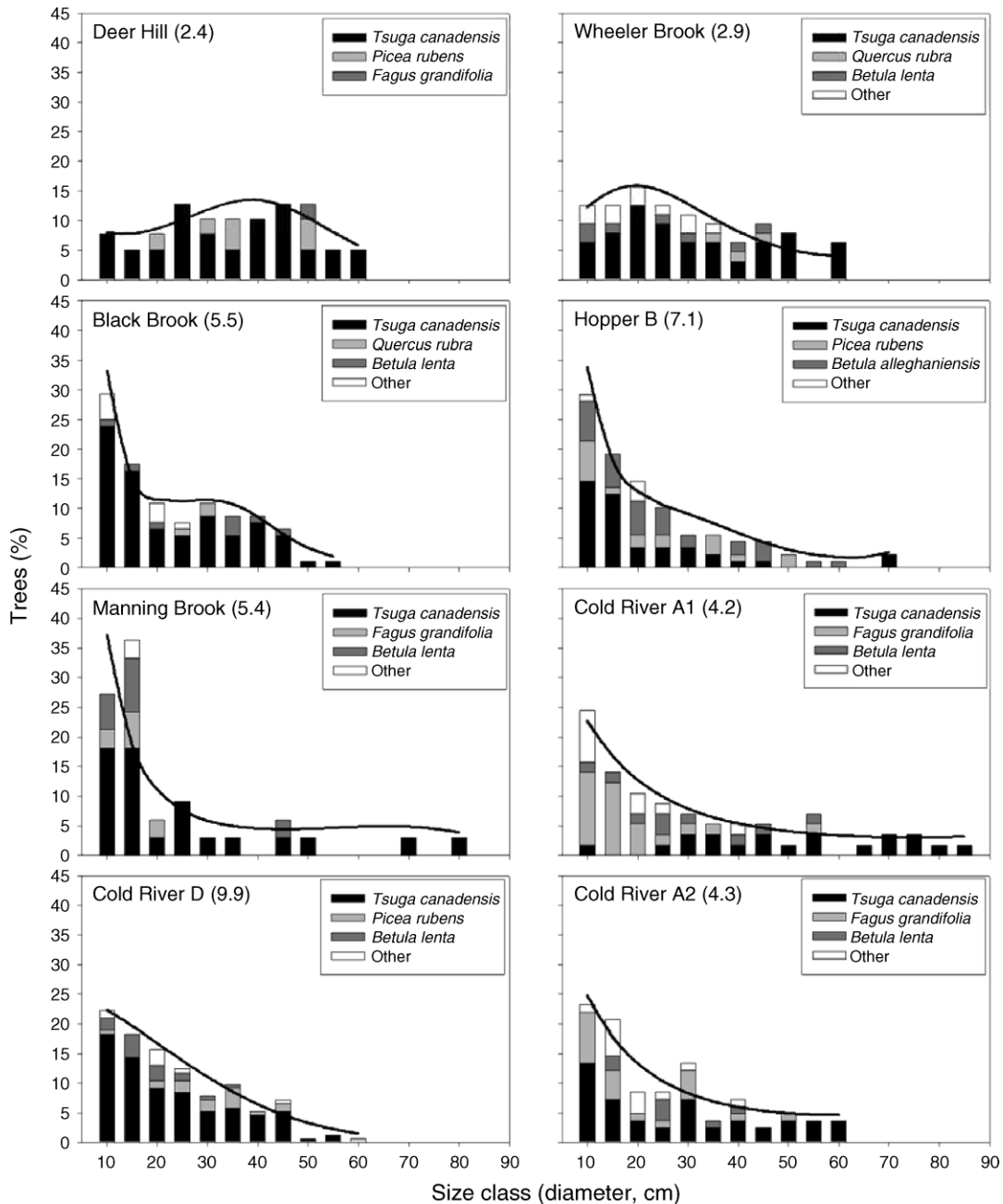


FIG. 2. Continued.

Fig. 2) or skewed unimodal distributions (e.g., Wheeler Brook in Fig. 2). An exception to this general trend was the Bash Bish Falls study site, which had a skewed unimodal distribution despite having a high mean level of canopy disturbance (Fig. 2). Interestingly, the youngest tree at this site ≥ 10 cm dbh was 103 years old, suggesting potential recruitment limitation at this site despite a high level of canopy disturbance.

Variation in disturbance history from 1910–1990 had a strong influence on the volume of downed CWD in

each old-growth stand, as the best single model for describing this structural attribute predicted a positive relationship between DISTDYN90 (model-averaged parameter = 36.7 ± 10.4 [\pm SE]) and downed CWD volume (Table 4). Pearson’s correlations between NMS scores used for calculating DISTDYN90 and the disturbance chronology data matrix indicated that the variables describing the percentage canopy area disturbed in the 1930s and 1980s, respectively, had the highest positive correlations with these NMS scores.

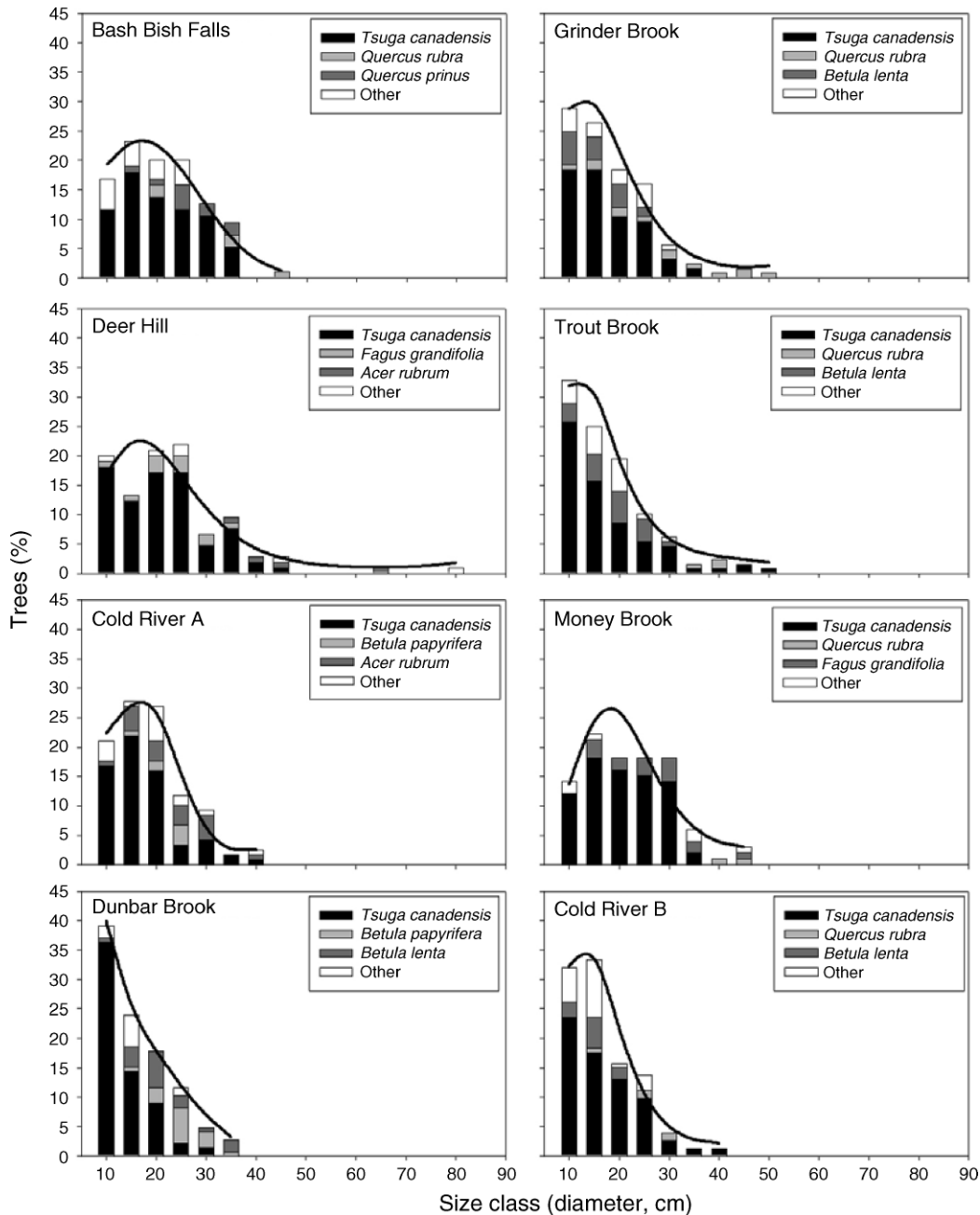


FIG. 3. Relative frequency distribution for all tree species combined within second-growth eastern hemlock stands. Regression curves are superimposed on the diameter distribution.

These correlations suggest that both historic and more recent disturbances have played a prominent role in structuring downed CWD pools in these sites. Correspondingly, there were significant differences in the distribution of downed CWD among decay classes between stands with positive and negative NMS scores (Fig. 6; Kolmogorov-Smirnov test $P < 0.05$). In particular, those stands experiencing higher levels of disturbance in the 1930s and 1980s (i.e., positive NMS scores) had greater volumes of decay class I, II, and IV

downed CWD compared to stands experiencing lower levels of disturbance during these decades (Fig. 6).

Mean dbh of living trees (AVGDBH) was the best predictor of snag volumes (Table 4) as old-growth stands with larger diameter living trees also contained higher snag volumes (model-averaged parameter = 1.8 ± 0.58). Four other models also had strong support as being the best approximating model for describing snag volumes (i.e., $\Delta_i < 2$; Table 4): variation in disturbance history from 1950–1990 (DISTDYN40), recent canopy

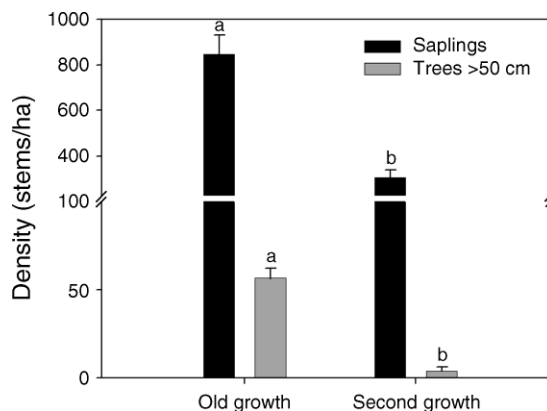


FIG. 4. Density of saplings and large trees (≥ 50 cm dbh) within old-growth and second-growth hemlock stands. Statistically significant differences ($P \leq 0.05$; Wilcoxon rank sum test) between successional stages are denoted with different letters.

disturbance (CANOPY80), mean disturbance rate from 1950–1990 (MEANDIST), and stand age (MAXAGE). Mean disturbance rate from 1950–1990 (MEANDIST) best described the density of snags at each site, as sites that experienced higher mean levels of canopy disturbance also exhibited greater snag densities (model-averaged parameter = 10.7 ± 3.1). Four other models also had strong support as being the best approximating model for describing snag densities (i.e., $\Delta_i < 2$; Table 4): variation in disturbance history from 1950 to 1990 (DISTDYN40), mean dbh of living trees (AVGDBH), recent canopy disturbance (CANOPY80), and stand age (MAXAGE). For all model comparisons, the null models had very little support of being the best model in the set (i.e., $\Delta_i < 10$; Table 4) indicating that the selected models were able to explain more variation in forest structure than other unmeasured factors.

DISCUSSION

Comparisons between successional stages

Our results indicate that old-growth hemlock forests exhibit a higher degree of structural complexity than second-growth hemlock forests in western Massachusetts, particularly live-tree size distributions and the

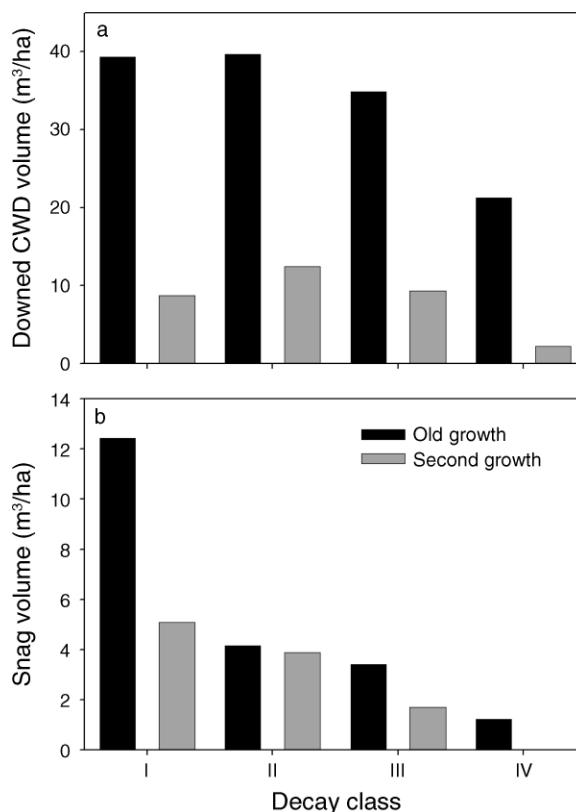


FIG. 5. Decay class distributions of (a) downed coarse woody debris and (b) snags in second-growth and old-growth eastern hemlock forests.

abundance and decay characteristics of downed coarse woody debris (CWD) and snags. These findings are consistent with other structural comparisons of second-growth and old-growth forest ecosystems in northeastern North America (Gore and Patterson 1986, McGee et al. 1999, Ziegler 1999, Crow et al. 2002) and are likely due to the differences in stand developmental history between the old-growth and second-growth stands. Specifically, the second-growth stands studied originated following stand-replacing disturbances (i.e., clear-cut harvesting) in the late 19th century, whereas the development of the old-growth areas had been primarily

TABLE 3. Characteristics of downed coarse woody debris (CWD) and snags in eastern hemlock stands in western Massachusetts.

Structural attribute	Old growth ($n = 16$)		Second growth ($n = 8$)	
	Mean \pm SE	Range	Mean \pm SE	Range
Downed CWD volume (m^3/ha)	$135.2^a \pm 10.5$	60.6–224.1	$33.2^b \pm 4.4$	19.9–47.8
Conifer downed CWD (%)	$87.0^a \pm 2.5$	68.6–98.4	$21.6^b \pm 6.1$	4.6–55.5
Snag volume (m^3/ha)	$21.2^a \pm 3.2$	1.0–44.0	$10.7^b \pm 2.3$	1.8–19.8
Total snag density (no./ha)	$30.0^a \pm 3.1$	6.3–50.0	$54.2^b \pm 10.0$	25.0–108.3
Large snag (≥ 35 cm) density (no./ha)	$13.4^a \pm 1.9$	6.3–25.0	$4.2^b \pm 3.1$	0–33.3
Snag diameter (cm)	$35.6^a \pm 2.5$	11.3–95.4	$21.4^b \pm 1.3$	10.1–46.6

Note: Statistically significant differences ($P \leq 0.05$; Wilcoxon rank sum test) between successional stages are denoted with different lowercase letters.

TABLE 4. Ranking of a priori hypothesized models relating forest structural attributes and disturbance history to downed coarse woody debris (CWD) volume, snag volume, and snag density in old-growth eastern hemlock forests.

Model	K^\dagger	AIC_c^\ddagger	$\Delta\§$	$W $
Downed CWD volume				
DISTDYN90	3	167.5	0	0.54
MAXAGE	3	169.9	2.36	0.17
AVGDBH	3	170.4	2.92	0.13
CANOPY80	3	171.4	3.89	0.08
MEANDIST	3	171.9	4.38	0.06
DISTDYN90 MAXAGE DISTDYN90 × MAXAGE	5	174.4	6.92	0.02
CANOPY80 MAXAGE CANOPY80 × MAXAGE	5	177.3	9.82	<0.01
MEANDIST MAXAGE MEANDIST × MAXAGE	5	177.3	9.82	<0.01
NULL MODEL	2	177.7	10.18	<0.01
Snag volume				
AVGDBH	3	131.8	0	0.35
DISTDYN40	3	133.1	1.31	0.18
CANOPY80	3	133.1	1.31	0.18
MEANDIST	3	133.7	1.93	0.13
MAXAGE	3	133.7	1.93	0.13
MEANDIST MAXAGE MEANDIST × MAXAGE	5	138.9	7.09	0.01
CANOPY80 MAXAGE CANOPY80 × MAXAGE	5	140.1	8.26	<0.01
DISTDYN40 MAXAGE DISTDYN40 × MAXAGE	5	140.2	8.44	<0.01
NULL MODEL	2	144.6	12.79	<0.01
Snag density				
MEANDIST	3	132.1	0	0.29
DISTDYN40	3	132.6	0.44	0.23
AVGDBH	3	133.3	1.14	0.16
CANOPY80	3	133.4	1.31	0.15
MAXAGE	3	133.4	1.32	0.15
MEANDIST MAXAGE MEANDIST × MAXAGE	5	139.9	7.79	0.01
DISTDYN40 MAXAGE DISTDYN40 × MAXAGE	5	140.4	8.29	<0.01
CANOPY80 MAXAGE CANOPY80 × MAXAGE	5	141.2	9.04	<0.01
NULL MODEL	2	145.6	13.45	<0.01

Notes: Rankings are based on the corrected Akaike Information Criterion. See Table 2 for variable definitions. Models ranking below the null model are not presented.

† Total number of model parameters including the intercept and variance parameters.

‡ Corrected Akaike Information Criterion.

$\§$ Difference between model AIC_c value and minimum AIC_c value.

$||$ Probability of model being the best in a given set.

influenced by more than three centuries of small to moderate gap-scale disturbances (D'Amato and Orwig 2008). As a result, there was a tremendous degree of disparity between successional stages in terms of forest structural attributes.

The variety of diameter distribution patterns observed for hemlock stands in this study were similar to those reported elsewhere for second-growth (Ward and Smith 1999) and old-growth eastern hemlock stands (Meyer and Stevenson 1943, Hett and Loucks 1976, Tyrrell and Crow 1994a, Ziegler 2000, Orwig et al. 2001). Skewed unimodal and reverse J-shaped patterns were the only distribution types observed in second-growth stands and these patterns largely reflected successional processes occurring during the stem exclusion phase (Hett and Loucks 1976, Oliver 1981, Orwig et al. 2001). Similarly, the reverse-J shaped patterns observed in several second-growth stands were likely due to the stratification of species into distinct size classes (Oliver 1978, Muller 1982, Lorimer and Krug 1983, Hornbeck and Leak 1992), as faster-growing species, including *Betula lenta*, *B. papyrifera*, and *Quercus rubra*, often occupied upper

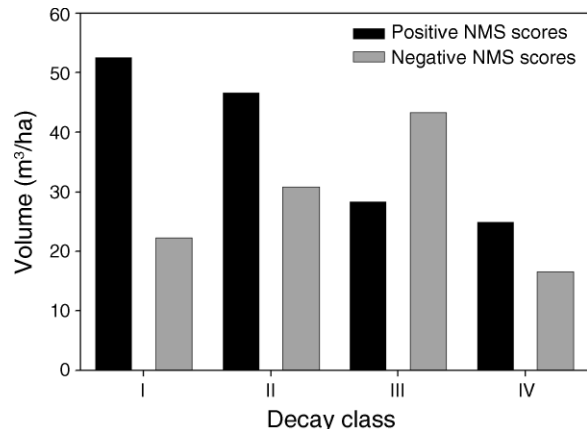


FIG. 6. Decay class distributions of downed coarse woody debris (CWD) between old-growth stands with high levels of canopy disturbance in the 1930s and 1980s (high NMS scores, $n = 9$ stands) and stands with lower levels of disturbance during these decades (low NMS scores, $n = 7$ stands).

canopy positions, whereas hemlock typically occurred in lower canopy strata (Fig. 3).

The only diameter distribution types unique to old-growth hemlock stands were bell-shaped and rotated sigmoid distributions. Rotated sigmoid distributions have been documented in other old-growth ecosystems dominated by shade tolerant species (Goff and West 1975, Goodburn and Lorimer 1999, Westphal et al. 2006) and have been suggested as a universal distribution type for smaller old-growth stands, such as those examined in this study (Goff and West 1975). In contrast, bell-shaped and skewed unimodal diameter distributions are typically associated with even-aged forests (Ford 1975); however, these diameter distributions have been observed in several uneven-aged old-growth eastern hemlock forests in the upper midwest (Frelich and Lorimer 1985, Tyrrell and Crow 1994a), New York (Ziegler 2000), and Massachusetts (Orwig et al. 2001). These distributions have been attributed to the lack of *Tsuga* recruitment due to deer browsing (Frelich and Lorimer 1985) or unfavorable understory light conditions for successful regeneration in dense hemlock stands (Hett and Loucks 1976, Orwig et al. 2001). In this study, the site exhibiting a bell-shaped size distribution (Deer Hill) had abundant evidence of deer browsing (i.e., clipped seedlings and shrubs, abundant deer sign) and the lowest density of saplings among old-growth stands (319 stems/ha) suggesting that sustained herbivory may have prevented the establishment of new *Tsuga* recruits in this area. In contrast, the two areas with skewed unimodal distributions (Bash Bish Falls, Wheeler Brook) had little evidence of herbivory, yet still had lower sapling densities (<700 stems/ha) indicating that the competitive effects of overstory trees on understory growing conditions may have prevented the successful recruitment of saplings into the canopy at these sites.

Our estimates of downed CWD volume were within the range reported elsewhere for old-growth (Tyrrell and Crow 1994a, Ziegler 2000) and second-growth (Mathewson 2006) eastern hemlock forests. In contrast, the range of snag volumes and densities in the old-growth stands we examined were much lower than those reported for other old-growth eastern hemlock forests (Tyrrell and Crow 1994a, Ziegler 2000). These differences in snag characteristics were likely due to higher snag fall rates in our study areas due to the steeper slopes they occupy (mean slope = $34.3^\circ \pm 1.3^\circ$). Moreover, the range of total CWD volumes (i.e., snags and downed CWD combined) in these study areas (97–234 m³/ha) was similar to those reported by Tyrrell and Crow (1994a), suggesting that similar levels of CWD are produced in the old-growth study areas we examined, although a larger proportion is in downed logs.

Differences in downed CWD and snag volumes between second-growth and old-growth stands were primarily due to larger CWD inputs within old-growth stands. In particular, old-growth stands had a higher

density of large diameter canopy trees resulting in larger diameter snags and greater downed CWD volumes compared to second-growth areas. In addition, the primary mortality processes in these two successional stages were quite distinct, subsequently affecting CWD input size. The higher amounts of mortality for overstory trees in old-growth stands due to disturbance processes (cf. Dahir and Lorimer 1996, Lorimer et al. 2001) led to larger CWD inputs within the old-growth stands. Conversely, the abundance of smaller diameter snags and downed *Betula papyrifera* CWD indicated that successional processes, such as mortality from self-thinning (Dahir and Lorimer 1996) and the death of shorter-lived, intolerant species (Lee et al. 1997), were influencing the development of snags and downed CWD in second-growth stands. This is consistent with findings of other studies examining CWD in younger forest stands in which the mortality of overtopped stems (McComb and Muller 1983, Dahir and Lorimer 1996, Goodburn and Lorimer 1998) and death of shorter-lived, pioneer species (Gore and Patterson 1986, Ziegler 2000) contributed to the abundance of snags and downed CWD. Due to the higher wood decomposition rates associated with most pioneer species, including *B. papyrifera* (McComb 2003), the potential for the accumulation of large volumes of downed CWD and snags within these second-growth systems is limited.

Disturbance processes did play an important role in promoting high volumes of downed CWD in several second-growth sites (Trout Brook, Deer Hill, Money Brook). Notably, canopy *F. grandifolia* killed by the beech bark disease complex (scale insect [*Cryptococcus fagisuga* Lindinger] and fungus [*Nectria* spp.]; Houston 1994) made up a significant portion of the snags and downed CWD in these stands (e.g., 51.5%, 40.2%, and 58.6% of the total downed CWD in the Trout Brook, Deer Hill, and Money Brook study areas, respectively).

Variation in structure among old-growth forests

Differences in disturbance history resulted in a range of variation in forest structure among old-growth stands, particularly in terms of live-tree distributions, downed CWD abundance, and snag densities. Although reverse-J shaped or descending monotonic diameter distributions have been suggested as emergent properties of old-growth forest ecosystems (e.g., Hough 1932, Meyer and Stevenson 1943, Meyer 1952, Lorimer 1980, Oliver and Larson 1996), these distributions were not observed for all of the old-growth stands examined in this study. Deviations from this general curve form have been ascribed to the influence of past disturbances, particularly in instances where rotated sigmoid distributions have been observed (Schmelz and Lindsey 1965, Lorimer 1980, Parker et al. 1985, Leak 1996, Lorimer and Frelich 1998). In this study, several of the stands (Black Brook, Money Brook, Tower Brook) exhibiting rotated sigmoid curve forms experienced moderate intensity disturbance events ($\geq 10.0\%$ canopy area

TABLE 5. Percentage of canopy disturbed during the 1930s and 1980s and volume of downed coarse woody debris (CWD) for each *Tsuga canadensis*-dominated old-growth study area.

Study site	Canopy disturbed (%) [†]		Downed CWD (m ³ /ha)
	1930s	1980s	
Bash Bish Falls	3.4	3.9	60.6
Black Brook	1.9	2.3	110.0
Cold River A1	6.7	2.4	201.7
Cold River A2	5.2	2.0	147.7
Cold River B	5.5	4.7	135.7
Cold River D	8.0	2.2	157.3
Deer Hill	3.2	0.2	100.9
Grinder Brook	3.8	0.8	115.7
Hopper A	11.4	6.0	117.2
Hopper B	5.2	6.2	134.5
Manning Brook	14.6	1.3	224.1
Mt. Everett	2.7	0.5	115.9
Money Brook	1.1	0.8	94.1
Tower Brook	8.8	2.4	171.8
Todd Mountain	3.2	4.6	169.1
Wheeler Brook	1.4	0.1	106.9

[†] Values represent reconstructions of percentage canopy area disturbed based on dendroecological methods outlined in Lorimer and Frelich (1989).

disturbed; D'Amato and Orwig 2008) within the past 110 years, suggesting that these distributions may be a reflection of recovery from past disturbance events (*sensu* Schmelz and Linsey 1965). However, the study areas with highest mean levels of canopy disturbance over the past 130 years (Hopper A, Hopper B, and Cold River D) had reverse-J shaped diameter distributions indicating that frequent, moderate intensity disturbances may result in the constant mortality rates across diameter classes required to generate and maintain this distribution (Leak 1964, Westphal et al. 2006).

An alternative explanation for failure to observe reverse-J shaped distributions in some of the old-growth stands is an insufficient sampling area to detect such a population structure (Rubin et al. 2006). Rubin et al. (2006) argue that sampling areas exceeding 1 ha are necessary to accurately assess the diameter distribution of old-growth stands due to the variable spatial distribution of different sized trees. In addition, the use of larger sampling areas increases the likelihood of encountering a wider range a range of structural conditions (e.g., saplings, pole-size trees, mature trees) resulting from historic gap-scale disturbances (cf. Meyer 1952). However, the reverse-J shaped distributions observed in study areas with the highest mean levels of canopy disturbance suggest that this disturbance regime may have resulted in the mosaic of size and age classes necessary to detect this population structure at the scales we sampled.

The abundance of downed CWD among old-growth stands was strongly related to past disturbance history. In particular, stands experiencing high levels of canopy disturbance in the 1930s and 1980s tended to have the highest volumes of downed CWD (Table 5), highlighting the role of past disturbance events in generating the

observed variation in downed CWD pools among old-growth study areas. In addition, several sites (Cold River A1, Cold River D, and Manning Brook) with the highest volumes of downed CWD had uniform downed-log orientations consistent with prevailing wind directions for storm events in this region, which likely generated the CWD in these stands (Boose et al. 2001; data *available online*).⁵ The importance of recent, gap-scale disturbances contributing to CWD pools has been shown by numerous studies in which disturbance events, including wind storms (Kirby et al. 1998, Spetich et al. 1999, Christensen et al. 2005), ice storms (Rebertus et al. 1997, Hooper et al. 2001, Bragg et al. 2003), and insect outbreaks (Sturtevant et al. 1997, Youngblood and Wickman 2002), have resulted in large pulses of downed CWD. Few studies have examined the role of historic disturbances on downed CWD abundance; however, Schoonmaker (1992) found that 63% of the downed CWD within an old-growth white pine (*Pinus strobus*)–hemlock stand was from a large-scale hurricane event occurring five decades prior to his sampling. Although maximum canopy disturbance levels at our study areas during the 1930s (14.7% of canopy area disturbed) were much lower than those for the areas studied by Schoonmaker (1992; ~75% disturbed based on Foster [1988]), the legacy of disturbance during this decade is still affecting downed CWD pools within these stands. This legacy is likely a reflection of the decay resistance of eastern hemlock logs as it can take nearly 200 years for their complete decomposition (Tyrrell and Crow 1994b).

Wind, insects, and diseases are common mortality agents resulting in snag formation in forest stands (e.g., Foster 1988, Peterson and Pickett 1991, Orwig and Foster 1998, Hansen and Goheen 2000, Wilson and McComb 2005). Although trees snapped by recent wind events are easily recognized (e.g., Putz et al. 1983, Peterson and Pickett 1991), assigning causes of tree death and subsequent snag formation for other disturbance agents and older disturbance events is often challenging (but see Worrall et al. 2005). While we could not determine the origin of all snags in these study areas, our results indicate that areas experiencing higher levels of canopy disturbance generally had higher snag densities. Moreover, all stands contained wind-snapped stems and a few stands had *F. grandifolia* snags resulting from beech bark disease. In contrast, differences in site productivity, as measured by mean overstory tree diameter, influenced the volume of snags in old-growth areas. This finding is consistent with other studies that reported higher snag volumes on more productive sites (Linder et al. 1997, Spetich et al. 1999).

Dendroecological reconstructions of disturbance history were very useful in elucidating the factors responsible for the observed variation in structure

⁵ www.ncdc.noaa.gov/oa/ncdc.html



PLATE 1. Several of the structural attributes characterizing old-growth *Tsuga canadensis* forests in western Massachusetts, USA, including a diversity of tree sizes and an abundance of downed coarse woody debris (CWD), are seen in this portion of the Cold River A2 study area. Note the recent pulses of CWD within this stand due to wind (*T. canadensis* log in background) and disease (*Fagus grandifolia* log in foreground resulting from mortality associated with beech bark disease complex [scale insect, *Cryptococcus fagisuga* Lindinger, and fungus, *Nectria* spp.]).

among old-growth hemlock stands. For example, these reconstructions highlighted the importance of recent and historic disturbance events in structuring the downed CWD pools, live-tree distributions, and snag densities within these old-growth areas. Despite the usefulness of this approach, it is important to recognize the limitations of relying solely on dendroecological data for relating disturbance history to forest structure. In particular, most dendroecological criteria used for detecting growth releases rely on at least a 10-year post-disturbance window (e.g., Lorimer and Frelich 1989, Nowacki and Abrams 1997, Fraver and White 2005a), preventing the inclusion of recent disturbance events. Likewise, trees in recent canopy gaps may not be large enough for coring at the time of sampling leading to an underestimate of the amount of canopy disturbed by recent disturbances (Frelich 2002). Future studies utilizing this approach for examining relationships between disturbance history and forest structure should incorporate measurements of recent gap areas, as well as estimates of gap creation dates (cf. Runkle 1992, Fraver and White 2005b) to account for these limitations.

Conclusions and management implications

The structure of the old-growth stands examined in this study is quite distinctive from the second-growth stands covering much of the landscape of western Massachusetts. Structural attributes of these older systems, including tree sizes and ages, sapling densities,

and the abundance of coarse woody debris, are much greater than those observed in second-growth areas. The live-tree distribution patterns and estimates of downed CWD in this study were similar to those in other old-growth eastern hemlock forests located on more moderate terrain in the upper midwest and New York (Tyrrell and Crow 1994a, Ziegler 2000), highlighting that many structural properties in the old-growth stands in western Massachusetts are representative of the natural range in variation for this forest type. While successional processes such as density-dependent mortality are influencing the structure of second-growth systems, our findings suggest that long-term gap-scale disturbances have been responsible for generating most of variation in structure currently observed in these old-growth areas.

The importance of disturbance in shaping forest structural characteristics has long been recognized; however, few studies have directly examined the role disturbance plays in generating the structural complexity commonly observed in old-growth forest ecosystems. Using stand disturbance chronologies constructed from tree-ring data, we were able to test specific hypotheses regarding the influence of disturbance dynamics on old-growth structure and demonstrate how these disturbances have affected factors such as downed CWD abundance. In particular, the high volumes of downed CWD found at several old-growth sites were linked to past, moderate intensity canopy disturbances that

resulted in pulses of deadwood at these areas. These episodic patterns of CWD recruitment are critical for maintaining a spatially heterogeneous distribution of deadwood within forest stands, as well as for maintaining a mosaic of logs in various stages of decay for deadwood-dependent organisms (e.g., McComb 2003, Mathewson 2006).

The mechanistic linkages we observed between disturbance processes and old-growth structural attributes highlight the importance of incorporating structural dynamics into ecosystem management strategies aimed at restoring old-growth structures to managed landscapes (cf. D'Amato and Catanzaro 2007). While natural-disturbance parameters, including the scale and frequency of canopy disturbance, have been incorporated into current management systems (Seymour et al. 2002), these approaches do not account for the structural legacies of disturbance, including large downed logs, that our results indicate are central to the development of old-growth structure. To account for these structural dynamics, natural disturbance-based harvesting systems could be modified to include the deliberate felling and retention of canopy trees within harvest gaps (*sensu* Keeton 2006), emulating the episodic nature of CWD recruitment found in these systems. The inclusion of CWD creation with each harvest entry would not only increase stand level CWD volumes, but also result in a diversity of decay classes within treated stands. In many cases, large canopy trees may be absent from second-growth systems, and therefore the use of crown release treatments (Singer and Lorimer 1997) and selection systems guided by rotated sigmoid target distributions (Keeton 2006) could be used to accelerate the development of large living trees and future, large dead wood inputs within these systems.

The diversity of diameter-distribution forms observed in this study reinforce the conclusions of other work regarding the prevalence of multiple distribution types common in uneven-aged forest stands (e.g., Lorimer and Frelich 1984, Leak 1996, O'Hara 1998, Westphal et al. 2006, Neuendorff et al. 2007). Notably, these results highlight that variations in disturbance history can result in spatial and temporal variation in size-class distribution forms across compositionally similar old-growth stands. As such, uneven-aged management approaches should consider multiple, target diameter distribution forms if objectives include maintaining natural levels of structural variation on the landscape (O'Hara 1998, 2001). Similarly, a range of natural disturbance frequencies should be applied in guiding natural disturbance-based, multi-cohort management (Seymour and Hunter 1999) to ensure that multiple size-distribution forms are maintained across the landscape.

ACKNOWLEDGMENTS

We thank Jessica Butler, Glenn Motzkin, Christian Foster, and Ben Ewing for assistance with fieldwork. This work was supported by NSF grant DEB-0236897 and USDA Focus

Funding Grant 01-DG-11244225-037. In addition, A.W. D'Amato received funding from the A. W. Mellon Foundation and Pisgah Fund at the Harvard Forest. Comments from Matthew Kelty, Brenda McComb, and two anonymous reviewers greatly improved this manuscript. This publication is a product of the Harvard Forest LTER program.

LITERATURE CITED

- Abrams, M. D., and D. A. Orwig. 1996. A 300-year history of disturbance and canopy recruitment for co-occurring white pine and hemlock on the Allegheny Plateau, USA. *Journal of Ecology* 84:353–363.
- Anderson, D. R., K. P. Burnham, and W. L. Thompson. 2000. Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wildlife Management* 64:912–923.
- Avery, J., and T. Slack. 1926. Map of Mohawk Trail State Forest. Massachusetts Department of Conservation and Recreation, Amherst, Massachusetts, USA.
- Boose, E. R., K. E. Chamberlain, and D. R. Foster. 2001. Landscape and regional impacts of hurricanes in New England. *Ecological Monographs* 71:27–48.
- Boulanger, Y., and L. Sirois. 2006. Postfire dynamics of black spruce coarse woody debris in northern boreal forest of Quebec. *Canadian Journal of Forest Research* 36:1770–1780.
- Bragg, D. C., M. G. Shelton, and B. Zeide. 2003. Impacts and management implications of ice storms on forests in the southern United States. *Forest Ecology and Management* 186:99–123.
- Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.
- Burnham, K. P., and D. R. Anderson. 2001. Kullback-Leibler information as a basis for strong inference in ecological studies. *Wildlife Research* 28:111–119.
- Busing, R. T. 2005. Tree mortality, canopy turnover, and woody detritus in old cove forests of the southern Appalachians. *Ecology* 86:73–84.
- Chokkalingam, U., and A. S. White. 2001. Structure and spatial patterns of trees in old-growth northern hardwood and mixed forests of northern Maine. *Plant Ecology* 156:139–160.
- Christensen, M., K. Hahn, E. P. Mountford, P. Ódor, T. Standovár, D. Rozenbergar, J. Diaci, S. Wijdeven, P. Meyer, S. Winter, and T. Vrska. 2005. Dead wood in European beech (*Fagus sylvatica*) forest reserves. *Forest Ecology and Management* 210:267–282.
- Clark, D. F., D. D. Kneeshaw, P. J. Burton, and J. A. Antos. 1998. Coarse woody debris in sub-boreal spruce forests of west-central British Columbia. *Canadian Journal of Forest Research* 28:284–290.
- Crow, T. R., D. S. Buckley, E. A. Nauertz, and J. C. Zasada. 2002. Effects of management on the composition and structure of northern hardwood forests in upper Michigan. *Forest Science* 48:129–145.
- Dahir, S. E., and C. G. Lorimer. 1996. Variation in canopy gap formation among developmental stages of northern hardwood stands. *Canadian Journal of Forest Research* 26: 1875–1892.
- D'Amato, A. W., and P. C. Catanzaro. 2007. Restoring old-growth characteristics. Cooperative Extension Landowner Outreach, University of Massachusetts, Amherst, Massachusetts, USA.
- D'Amato, A. W., and D. A. Orwig. 2008. Stand and landscape-level disturbance dynamics in old-growth forest ecosystems in western Massachusetts. *Ecology* 89: *in press*.
- D'Amato, A. W., D. A. Orwig, and D. R. Foster. 2006. New estimates of Massachusetts old-growth forests: useful data for regional conservation and forest reserve planning. *Northeastern Naturalist* 13:495–506.
- Dunwiddie, P. W., and R. T. Leverett. 1996. Survey of old-growth forests in Massachusetts. *Rhodora* 98:419–444.

- Durand, D., and J. A. Greenwood. 1958. Modifications of the Rayleigh test for uniformity in analysis of two-dimensional orientation of data. *Journal of Geology* 66:229–238.
- Field, D. D., and C. Dewey. 1829. A history of the county of Berkshire, Massachusetts, in two parts. S.W. Bush, Pittsfield, Massachusetts, USA.
- FIA (Forest Inventory and Analysis). 2005. Forest inventory and analysis national core field guide. Volume 1: field data collection procedures for phase 2 plots, Version 3.0. U.S. Forest Service, Arlington, Virginia, USA.
- Filip, S. M., D. A. Marquis, and W. B. Leak. 1960. Development of old-growth northern hardwoods on Bartlett Experimental Forest—a 22-year record. U.S. Forest Service, Northeastern Forest Experiment Station Paper 135. U.S. Forest Service, Washington, D.C., USA.
- Ford, E. D. 1975. Competition and stand structure in some even-aged plant monocultures. *Journal of Ecology* 63: 311–333.
- Foster, D. R. 1988. Disturbance history, community organization and vegetation dynamics of the old-growth Pisgah Forest, southwestern New Hampshire, USA. *Journal of Ecology* 76:105–34.
- Fraver, S. 2004. Spatial and temporal patterns of natural disturbance in old-growth forests of northern Maine, USA. Dissertation. University of Maine, Orono, Maine, USA.
- Fraver, S., R. G. Wagner, and M. Day. 2002. Dynamics of coarse woody debris following gap harvesting in an Acadian forest of central Maine, USA. *Canadian Journal of Forest Research* 32:2094–2105.
- Fraver, S., and A. S. White. 2005a. Identifying growth releases in dendrochronological studies of forest disturbance. *Canadian Journal of Forest Research* 35:1648–1656.
- Fraver, S., and A. S. White. 2005b. Disturbance dynamics of old-growth *Picea rubens* forests of northern Maine. *Journal of Vegetation Science* 16:597–610.
- Frelich, L. E. 2002. Forest dynamics and disturbance regimes. Cambridge University Press, Cambridge, UK.
- Frelich, L. E., and C. G. Lorimer. 1985. Current and predicted long-term effects of deer browsing in hemlock forests in Michigan, USA. *Biological Conservation* 34:99–120.
- Fritts, H. C., and T. W. Swetnam. 1989. Dendrochronology: a tool for evaluating variations in past and present environment. *Advances in Ecological Research* 19:111–189.
- Goff, F. G., and D. West. 1975. Canopy–understory interaction effects on forest population structure. *Forest Science* 21: 98–108.
- Goodburn, J. M., and C. G. Lorimer. 1998. Cavity and coarse woody debris in old-growth and managed northern hardwood forests in Wisconsin and Michigan. *Canadian Journal of Forest Research* 28:427–438.
- Goodburn, J. M., and C. G. Lorimer. 1999. Population structure in old-growth and managed northern hardwoods: an examination of the balanced diameter distribution concept. *Forest Ecology and Management* 118:11–29.
- Gore, J. A., and W. A. Patterson III. 1986. Mass of downed wood in northern hardwood forests in New Hampshire: potential effects of forest management. *Canadian Journal of Forest Research* 16:335–339.
- Greenwood, J. A., and D. Durand. 1955. The distribution of length and components of the sum of n random unit vectors. *Annals of Mathematics and Statistics* 26:233–246.
- Hansen, E. M., and E. M. Goheen. 2000. *Phellinus weirii* and other native root pathogens as determinants of forest structure and process in western North America. *Annual Review of Phytopathology* 38:515–539.
- Harmon, M. E., et al. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* 15: 133–302.
- Harmon, M. E., and J. Sexton. 1996. Guidelines for measurements of woody detritus in forest ecosystems. Publication number 20. U.S. Long-term Ecological Research Network Office, University of Washington, Seattle, Washington, USA.
- Hély, C., Y. Bergeron, and M. D. Flannigan. 2000. Coarse woody debris in the southeastern Canadian boreal forest: composition and load variations in relation to stand replacement. *Canadian Journal of Forest Research* 30: 674–687.
- Hennon, P. E., and M. H. McClellan. 2003. Tree mortality and forest structure in the temperate rain forests of southeast Alaska. *Canadian Journal of Forest Research* 33:1621–1634.
- Henry, J. D., and J. M. A. Swan. 1974. Reconstructing forest history from live and dead plant material—an approach to the study of forest succession in southwest New Hampshire. *Ecology* 55:772–783.
- Hett, J. M., and O. L. Loucks. 1976. Age structure models of balsam fir and eastern hemlock. *Journal of Ecology* 64: 1029–1044.
- Hooper, M. C., K. Aarii, and M. J. Lechowicz. 2001. Impact of a major ice storm on an old-growth northern hardwood forest. *Canadian Journal of Botany* 79:70–75.
- Hornbeck, J. W., and W. B. Leak. 1992. Ecology and management of northern hardwood forests in New England. U.S. Forest Service General Technical Report NE-159. U.S. Forest Service, Washington, D.C., USA.
- Hough, A. F. 1932. Some diameter distributions in forest stands of northwestern Pennsylvania. *Journal of Forestry* 30: 933–943.
- Houston, D. R. 1994. Major new tree disease epidemics: beech bark disease. *Annual Review of Phytopathology* 32:75–87.
- Hunter, M. L., Jr. 1999. Maintaining biodiversity in forest ecosystems. Cambridge University Press, Cambridge, UK.
- Keeton, W. S. 2006. Managing for late-successional/old-growth characteristics in northern hardwood–conifer forests. *Forest Ecology and Management* 235:129–142.
- Kirby, K. J., C. M. Reid, R. C. Thomas, and F. B. Goldsmith. 1998. Preliminary estimates of fallen deadwood and standing dead trees in managed and unmanaged forests in Britain. *Journal of Applied Ecology* 35:148–155.
- Kovach, W. L. 1994. Oriana for Windows, version 2.0. Kovach Computing Services, Pentraeth, Wales, UK.
- Kulakowski, D., and T. T. Veblen. 2003. Subalpine forest development following a blowdown in the Mount Zirkel Wilderness, Colorado. *Journal of Vegetation Science* 14:653–660.
- Leak, W. B. 1964. An expression of diameter distribution for unbalanced, uneven-aged stands and forests. *Forest Science* 10:39–50.
- Leak, W. B. 1996. Long-term structural change in uneven-aged northern hardwoods. *Forest Science* 42:160–165.
- Lee, P. C., S. Crites, M. Nietfield, H. Van Nguyen, and J. B. Stelfox. 1997. Characteristics and origins of deadwood material in aspen-dominated boreal forests. *Ecological Applications* 7:691–701.
- Lester, A. M. 2003. Dynamics of coarse woody debris in transitional northern hardwood forests. Thesis. University of Massachusetts, Amherst, Massachusetts, USA.
- Lindenmayer, D. B., and J. F. Franklin. 2002. Conserving forest biodiversity: a comprehensive multiscale approach. Island Press, Washington, D.C., USA.
- Linder, P., B. Elfving, and O. Zackrisson. 1997. Stand structure and successional trends in virgin boreal forest reserves in Sweden. *Forest Ecology and Management* 98:17–33.
- Lorimer, C. G. 1980. Age structure and disturbance history of a southern Appalachian virgin forest. *Ecology* 61:1169–1184.
- 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.
- Lorimer, C. G., and L. E. Frelich. 1984. A simulation of equilibrium diameter distributions of sugar maple (*Acer*

- saccharum*). Bulletin of the Torrey Botanical Club 111: 193–199.
- Lorimer, C. G., and L. E. Frelich. 1989. A method for estimating canopy disturbance frequency and intensity in dense temperate forests. *Canadian Journal of Forest Research* 19:651–663.
- Lorimer, C. G., and L. E. Frelich. 1998. A structural alternative to chronosequence analysis for uneven-aged northern hardwood forests. *Journal of Sustainable Forestry* 6:347–366.
- Lorimer, C. G., L. E. Frelich, and E. V. Nordheim. 1988. Estimating gap origin probabilities for canopy trees. *Ecology* 69:778–785.
- Lorimer, C. G., and A. G. Krug. 1983. Diameter distributions in even-aged stands of shade-tolerant and midtolerant tree species. *American Midland Naturalist* 109:331–345.
- Maguire, C. C., and C. L. Chambers. 2005. College of forestry integrated research project: ecological and socioeconomic responses to alternative silvicultural treatments. Research Contribution 46, Forest Research Laboratory, Oregon State University, Corvallis, Oregon, USA.
- Mathewson, B. 2006. A comparison of eastern red-backed salamander populations in hemlock-dominated and mixed deciduous forests in north central Massachusetts. Thesis. Harvard Forest, Harvard University, Cambridge, Massachusetts, USA.
- McComb, W. C. 2003. Ecology of coarse woody debris and its role as habitat for mammals. Pages 335–372 in C. J. Zabel and R. G. Anthony, editors. *Mammal community dynamics: management and conservation in the coniferous forests of western North America*. Cambridge University Press, Cambridge, UK.
- McComb, W. C., and R. N. Muller. 1983. Snag densities in old-growth and second-growth Appalachian forests. *Journal of Wildlife Management* 47:376–382.
- McComb, W. C., T. A. Spies, and W. H. Emmingham. 1993. Douglas-fir forests: managing for timber and mature forest habitat. *Journal of Forestry* 91:31–42.
- McGee, G. G., D. J. Leopold, and R. D. Nyland. 1999. Structural characteristics of old-growth, maturing, and partially cut northern hardwood forests. *Ecological Applications* 9:1316–1329.
- McLachlan, J., D. R. Foster, and F. Menalled. 2000. Anthropogenic ties to late-successional structure and composition in four New England hemlock stands. *Ecology* 81: 717–733.
- Meyer, H. A. 1952. Structure, growth, and drain in balanced, uneven-aged forests. *Journal of Forestry* 52:85–92.
- Meyer, H. A., and D. D. Stevenson. 1943. The structure and growth of virgin beech–birch–maple–hemlock forests in northern Pennsylvania. *Journal of Agricultural Research* 67:465–484.
- Muller, R. N. 1982. Vegetation patterns in the mixed mesophytic forests of eastern Kentucky. *Ecology* 63:1901–1907.
- Muller, R. N. 2003. Landscape patterns of change in coarse woody debris accumulation in an old-growth deciduous forest on the Cumberland Plateau, southeastern Kentucky. *Canadian Journal of Forest Research* 33:763–769.
- Neuendorf, J. K., L. M. Nagel, C. R. Webster, and M. K. Janowiak. 2007. Stand structure and composition in a northern hardwood forests after 40 years of single-tree selection. *Northern Journal of Applied Forestry* 24:197–202.
- Nowacki, G. J., and M. D. Abrams. 1997. Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. *Ecological Monographs* 67: 225–249.
- O'Hara, K. L. 1998. Silviculture for structural diversity: a new look at multi-aged systems. *Journal of Forestry* 96:4–10.
- O'Hara, K. L. 2001. The silviculture of transformation—a commentary. *Forest Ecology and Management* 151:81–86.
- Oliver, C. D. 1978. The development of northern red oak in mixed stands in central New England. School of Forestry and Environmental Studies Bulletin Number 91. Yale University New Haven Connecticut, USA.
- Oliver, C. D. 1981. Forest development in North America following major disturbances. *Forest Ecology and Management* 3:153–168.
- Oliver, C. D., and B. C. Larson. 1996. *Forest stand dynamics*. John Wiley and Sons, New York, New York, USA.
- Oliver, C. D., and E. P. Stephens. 1977. Reconstruction of a mixed-species forest in central New England. *Ecology* 58: 562–572.
- Orwig, D. A., C. V. Cogbill, D. R. Foster, and J. F. O'Keefe. 2001. Variations in old-growth structure and definitions: forest dynamics on Wachusett Mountain, Massachusetts. *Ecological Applications* 11:437–452.
- Orwig, D. A., and D. R. Foster. 1998. Forest response to the introduced hemlock woolly adelgid in southern New England, USA. *Journal of the Torrey Botanical Society* 125:60–73.
- Palik, B. J., and J. Robl. 1999. Structural legacies of catastrophic windstorm in a mature Great Lakes aspen forest. U.S. Forest Service, Research Paper, NC-337. U.S. Forest Service, Washington, D.C., USA.
- 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.
- Peterken, G. F. 1996. *Natural woodland: ecology and conservation in northern temperate regions*. Cambridge University Press, Cambridge, UK.
- Peterson, C. J., and S. T. A. Pickett. 1991. Treefall and resprouting following catastrophic windthrow in an old-growth hemlock–hardwoods forest. *Forest Ecology and Management* 42:205–217.
- Putz, F. E., P. D. Coley, K. Lu, A. Montvallo, and A. Aiello. 1983. Uprooting and snapping of trees: structural determinants and ecological consequences. *Canadian Journal of Forest Research* 13:1011–1020.
- Rebertus, A. J., S. R. Shifley, R. H. Richards, and L. M. Roovers. 1997. Ice storm damage to an old-growth oak–hickory forest in Missouri. *American Midland Naturalist* 137:48–61.
- Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223–225.
- Robertson, P. A., G. T. Weaver, and J. A. Cavanaugh. 1978. Vegetation and tree species patterns near the northern terminus of the southern floodplain forest. *Ecological Monographs* 48:249–267.
- Rose, C. L., B. G. Marcot, T. K. Mellen, J. L. Ohman, K. L. Waddell, D. L. Lindley, and B. Schreiber. 2001. Decaying wood in Pacific Northwest forests: concepts and tools for habitat management. Pages 580–623 in D. H. Johnson and T. A. O'Neill, editors. *Wildlife-habitat relationships in Oregon and Washington*. Oregon State University Press, Corvallis, Oregon, USA.
- Rubin, B. D., P. D. Manion, and D. Faber-Langendoen. 2006. Diameter distributions and structural sustainability in forests. *Forest Ecology and Management* 222:427–438.
- Runkle, J. R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology* 63: 1533–1546.
- Runkle, J. R. 1992. Guidelines and sample protocol for sampling forest gaps. U.S. Forest Service General Technical Report PNW-GTR-283. U.S. Forest Service, Washington, D.C., USA.
- Runkle, J. R. 2000. Canopy tree turnover in old-growth mesic forests of eastern North America. *Ecology* 81:554–567.
- SAS Institute. 2004. *SAS/STAT user's guide: version 9.1*. SAS Institute, Cary, North Carolina, USA.
- Scanu, R. J. 1988. Soil survey of Berkshire County, Massachusetts. USDA, Soil Conservation Service, Amherst, Massachusetts, USA.

- Schmelz, D. V., and A. A. Lindsey. 1965. Size-class structure of old-growth forests in Indiana. *Forest Science* 11:258–264.
- Schoonmaker, P. K., Jr. 1992. Long-term vegetation dynamics in southwestern New Hampshire. Dissertation. Harvard University, Cambridge, Massachusetts, USA.
- Seymour, R. S., and M. L. Hunter, Jr. 1999. Principles of ecological forestry. Pages 22–61 in M. L. Hunter, Jr., editor. *Maintaining biodiversity in forest ecosystems*. Cambridge University Press, Cambridge, UK.
- Seymour, R. S., A. S. White, and P. G. deMaynadier. 2002. Natural disturbance regimes in northeastern North America—evaluating silvicultural systems using natural scales and frequencies. *Forest Ecology and Management* 155:357–367.
- Singer, M. T., and C. G. Lorimer. 1997. Crown release as a potential old-growth restoration approach in northern hardwoods. *Canadian Journal of Forest Research* 27:1222–1232.
- 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.
- Spies, T. A. 1998. Forest structure: a key to the ecosystem. *Northwest Science* 72:34–39.
- Spies, T. A., and J. F. Franklin. 1991. The structure of natural young, mature, and old-growth Douglas-fir forests. Pages 91–110 in L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, technical coordinators. *Wildlife and vegetation of unmanaged Douglas-fir forests*. U.S. Forest Service General Technical Report PNW-GTR-285.
- Spies, T. A., J. F. Franklin, and M. Klopsch. 1990. Canopy gaps in Douglas-fir forests of the Cascade Mountains. *Canadian Journal of Forest Research* 20:649–658.
- Spies, T. A., J. F. Franklin, and T. B. Thomas. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. *Ecology* 69:1689–1702.
- Sturtevant, B. R., J. A. Bissonette, J. N. Long, and D. W. Roberts. 1997. Coarse woody debris as a function of age, stand structure, and disturbance in boreal Newfoundland. *Ecological Applications* 7:702–712.
- Tappeiner, J. C., D. Huffman, D. Marshall, T. A. Spies, and J. D. Bailey. 1997. Density, ages, and growth rates in old-growth and young-growth forests in coastal Oregon. *Canadian Journal of Forest Research* 27:638–648.
- Tinker, D. B., and D. H. Knight. 2000. Coarse woody debris following fire and logging in Wyoming lodgepole pine forests. *Ecosystems* 3:472–483.
- Tyrrell, L. E., and T. R. Crow. 1994a. Structural characteristics of old-growth hemlock–hardwood forests in relation to age. *Ecology* 75:370–386.
- Tyrrell, L. E., and T. R. Crow. 1994b. 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. 1986. Age and size structure of subalpine forests in the Colorado Front Range. *Bulletin of the Torrey Botanical Club* 113:225–240.
- van Wagner, C. E. 1968. The line intersect method in forest fuel sampling. *Forest Science* 14:20–26.
- Ward, J. S., and D. M. Smith. 1999. Dynamics of Connecticut hemlock stands. Pages 50–54 in K. A. McManus, K. S. Shields, and D. R. Souto, editors. *Proceedings: Symposium on Sustainable Management of Hemlock Ecosystems in Eastern North America*, June 22–24, 1999. U.S. Forest Service General Technical Report NE-267. U.S. Forest Service, Washington, D.C., USA.
- Weisburg, P. J. 2004. The importance of non-stand-replacing fire for the development of forest structure in the Pacific Northwest, USA. *Forest Science* 50:245–258.
- Westphal, C., N. Tremer, G. von Oheimb, J. Hansen, K. von Gadow, and W. Härdtle. 2006. Is the reverse J-shaped diameter distribution universally applicable in European virgin beech forests? *Forest Ecology and Management* 223:75–83.
- Wilson, B. F., and B. C. McComb. 2005. Dynamics of dead wood over 20 years in a New England oak forest. *Canadian Journal of Forest Research* 35:682–692.
- Winter, L. E., L. B. Brubaker, J. F. Franklin, E. A. Miller, and D. Q. DeWitt. 2002. Canopy disturbances over the five-century lifetime of an old-growth Douglas-fir stand in the Pacific Northwest. *Canadian Journal of Forest Research* 32:1057–1070.
- Woldendorp, G., R. J. Keenan, S. Barry, and R. D. Spencer. 2004. Analysis of sampling methods for coarse woody debris. *Forest Ecology and Management* 198:133–148.
- Woods, K. D. 2000a. Dynamics in late-successional hemlock-hardwood forests over three decades. *Ecology* 81:110–126.
- Woods, K. D. 2000b. Long-term change and spatial pattern in a late-successional hemlock–northern hardwood forest. *Journal of Ecology* 88:267–282.
- Worrall, J. J., T. D. Lee, and T. C. Harrington. 2005. Forest dynamics and agents that initiate and expand canopy gaps in *Picea–Abies* forests of Crawford Notch, New Hampshire, USA. *Journal of Ecology* 93:178–190.
- Youngblood, A., and B. E. Wickman. 2002. The role of disturbance in creating dead wood: insect defoliation and tree mortality in northeastern Oregon. U.S. Forest Service General Technical Report PSW-GTR-181.
- Zen, E., G. R. Goldsmith, N. L. Ratcliffe, P. Robinson, and R. S. Stanley. 1983. Bedrock geologic map of Massachusetts. U.S. Department of the Interior, U.S. Geologic Survey, Washington, D.C., USA.
- Zenner, E. K. 2005. Development of tree-size distributions in Douglas-fir forests under differing disturbance regimes. *Ecological Applications* 15:701–714.
- Ziegler, S. S. 2000. A comparison of structural characteristics between old-growth and post-fire second-growth hemlock-hardwood forests in Adirondack Park, New York, U.S.A. *Global Ecology and Biogeography* 9:373–389.
- Ziegler, S. S. 2002. Disturbance regimes of hemlock-dominated old-growth forests in northern New York, U.S.A. *Canadian Journal of Forest Research* 32:2106–2115.