Ecological Monographs, 78(4), 2008, pp. 507–522

STAND AND LANDSCAPE-LEVEL DISTURBANCE DYNAMICS IN OLD-GROWTH FORESTS IN WESTERN MASSACHUSETTS

Anthony W. D'Amato[1,2,3] and David A. Orwig[2]

[1]*Department of Natural Resources Conservation, University of Massachusetts, Amherst, Massachusetts 01003 USA*
[2]*Harvard Forest, Harvard University, 324 North Main Street, Petersham, Massachusetts 01366 USA*

Abstract. Natural disturbances strongly influence the dynamics and developmental patterns of forest ecosystems; however, relatively little is known about the historic patterns of natural disturbance for many portions of eastern North America, such as southern New England, where human disturbance has predominated for centuries. For these regions, much of our understanding of natural disturbance dynamics comes from studies of younger second-growth forests or isolated old-growth stands, thus limiting the temporal and spatial resolution of our knowledge of dynamics in these regions. To address these limitations, we analyzed dendroecological data from the 18 largest remaining old-growth stands in western Massachusetts, ranging in proximity from 1–60 km apart, in an effort to characterize the historic stand and landscape-level patterns of natural disturbance. Our results indicate that disturbance regimes for these systems were dominated by relatively frequent, low-intensity disturbances (average 5.0% ± 0.2% canopy area disturbed per decade) operating somewhat randomly on the landscape. Across the study areas, most decadal disturbances (86.2%) involved <10% canopy loss. There was no evidence of stand-replacing disturbances during the period examined (1700–1989), and the maximum canopy area disturbed in any given decade was 26.3%. Nonmetric multidimensional scaling demonstrated that several forests shared similar disturbance histories despite being separated by >50 km. Comparisons of these patterns with model simulations of past hurricane events and historical documents suggest that broadscale disturbances, such as hurricanes and ice storms, resulted in common disturbance peaks and subsequent recruitment peaks at spatially disparate areas in the 1790s, 1870s, 1900s, and 1920s. Conversely, the lack of synchrony in proximate areas during these events highlights the patchy nature of these disturbances on the landscape. Compositional and physiographic factors influenced disturbance patterns, as stands located on northwest-facing slopes or containing significant *Picea rubens* components in the forest overstory experienced the highest levels of disturbance. Our results highlight the utility of incorporating dendroecological reconstructions across numerous old-growth stands to interpret the historic stand and landscape-level disturbance dynamics in areas devoid of large, contiguous old-growth landscapes.

Key words: dendroecology; HURRECON; hurricanes; landscape dynamics; Massachusetts; natural disturbance; nonmetric multidimensional scaling; old-growth forests; Tsuga canadensis.

Introduction

Natural disturbances are primary drivers of forest ecosystem dynamics that influence species assemblages, nutrient cycling patterns, and ecosystem structures (White 1979). Characterizations of the disturbance regimes of natural forest ecosystems have strongly influenced modern theories of forest dynamics and succession and play a critical role in the development of ecosystem management strategies aimed at emulating natural disturbance processes (Runkle 1985, Attiwill 1994, Peterken 1996, Engstrom et al. 1999, Frelich 2002, Seymour et al. 2002).

Due to the scarcity of old-growth forest ecosystems in eastern North America, much of our understanding of natural disturbance dynamics for a given region or forest type comes from studies of younger second-growth forests and isolated old-growth stands. These studies suggest that the disturbance regime for many eastern hemlock–northern hardwood forests in eastern North America is dominated by frequent, gap-scale disturbance events, especially windstorms (Whitney 1990, Abrams and Orwig 1996, Engstrom et al. 1999, Lorimer and White 2003). In most cases, these disturbances create small (<400 m^2), isolated canopy openings resulting from the death of single canopy trees or small groups of trees (Runkle 1982, Ward and Parker 1989); however, less-frequent, broadscale disturbances by hurricanes and derechos can result in much larger patches of mortality (>1 ha), occasionally exceeding 500 ha in scale (Canham and Loucks 1984, Foster and Boose 1992, Jenkins 1995). Although average frequencies of

Manuscript received 9 April 2007; revised 20 December 2007; accepted 31 January 2008; final version received 11 March 2008. Corresponding Editor: R. Muzika.

[3] Present address: Department of Forest Resources, University of Minnesota, St. Paul, Minnesota 55108 USA. E-mail: damato@umn.edu

gap formation tend to be similar among forest types for the region (0.55–2.0%; Runkle 1985), the spatial and temporal distribution of these events at the stand and landscape scale is rarely uniform, resulting in a mosaic of forest successional and structural stages at these two spatial scales (Foster 1988, Frelich and Lorimer 1991*a*).

Several studies within large remaining old-growth forests have increased our understanding of landscape-level patterns of disturbance in areas such as the Upper Peninsula of Michigan (Frelich and Lorimer 1991*b*), the Adirondack Park in New York (Ziegler 2002), and northern Maine (Fraver 2004); however, little opportunity exists for characterizing these dynamics at similar spatial scales across much of eastern North America where old-growth stands occur in scattered small, isolated stands (Henry and Swan 1974, Foster 1988, Davis 1996, Abrams et al. 2000, Orwig et al. 2001). The recent discovery of numerous small, old-growth stands in western Massachusetts (Dunwiddie and Leverett 1996, D'Amato et al. 2006) provides an opportunity to characterize the natural disturbance dynamics for a region once considered devoid of any old-growth forests (cf. Egler 1940). While most of these areas are <15 ha in size, their geographic distribution is highly concentrated within three main regions (D'Amato et al. 2006), allowing for the examination of disturbance patterns within and among stands occupying similar spatial contexts. For this study, we were particularly interested in (1) reconstructing the historic patterns of disturbance within these stands using dendroecological methods (cf. Lorimer and Frelich 1989), (2) examining landscape-level gradients in disturbance history among old-growth stands using ordination techniques, and (3) investigating the relative influence of known disturbance events on these areas using a hurricane simulation model (HURRECON; Boose et al. 2001) and other historical records of disturbance for this region.

Dendroecological methods provide an effective means to develop a detailed understanding of stand-level disturbance patterns (e.g., Frelich and Lorimer 1991*b*, Abrams and Orwig 1996, Nowacki and Abrams 1997, Ziegler 2002), yet the labor-intensive nature of this work prevents its application across large, contiguous landscape units. Likewise, disturbance models such as HURRECON (Boose et al. 2001) can increase our understanding of broadscale disturbance patterns; however, these approaches often miss fine-scale variation in disturbance effects on the landscape. As such, a combination of these methods will be useful in determining how disturbance affects forests at broad temporal and spatial scales within the region.

STUDY AREA

This research was conducted within the largest known remaining old-growth forests in western Massachusetts (D'Amato et al. 2006). Old-growth forests were defined as forests lacking any evidence of past land use and containing at least five canopy trees per hectare >225 yr old, indicating establishment prior to European settlement (Field and Dewey 1829) and exceeding 50% of the maximum longevity for species commonly encountered in these forests (Dunwiddie and Leverett 1996, Leverett 1996, McGee et al. 1999). Extensive analysis of historical documents and increment cores collected at each site confirmed these criteria (D'Amato et al. 2006). These forests are located within the Berkshire Hills and Taconic Mountains. They are relatively low (215–1064 m above sea level), mostly flat-topped mountains located in the westernmost portion of the state (Fig. 1). This region has a humid continental climate with average annual precipitation ranging from 116.2 to 129.5 cm and mean monthly temperatures from −7.7°C in January to 22.2°C in July (National Climatic Data Center 2006). Bedrock composition varies considerably throughout this region, with the Berkshire Hills being composed predominantly of gneisses and schists, and the Taconic Mountains composed predominantly of schists, phyllites, and quartzites (Zen et al. 1983). Elevations of old-growth study areas range from 360 m to 800 m a.s.l., and soils within these areas are predominantly well-drained spodosols (Scanu 1988). All sites occupy steep, midslope positions characteristic of large portions of the Berkshire Hills and Taconic Mountains.

METHODS

Depending on stand size, three to five 0.04-ha plots were established and permanently marked along transects orientated through the central portion of each study area. Species and diameter at breast height (dbh) were recorded for every tree (stems $\geq$1.37 m tall and $\geq$10 cm dbh) rooted within these plots. In addition, all saplings (stems $\geq$1.37 m tall and $\leq$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. Additional increment cores were taken from trees with bark and crown characteristics indicative of advanced age (cf. Leverett 1996) located outside of these plots (8–33 trees per study area) to aid in reconstructing age distributions and disturbance chronologies for each study site (see *Methods: Disturbance chronologies*). All increment cores were air dried, sanded, aged, and visually cross-dated (Yamaguchi 1991) with a dissecting microscope, and annual ring-widths were measured to the nearest 0.01 mm using a Velmex measuring system (Velmex, East Bloomfield, New York, USA). In cases in which increment cores missed the pith, tree ages were determined graphically using a pith locator (Applequist 1958). Incomplete cores were used in the reconstruction of disturbance dynamics, but not for age reconstructions. Physiographic attributes of each study plot (e.g., slope steepness, slope aspect, elevation) were determined by recording plot positions on digital elevation models. Aspect values were transformed using the following formula by Beers et al. (1966): aspect = cosine (45-azimuth degrees) + 1. Based

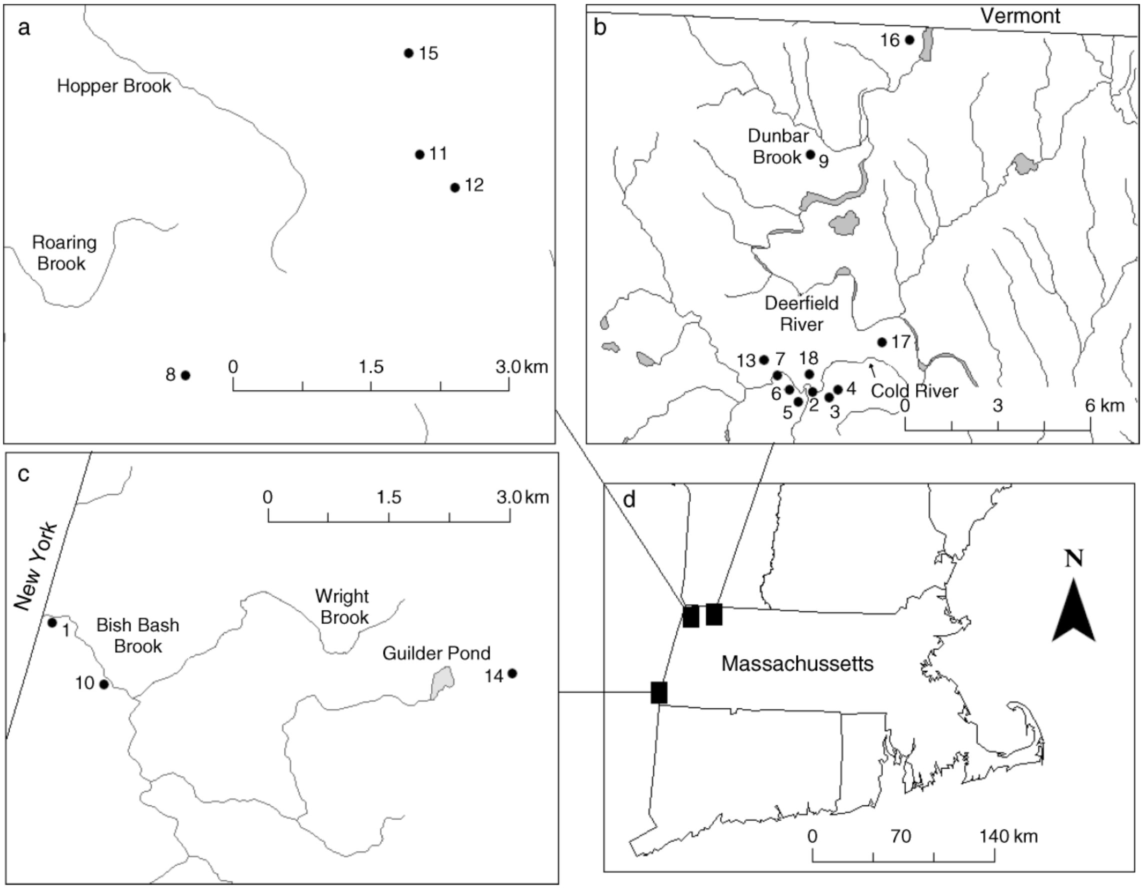

FIG. 1. Location of old-growth study areas within the (a) Greylock, (b) Berkshire Plateau, and (c) Southern Taconic study regions in western Massachusetts. (d) Location of study regions. See Table 1 for study site information.

on this transformation, values ranged from 0° for southwestern slopes to 2° on northeastern slopes.

Reconstruction of disturbance dynamics

Radial increment patterns of 1429 increment cores collected from the 18 sites were analyzed for historical disturbance events. In particular, each core was screened for (1) 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 average growth rates $\geq$1.2 mm/yr over the initial five years of radial growth were considered to be gap-recruited trees. As such, the date of the innermost ring for these individuals was recorded as the date of canopy accession (i.e., the date of gap formation that provides understory trees access to the forest canopy; Lorimer et al. 1988, Frelich 2002, Ziegler 2002). Due to their gap-obligate nature (cf. Orwig and Abrams 1994), all *Betula* spp. were classified as gap-recruited trees independent of their initial growth rates (Lorimer and Frelich 1989).

All cores were evaluated separately for growth releases (i.e., abrupt increases in radial growth) using the criteria established by Lorimer and Frelich (1989), who defined a "major sustained release" as an average growth increase $\geq$100% lasting at least 15 yr relative to the previous 15 yr, and a "moderate temporary release" as an average growth increase $\geq$50% lasting 10–15 yr relative to the previous 10–15 yr. Although lags in growth response of released trees may occur, we assumed that the year in which the growth release began represented the date of canopy accession. The use of 10- and 15-yr release windows to remove the effects of short-term growth responses due to climatic events (e.g., drought) allowed us to focus specifically on radial growth changes due to canopy disturbance (Leak 1987, Lorimer and Frelich 1989, Nowacki and Abrams 1997, Frelich 2002) and eliminated the need for additional age–size detrending (cf. Nowacki and Abrams 1997).

In some cases, initial growth rates and release criteria are ineffective at identifying the dates of gap recruitment and canopy accession, respectively (Lorimer and Frelich 1989). Radial increment patterns for each core not qualifying as a gap-recruited individual or containing a release date based on the criteria described above were plotted and screened for growth patterns indicative of gap origin (e.g., declining, parabolic, or flat) or release from suppression (e.g., "ambiguous" or "irregular";

Lorimer and Frelich 1989). Dates of gap recruitment and canopy accession were assigned using the same methodology described in the previous two paragraphs.

One of the prime areas of interest was reconstructing the amount of canopy area disturbed by past disturbance events (see *Methods: Disturbance chronologies*). As such, the growth release of canopy trees adjacent to gaps was not tallied to prevent overestimating the proportion of canopy area disturbed during a given disturbance event (Frelich 2002). The likelihood of a tree being in the canopy during a disturbance event was determined based on its dbh (Lorimer and Frelich 1989). Size thresholds were created for each tree species based on the size structure of the canopy and understory of our study areas using the methodology outlined by Lorimer and Frelich (1989): *Tsuga canadensis* = 28.0 cm, *Fagus grandifolia* = 20.0 cm, *Picea rubens* = 20.5 cm, *Acer saccharum* = 25.0 cm, and *Betula* spp. = 18.0 cm. Release events were not tallied for individuals with diameters greater than or equal to these thresholds at the time of disturbance, allowing us to focus solely on the release of understory trees due to loss of overtopping canopy trees. Diameters were estimated for every year a tree was in the record using cumulative radial increment and species-specific equations for bark thickness from NE-TWIGS (Bush 1995). Moderate releases were tallied only if they were the first or only significant growth release displayed for a given understory tree (Lorimer and Frelich 1989). In contrast, all major releases were tallied, and multiple major releases were allowed for a given individual because several disturbance events are often needed for shade-tolerant tree species to attain canopy status (Oliver and Stephens 1977, Canham 1985, 1990, Lorimer and Frelich 1989).

Disturbance chronologies

Disturbance chronologies were constructed for each study area by tallying the number of release events and gap-recruitment events by decade (Lorimer and Frelich 1989). The number of releases per decade was weighted by the current exposed crown area (ECA; see Appendix A for equations used to predict ECA) of each released tree to derive an estimate of canopy area disturbed (Lorimer and Frelich 1989). This method assumes that the percent area of the current canopy occupied by trees released in a given decade represents an estimate of the proportion of canopy area disturbed during that decade (Lorimer and Frelich 1989; Frelich 2002). Because every tree on each plot was cored, ECA estimates were corrected to prevent overestimating canopy area disturbed due to more intensive sampling of smaller trees (Frelich 2002). These estimates were corrected using the following formula from Lorimer and Frelich (1989):

$$W_i = \frac{(\mathrm{ECA}_i/\mathrm{ECA})}{n_i/N}$$

where W_i is the weighting factor for diameter class i, ECA_i is the cumulative exposed crown area of trees in diameter class i, ECA is the exposed crown area of all trees on the plot, n_i is the number of cores in diameter class i, and N is the total number of cored trees in the plot.

The length of each study area's disturbance chronology was determined by the number of living trees present in each decade and was truncated when the number of living trees dropped below 15 (Fraver and White 2005). The last decade of each chronology was 1980–1989 because trees recruited by disturbance events in the 1990s were not large enough to core during our sampling period (Frelich 2002). In addition, the use of 10- and 15-yr windows for analyzing release events precluded us from including disturbance events after 1989 in the chronologies, and therefore our estimates of canopy area disturbed during 1980–1989 may be low.

Release of overstory trees and growth declines

In addition to using the growth responses of understory trees to determine the amount of canopy area disturbed, the responses of canopy trees to disturbance events were also analyzed. Because the growth response of overstory trees to surrounding canopy openings is typically much smaller than those elicited by released understory trees (Lorimer and Frelich 1989, Nowacki and Abrams 1997), we used growth release criteria developed specifically for detecting the response of overstory trees to canopy disturbance (Nowacki and Abrams 1997). Following these criteria, average 10-yr growth increases ≥50% relative to the previous 10 yr were tallied for each tree deemed to be a canopy tree at the time of disturbance, based on the dbh thresholds listed in *Methods: Reconstruction of disturbance dynamics*. In addition, abrupt growth decreases ≥50% and lasting 10 yr relative to the previous 10 yr were tallied for each canopy tree as an indication of canopy damage (cf. Foster 1988, Orwig et al. 2001, Lafon and Speer 2002). The same growth decrease criteria were applied to understory trees to detect events in which understory trees (i.e., trees that were less than dbh threshold) were also damaged. Growth releases and declines of canopy trees and growth declines of understory trees were examined in concert with our reconstructions of canopy area disturbed to determine the nature and intensity of disturbance (e.g., wind and ice storms, insect outbreaks) at each study area (see *Methods: Historical evidence of disturbance*).

Ordination analysis of disturbance chronologies

Traditional approaches for examining patterns of disturbance across multiple study sites have involved qualitative comparisons of histograms or tables containing the distribution of canopy area disturbed each decade (e.g., Nowacki and Abrams 1997, Orwig et al. 2001, Ziegler 2002). These approaches have proven useful when only a few study areas are being compared (e.g., Fraver and White 2005); however, this approach becomes increasingly subjective and cumbersome when large numbers of disturbance chronologies are examined. To address this issue, we developed a multivariate approach for examining disturbance chronologies that allowed for comparisons and characterizations of disturbance history across numerous study areas. This approach used nonmetric multidimensional scaling (NMS), a nonparametric ordination technique particularly well suited for analyzing disturbance chronologies due to its ability to deal with data that are nonnormal or discontinuous in scale (McCune and Grace 2002).

For this approach, a matrix of study site by decade was constructed and the percentage of canopy area disturbed entered for each site and decade. To maximize redundancy among study areas, the length of the chronology was entered into the data matrix was limited to the shortest chronology common among the study areas (1870–1989). A subset of this matrix including only sites with chronologies extending back to 1780 was also created to examine older patterns of disturbance not represented in the main data matrix. Additional secondary matrices containing physiographic (e.g., aspect, slope steepness, and elevation), compositional (e.g., percent hemlock), and geographic (e.g., longitude and latitude) variables were created to examine relationships between disturbance patterns and environmental, compositional, and geographic factors using the bi-plot function in PC-ORD (McCune and Mefford 1999). The "slow-and-thorough" autopilot mode of NMS in PC-ORD was used to generate NMS solutions. This procedure determines the optimal ordination solution by stepping down in dimensionality from a six-axis to a one-axis solution using 40 runs performed on real data followed by 50 Monte Carlo runs using random data (McCune and Mefford 1999). Optimal dimensionality was based on the number of dimensions with the lowest stress (i.e., smallest departure from monotonicity in the relationship between distance in the original space and distance in the reduced ordination space; McCune and Grace 2002). Sørensen distances were used to express resemblances in disturbance history.

Historical evidence of disturbance

To develop a disturbance etiology for each study area, several sources of information were used, including historical references of known disturbance events. Geographic Information System (GIS) data layers developed by the Massachusetts Department of Conservation and Recreation depicting the extent of forest defoliation from insects, disease, and weather events from 1934–1946 and 1961–1994 (MassGIS 2006) were also analyzed to determine the effect these factors may have had on each study area. The HURRECON meteorological model (Boose et al. 2001) was used to determine the broadscale wind conditions at each study area during known hurricane events over the past three centuries (e.g., 1788, 1815, 1869, 1938; Smith 1946). The HURRECON model generates estimates of wind speed and direction based on the track, size, and intensity of a hurricane, as well as the surface type (i.e., land or water; see Boose et al. 2001 for a detailed description of the HURRECON model). Because the spatial extent of model predictions was 10 km^2, simulations were run for points located equidistantly between study areas. For each hurricane event predicted to have caused at least minor damage (loss of leaves or branches; F0 on the Fujita Scale; Fujita 1971) at a study site, the EXPOS topographic exposure model (Boose et al. 1994) was run to determine if a given study area was protected from or exposed to damaging winds during these hurricane events. This model determines topographic exposure to wind based on digital elevation models and the direction of peak wind gusts during a given hurricane event (Boose et al. 1994). All historical references and model simulations were compared with each disturbance chronology to explore potential relationships between these historic disturbance events and identified periods of suppression and release in the tree ring record.

RESULTS

Species composition

Tsuga canadensis was the most common canopy dominant within the old-growth areas, comprising 39% to 92% of the basal area on 16 of the 18 sites where it was present (Table 1). Other species commonly co-occurring with *T. canadensis* in these areas included *Betula lenta, B. alleghaniensis*, *Fagus grandifolia*, and *Picea rubens*. In stands not dominated by *T. canadensis*, *Acer saccharum* was the dominant species, with *Fraxinus americana*, *F. grandifolia*, and *B. alleghaniensis* making up lesser components of these stands (Table 1).

Disturbance dynamics

Stands either contained two age classes (e.g., BB, CRB; Fig. 2) or were uneven-aged (e.g., CRA2, CRD; Fig. 2) and contained distinct establishment peaks indicative of past gap-scale disturbances (cf. Smith et al. 1997). There was little synchrony in establishment peaks across all 18 study areas; however, several establishment peaks were common at the regional scale (Fig. 2). For example, two establishment peaks (1770–1790 and 1850–1870) were common to all sites in the Southern Taconics, suggesting broadscale disturbances may have occurred during these decades. Similarly, establishment peaks during 1780–1800 and 1850–1870 were observed at the majority of sites within the Greylock region. Numerous sites within the Berkshire Plateau region exhibited comparable establishment patterns during 1780–1800, 1880–1910, and 1940–1960. In most study areas, the establishment of hardwood species such as *A. saccharum*, *F. grandifolia*, *B. lenta*, and *B. alleghaniensis* occurred during episodic establishment events (e.g., CRC, ME, MB, DB, TB; Fig. 2). In contrast, a combination of episodic and low but continuous establishment patterns was observed for *T. canadensis* and *P. rubens* at several sites (e.g., GR, CRA2, CRD, DH, HB; Fig. 2).

TABLE 1. Site and stand structural characteristics for each old-growth study area in western Massachusetts.

Characteristic	Study site BASH	BB	CRA1	CRA2	CRB	CRC	CRD	DH
Number on map	1	2	3	4	5	6	7	8
Elevation (m)	370–450	470–520	390–480	400–490	330–490	355–370	350–390	550–580
Study region†	S	B	B	B	B	B	B	G
Aspect (°)	353°–4°	350°–10°	336°–340°	296°–320°	332°–340°	48°–56°	272°–321°	270°–336°
Slope (°)	26°–46°	23°–38°	36°–40°	33°–41°	40°–42°	30°–37°	20°–31°	33°–38°
Size (ha)	7.8	6.7	8.2	7.3	5.2	7.0	13.0	12.9
Mean dbh of canopy trees (cm)	44.1	36.9	57.2	42.8	44.5	47.7	39.9	48.5
Basal area (m^2/ha)	48.3	47.3	44.1	39.7	38.6	28.1	49	41.5
Composition‡ (% basal area)	TSCA (72), PIST (22), BELE (2)	TSCA (79), BELE (13), QURU (4)	TSCA (71), FAGR (12), BELE (11)	TSCA (69), FAGR (15), BELE (8)	TSCA (80), BELE (8), BEAL (5)	ACSA (61), FAGR (19), BEAL (19)	TSCA (70), PIRU (19), BELE (7)	TSCA (81), PIRU (15), FAGR (4)

Notes: See Fig. 1 for study site locations; dbh, diameter at breast height.

† B = Berkshire Plateau, G = Greylock (located in the Taconic Mountains), S = Southern Taconics.

‡ ACRU = *Acer rubrum*, ACSA = *Acer saccharum*, BEAL = *Betula alleghaniensis*, BELE = *Betula lenta*, FAGR = *Fagus grandifolia*, FRAM = *Fraxinus americana*, PIRU = *Picea rubens*, PIST = *Pinus strobus*, QURU = *Quercus rubra*, TSCA = *Tsuga canadensis*.

Mean decadal rates of disturbance differed among stands (Kruskall-Wallis; $\chi^2 = 69.5$, 17 df, $P < 0.0001$), and the overall mean rate of disturbance across sites was 5.0% ± 0.2% canopy area disturbed per decade. Most decadal disturbance rates (86.2%) resulted in <10% canopy loss. In addition, there was no evidence of stand-replacing disturbances in any study area, as the maximum canopy area disturbed in any given decade was 26.3% (Table 2). Based on average disturbance rates, the mean residence time of canopy trees in these areas ranged from 118 yr to 357 yr (inverse of disturbance rates; Table 2). Nonetheless, many canopy trees had residence times well beyond these average values (Fig. 2). Among common canopy species, *T. canadensis*, *P. rubens*, and *F. grandifolia* established primarily as advance regeneration (i.e., were present in the forest understory prior to gap formation) and gained canopy status through gap-release events (Appendix B). In contrast, roughly half of the *A. saccharum* sampled originated in canopy gaps (i.e., were not present in the forest understory prior to gap formation).

Gradients in disturbance history

The disturbance chronologies constructed for each study area indicated that disturbance events varied considerably over time within and among study areas (Fig. 3). Nonmetric multidimensional scaling (NMS) ordination of the disturbance chronologies from 1870–1989 was able to explain 76.1% of the variation in disturbance history among study sites during this time period (Fig. 4a). Most of the variation in disturbance history (46.7%) was explained by the axis aligned with average decadal disturbance rate, which ranged from low, average levels of disturbance in the negative portion of axis 1 to higher levels of disturbance in the positive portion (Fig. 4a). Pearson correlations with this axis indicated that study sites located in the positive portion of axis 1 tended to have higher disturbance rates during the 1910s, 1920s, 1940s, 1950s, and 1980s (Table 3).

The distribution of study areas along axis 2, which explained 29.4% of the variation, generally ranged from more northern sites in the positive portion to more southern sites in the negative portion (Fig. 4a). Study areas in the northern portion of the state experienced higher levels of disturbances during the 1880s, as there was a significant negative correlation between disturbance rates in this decade and axis 2 (Table 3). Sites from within the same study region generally occupied different portions of ordination space, which suggests there was little relationship between study region and disturbance history from 1870–1989 (Fig. 4a).

NMS ordination of the disturbance dynamics for the older subset of study areas (1780–1869; $n = 11$) was effective in explaining the majority of variation in disturbance history among study sites during this time period (83.6% of total variation, Fig. 4b). As was the case from 1870–1989, the dominant gradient in variation among study areas during the 1780s–1860s was the average decadal disturbance rate (71.2% of total variation; Fig. 4b), with sites experiencing lower levels of disturbance occupying negative portions of NMS axis 1 and areas experiencing higher average rates of disturbance occupying the positive portions of this axis. Differences in forest composition and physiographic setting also influenced the range of variation in disturbance history among study areas, as percent *P. rubens* and aspect (Beer's transformed) were positively correlated with axis 1. Study areas located in the positive portion of axis 1 experienced higher levels of disturbance during the 1780s and 1790s, whereas study areas experiencing disturbances in the 1840s occupied negative portions of this axis (Fig. 4b; Table 3).

Differences in geographic location among study areas structured the distribution of study sites along NMS axis 2. In particular, the westernmost Greylock and Southern

Table 1. Extended.

Study site									
DB	GR	HA	HB	MB	ME	MO	TB	TM	WB
9	10	11	12	13	14	15	16	17	18
410–460	360–450	580–700	600–680	360–420	470–530	600–660	450–470	450–470	330–370
B	S	G	G	B	S	G	B	B	B
45°–53°	27°–50°	225°–270°	280°–321°	45°–77°	35°–50°	308°–33°	70°–88°	315°–358°	107°–143°
25°–30°	38°–43°	26°–40°	31°–35°	29°–35°	31°–45°	24°–32°	33°–42°	28°–35°	19°–28°
7.7	7.8	9.6	10.4	7.3	10.6	11.3	6.9	11.2	5.7
52.2	47.0	39.2	43.4	42.4	51.4	53.8	49.7	40.5	47.5
36.4	38	41.3	35.4	32.2	35.6	50.5	48.9	45.1	52.2
ACSA (41), FRAM (22), FAGR (19)	TSCA (92), BELE (5), BEAL (3)	TSCA (63), BEAL (16), PIRU (15)	TSCA (40), BEAL (37), PIRU (20)	TSCA (39), ACSA (36), FAGR (13)	TSCA (82), BELE (8), BEAL (6)	TSCA (44), ACSA (35), FRAM (8)	TSCA (56), ACSA (19), BEAL (17)	TSCA (81), ACRU (9), BELE (6)	TSCA (77), BELE (8), QURU (7)

Taconic study areas tended to occupy the negative portion of axis 2, whereas, the easternmost Berkshire Plateau study areas occupied the positive portions of this axis. A similar pattern regarding latitude also existed along this axis. The distribution of study areas along axis 2 and the negative correlation between this axis and disturbance rates in the 1820s (Table 3) suggest that areas in the southern and western portions of our study region were more affected by disturbance events during this decade. Despite these general patterns, there was no significant difference in the disturbance history from 1780–1869 among study regions (multiresponse permutation procedure; $P = 0.07$). Overall, final stress (16.8 and 11.6 for 1870–1989 and 1780–1869, respectively) and instability (0.00001 and 0.002 for 1870–1989 and 1780–1869, respectively) were well within acceptable ranges for both NMS ordinations (McCune and Grace 2002).

Discussion

Disturbance history

The following is a summary of the disturbance history for the old-growth areas based on evidence from the age class distributions, disturbance chronologies, and release and decline events developed from tree ring records. Model simulations of past hurricane events (Appendix C) and historical information on other known disturbance events (Appendix D) are used to assist in determining disturbance etiologies. The discussion of disturbance history across study areas is divided into three main periods: 1730–1829, 1830–1909, and 1910–1989. It is important to note that peak periods of disturbance fluctuated markedly within and among study regions, and we have chosen to focus the disturbance history mainly on disturbance periods in which moderate to high disturbance peaks in the form of tree establishment pulses, canopy disturbances, and/or releases and decline events were observed across study regions. Furthermore, historic events are discussed as known disturbance events that may have contributed to these periods and are not meant to imply absolute causation. In many cases, disturbance peaks observed at decadal scales are likely an aggregation of numerous disturbance events occurring during that time frame.

1730–1829

Disturbance peaks from 1730–1760 observed at sites within the Berkshire Plateau (BB and CRD) and Southern Taconics (BASH) suggest a period of widespread forest disturbance that resulted in *Tsuga canadensis* establishment; however, no specific disturbance events are historically noted for this period. Peak periods of disturbance activity across old-growth areas during the 1780s–1800s and 1820s corresponded to major hurricane events predicted to have affected these areas in 1788, 1804, 1815, and 1821, respectively (Appendix C; Ludlum 1963). Although the damaging effects of these hurricane events were much greater in other portions of New England (Boose et al. 2001), several study areas sustained moderate levels of canopy disturbance (>10% canopy area disturbed) during these decades (e.g., 1800s at BASH and 1820s at HA; Fig. 3). In addition, the establishment of midtolerant species, such as *Betula lenta* and *B. alleghaniensis*, at several sites (e.g., MO, GR, HA; Fig. 2) suggests that larger canopy gaps (>100 m^2; Webster and Lorimer 2005) were created during these disturbance periods. Multiple tornadoes affecting western Massachusetts in 1782 (Ludlum 1976) may have also contributed to the disturbance peak observed at sites such as GR in the 1780s (Fig. 3).

1830–1909

The highest level of canopy disturbance recorded in this study occurred during the 1860s at the CRD study area (26.3% canopy area). This disturbance era coincided with two predicted hurricane events (1861 and 1869; Appendix C) and resulted in the peak period of establishment for *T. canadensis*, *Picea rubens*, and hardwood species at this site. Extensive growth decline and release events also occurred at several other adjacent study areas during this decade but did not result in dramatic establishment of new individuals (CRB, MB, TM, WB; Figs. 2 and 3).

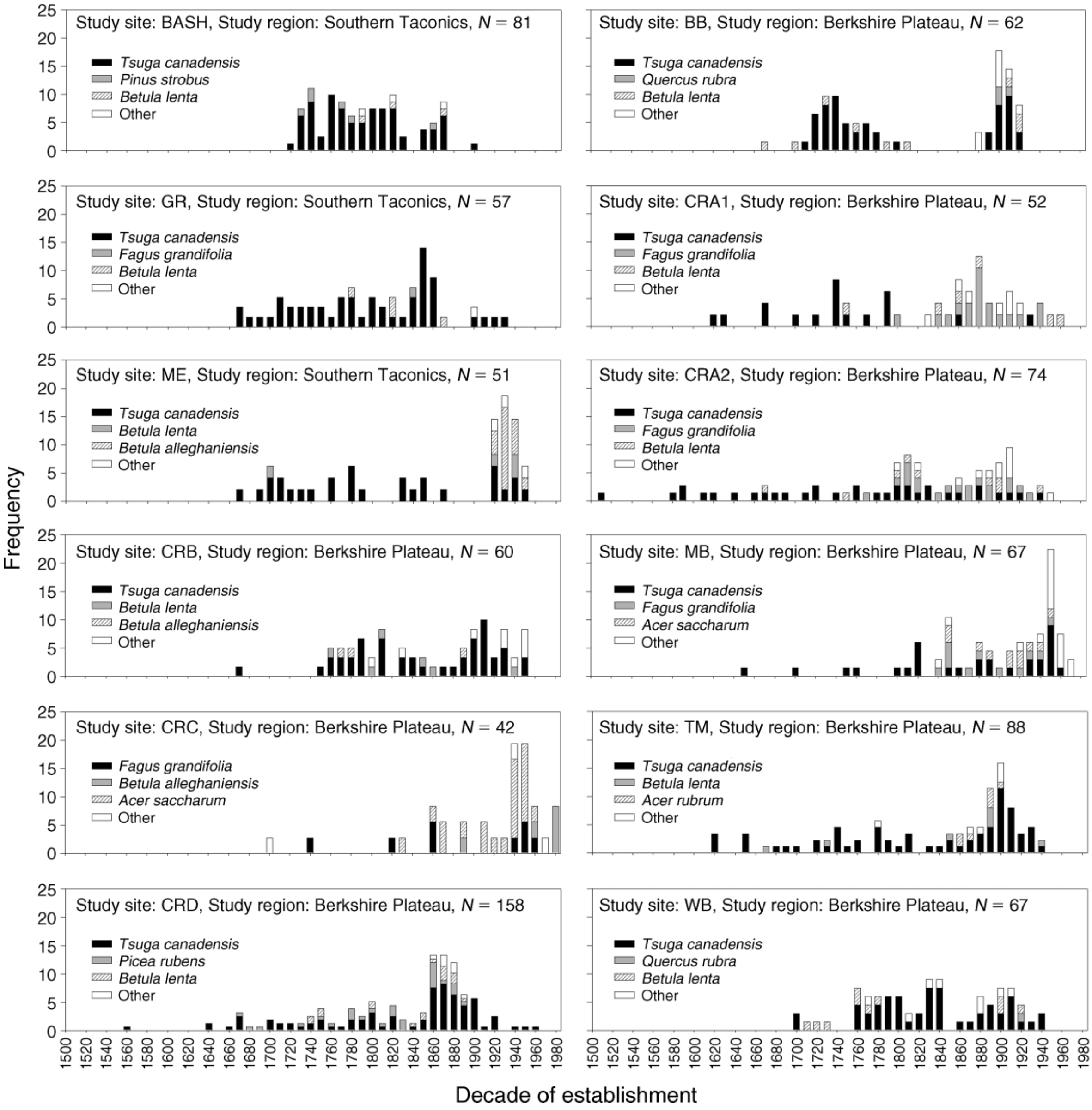

FIG. 2. Age class distributions for old-growth study areas. Distributions are based only on complete increment cores that reached the pith or contained strongly curved innermost rings allowing for age estimation using a pith locator (90.7% of total sample). N = total number of trees aged per study site. See Table 1 for study site information.

From 1830–1909 the only synchronous disturbance peaks across study regions occurred during the 1870s and 1900s. Moderate-intensity hurricane events in 1869 and 1878 (Appendix C), as well as region-wide severe thunderstorms in 1874 (Ludlum 1976) likely contributed to the peaks of canopy disturbance, canopy release, and tree damage (abrupt declines) experienced at many sites during this time. In addition, these events led to high subsequent establishment periods at several sites like CRA1 and CRD.

The peaks in disturbance within the Greylock region during the early 1900s were potentially due to a series of severe thunderstorms affecting this region during 1901 (Mount Greylock Reservation Commission [MGRC] 1919); however, little historical evidence exists to explain the disturbance peaks observed at other study areas during this time period. The high incidence of growth declines and subsequent canopy releases at several of the study areas suggest that canopy disturbances due to ice (cf. Lafon and Speer 2002) or windstorms (Foster 1988) were likely disturbance agents in these areas. Interestingly, disturbance peaks in the 1890s were only observed at study areas in the Berkshire Plateau (e.g., BB, WB; Fig. 3), despite the fact that the track of the hurricane of

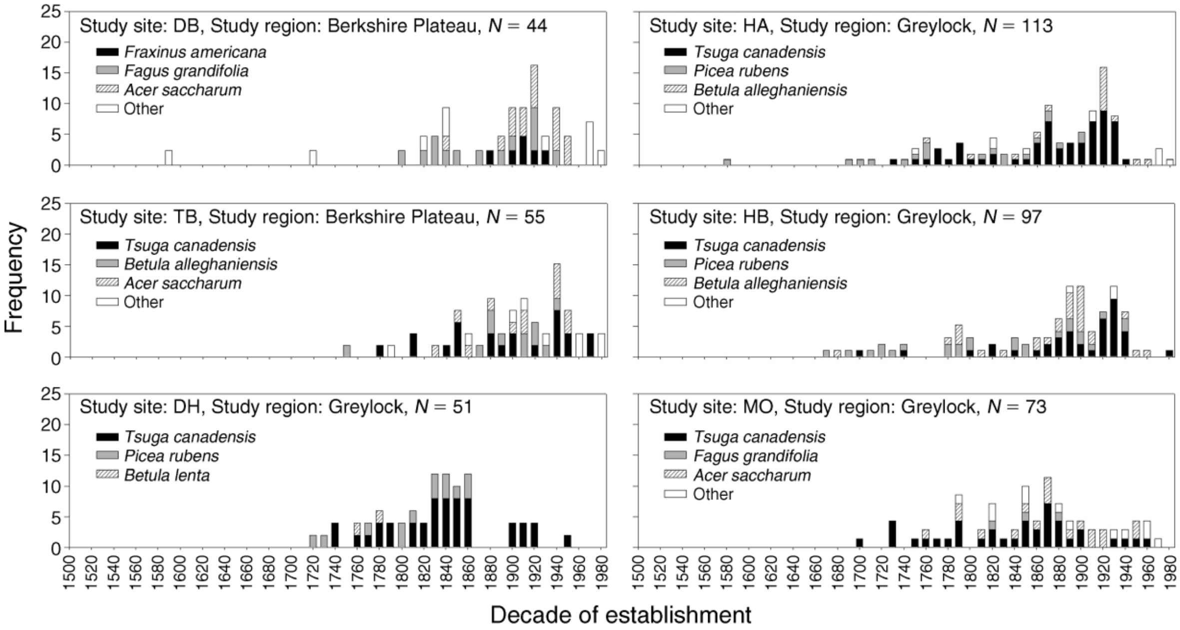

FIG. 2. Continued.

1893 passed in very close proximity to all three study regions (Smith 1946). These results highlight the patchy nature of disturbance on these landscapes with disturbance effects ranging from localized areas of extensive canopy disturbance (e.g., CRD in 1860s; Fig. 3) to smaller patches of disturbance within similar portions of the landscape (e.g., CRA1, CRA2, CRB, CRC, TM, WB in 1860s; Fig. 3).

1910–1989

The period from 1910–1989 was marked by several broadscale disturbance events in western Massachusetts that were recorded in both the dendroecological and historical records for all three study regions. Synchronous, interregion disturbance peaks in the 1920s were likely caused by two broadscale disturbance events. Based on historical records, it is likely that the 1921 ice storm significantly impacted all three study regions (Henry 1921). Specific accounts for each region document extensive damage to the forests during this time, including widespread uprooting of trees and extensive crown damage (Massachusetts Department of Conservation [MDC] 1922, MGRC 1922). A severe windstorm on 23 September 1920 caused substantial damage to forests and buildings within the Taconic Mountains (MGRC 1920) and may have contributed to the observed disturbance peaks during this decade. There were no records of this disturbance event for the Southern Taconic and Berkshire Plateau regions, but an account of the event in the *Annual Report of the Greylock Reservation Commission* suggests that this storm was locally destructive to the forests within the Greylock study region (MGRC 1920).

The hurricane of 1938 was the most destructive contemporary hurricane in southern New England, causing extensive canopy damage to forests throughout the central portion of the region (Foster 1988, Foster and Boose 1992). Although the effects of this disturbance were less severe in western Massachusetts (Appendix C), this event likely contributed to the moderate canopy disturbance and subsequent growth declines observed in the 1930s and 1940s across most study areas. A severe ice storm in 1942 (New England Power Service Company 1942, Winer 1955, Reid 1978)

TABLE 2. Mean (±SE) and maximum decadal disturbance rates and mean residence times for canopy trees in old-growth study areas in western Massachusetts.

Study area	Decadal disturbance rate (% canopy area disturbed)		Residence time of canopy trees (yr)
	Mean	Maximum	
BASH	6.6 ± 1	19.3	152
BB	5.5 ± 0.7	14.3	182
CRA1	4 ± 0.6	11.2	250
CRA2	4.6 ± 0.7	15.2	217
CRB	5.3 ± 0.8	15.8	189
CRC	3.1 ± 0.5	8.3	323
CRD	8.5 ± 1	26.3	118
DH	3.6 ± 0.6	7.9	278
DB	3.5 ± 0.5	8.8	286
GR	3.8 ± 0.5	9.3	263
HA	8.1 ± 1.1	21.3	123
HB	7.3 ± 0.8	16.1	137
MB	5.6 ± 1.1	14.6	179
ME	2.8 ± 0.6	9.2	357
MO	3.5 ± 0.8	13.7	286
TB	4.6 ± 1	12.8	217
TM	4.3 ± 0.6	11.7	233
WB	3.4 ± 0.5	9.5	294

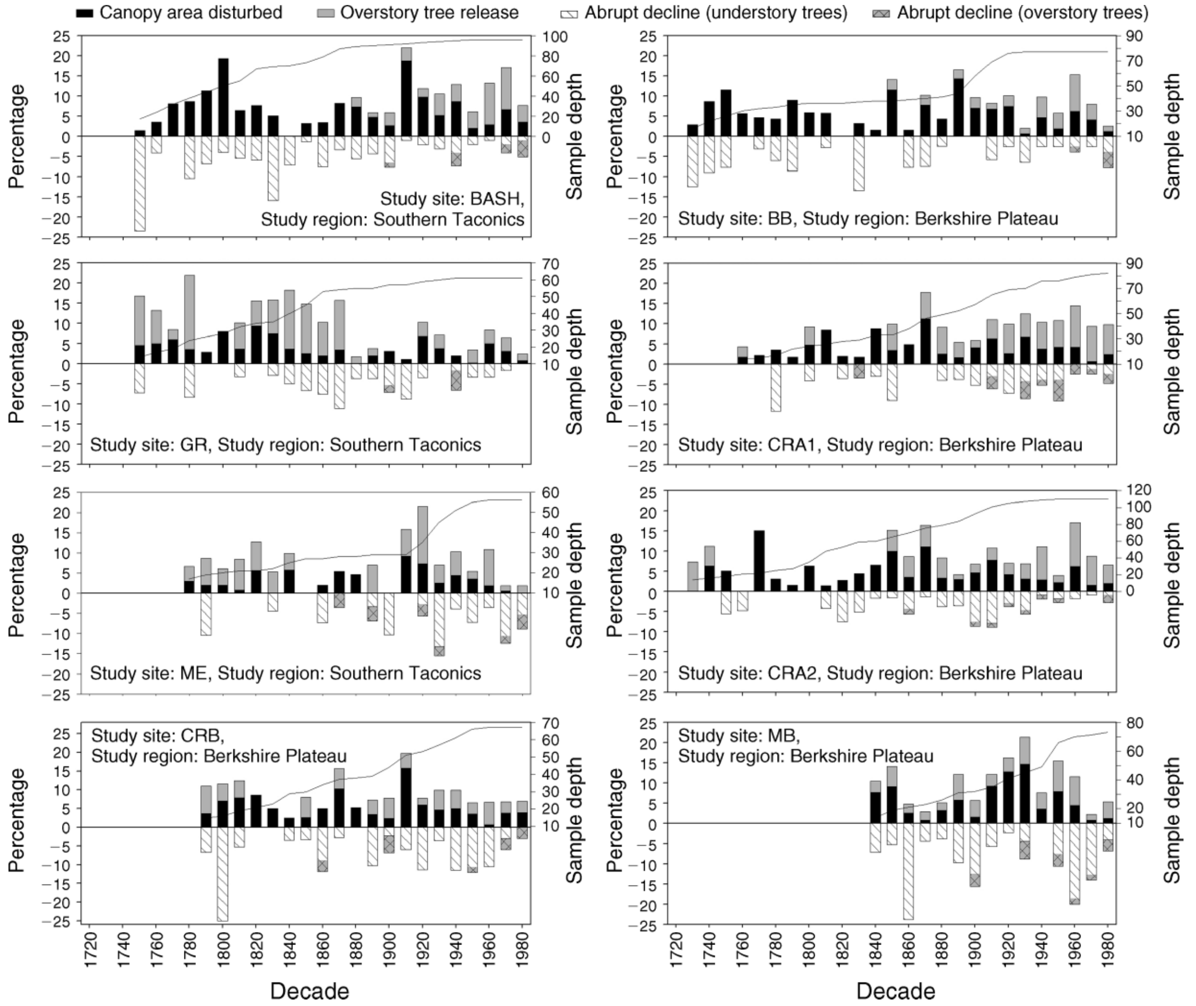

FIG. 3. Disturbance chronologies and growth release and decline events for old-growth study areas. Black bars represent reconstructed percentage of canopy area disturbed, gray bars represent percentage of overstory trees exhibiting growth release, and white hashed and gray hashed bars represent the percentage of understory and overstory trees, respectively, exhibiting a significant growth decline (see *Methods: Reconstruction of disturbance dynamics* and *Methods: Release of overstory trees and growth declines* for details on release and decline criteria). Sample depth refers to the number of canopy trees contributing to the chronology. Chronology length was truncated when sample depth dropped below 15 trees. See Table 1 for study site information.

and a low severity hurricane in 1944 (Appendix C) likely contributed to the widespread canopy disturbance, growth declines, and establishment peaks observed in the 1940s at the TB, ME, and CRC sites.

For most study areas, the 1950s through the 1980s was a period of relative quiescence, with no broadscale disturbance peaks or stand-level disturbance events affecting >7% of the canopy area during this time (Fig. 3). Nevertheless, several localized and more moderate disturbance peaks warrant further discussion. In particular, the establishment peaks observed at the CRC and MB study areas in the 1950s were two of the largest such events observed in this study (Fig. 2) and were probably due to the 1950 extra-tropical cyclone that affected portions of this region (MDC 1952). Drought has been suggested as a primary cause of canopy tree mortality in old-growth *T. canadensis* forests (Parshall 1995), and it is likely that the prolonged drought affecting the northeastern United States from 1962–1966 (Cook and Jacoby 1977) may have caused the substantial growth declines and subsequent canopy tree releases observed at numerous study areas during the 1960s. In addition, widespread mortality of *Fagus grandifolia* due to beech bark disease (caused by the fungi *Nectria* spp., preceded by the beech scale, *Cryptococcus fagisuga*) was documented in the 1960s in western Massachusetts (Reid 1978, Twery 1983) and may have contributed to the canopy disturbance and growth releases observed at several study areas with significant beech components (e.g., CRA2, DB, MB; Fig. 3). More specifically, *F. grandifolia* exhibited declining growth patterns at several of these sites during

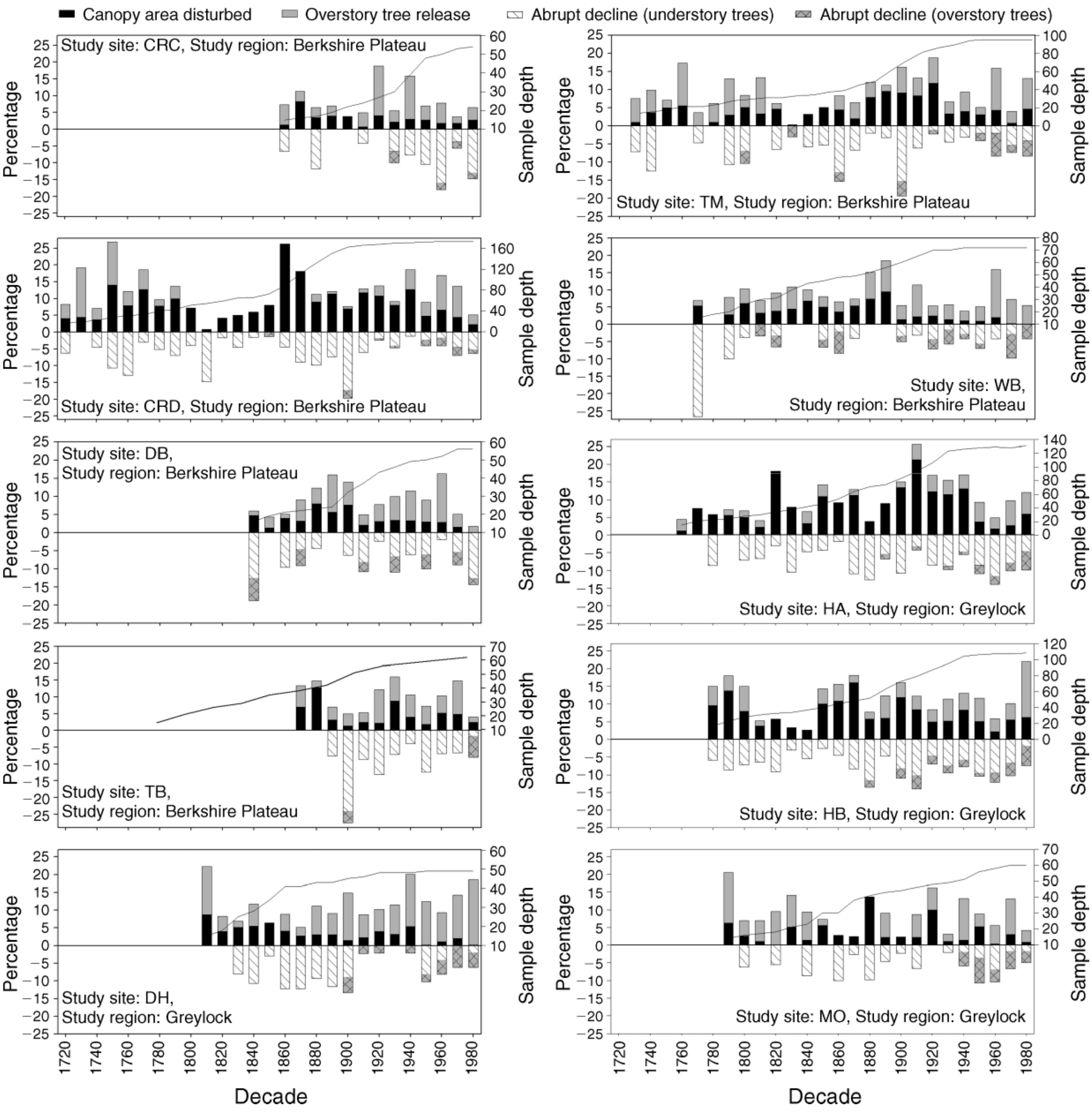

FIG. 3. Continued.

this decade, while other canopy species, such as *T. canadensis*, had concomitant growth releases.

Similarly, it is likely that the localized canopy disturbance and releases observed in several *Picea rubens*-dominated sites (HA, HB, DH) in the Greylock region during the 1980s were due to spruce decline reported for other parts of the northeastern United States during this time period (Siccama et al. 1982, Battles and Fahey 2000). In particular, canopy *P. rubens* exhibited declining growth patterns and increased rates of mortality (based on downed woody debris pools; D'Amato et al. 2008), while other species, including *T. canadensis* and *B. alleghaniensis*, exhibited growth releases.

Disturbance rates

The range of average canopy disturbance rates determined for old-growth sites in western Massachusetts was similar to those reported elsewhere for old-growth *T. canadensis* and northern hardwood forests (Runkle 1982, Frelich and Lorimer 1991*b*, Ziegler 2002). Similarly, the lack of evidence of stand-replacing disturbance is consistent with the findings of previous studies documenting the infrequent nature of such disturbances within northern hardwood and *T. canadensis* old-growth ecosystems (Hough and Forbes 1943, Whitney 1990, Nowacki and Abrams 1994, Abrams and Orwig 1996, Lorimer and White 2003). Nonetheless, it is

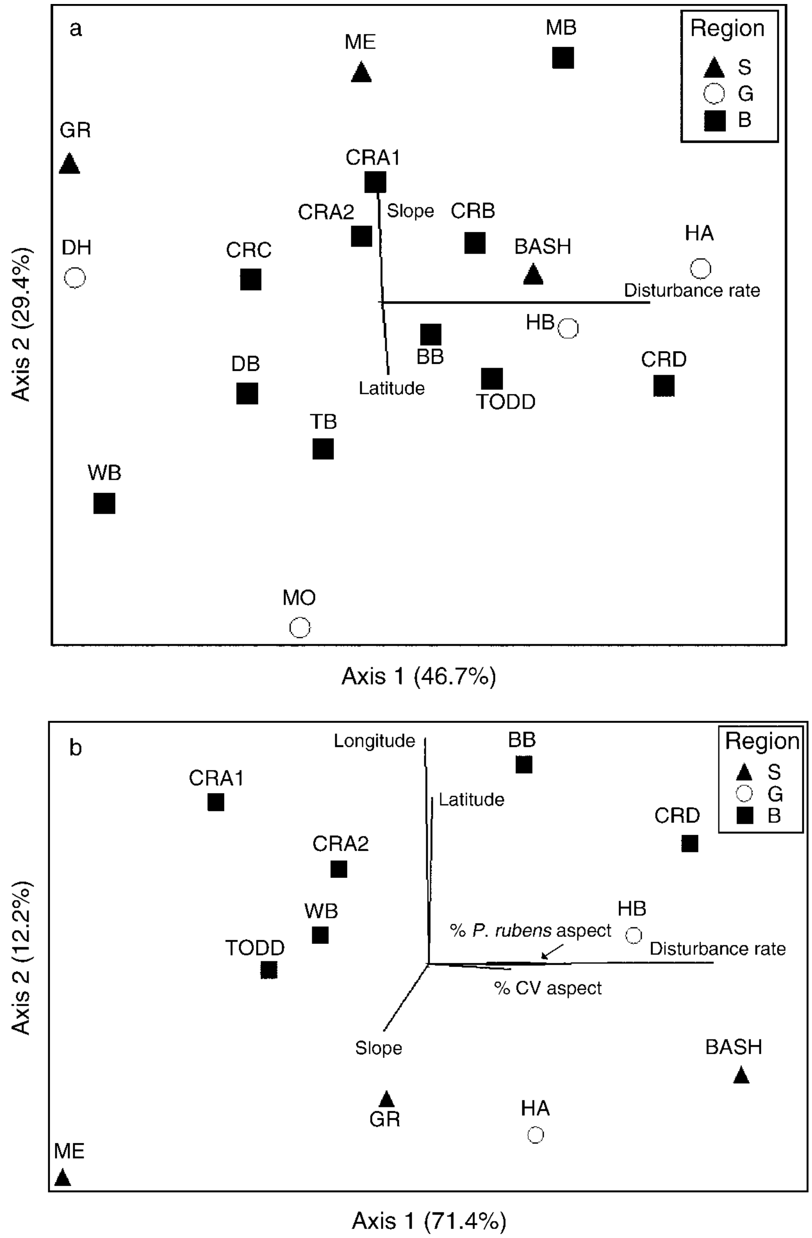

FIG. 4. Nonmetric multidimensional scaling (NMS) ordination of disturbance chronologies from (a) 1870–1989 and (b) 1780–1869. Study area locations in ordination space are depicted by symbols representing each study region. Vector length represents the explanatory power of the environmental, compositional, and geographic variables (only variables with $r^2 \geq 0.2$ are depicted). Both ordination diagrams were rigidly rotated to place the variable "average decadal disturbance rate" parallel with NMS axis 1. This variable corresponds to the average proportion of canopy disturbed for a given study site over the chronology used in the ordination. See Table 1 for study site information.

possible that stand-replacing disturbances may have historically affected similar portions of the landscape occupied by these old-growth forest types, as sites experiencing large-scale, stand-replacing disturbances may have been indecipherable from previously logged areas or stands subject to salvage operations at the time of this study. Despite this consideration, the findings of landscape-level studies of this forest type in other regions of North America suggest that these disturbance events are very infrequent (e.g., Frelich and Lorimer 1991*b*, Ziegler 2002, Fraver 2004).

Regional gradients in disturbance history

The effects of natural disturbances are rarely uniform on the landscape, resulting in a mosaic of conditions ranging from lightly disturbed to heavily disturbed areas at various spatial scales (e.g., Heinselman 1973, White 1979, Foster 1988, Frelich and Lorimer 1991, Foster and

Boose 1992, Turner et al. 1997). Intuitively, the scales at which we examined disturbance dynamics in this study constrain our observations to gap- and stand-scale dynamics and likely underestimate how extensive and severe the impacts of landscape-scale disturbances may have been across the landscapes of western Massachusetts. Nevertheless, the gradients in disturbance severity found within and among study sites suggest that historical disturbances had differential effects on these portions of the landscape at local and regional scales within western Massachusetts. In particular, temporal patterns of species establishment and disturbance were highly variable at the regional scale, and in several cases, geographically adjacent study areas occupied polar ends of ordination space (e.g., HA and DH; Fig. 4). Conversely, several geographically disparate areas shared similar disturbance histories, suggesting that broadscale disturbances, such as hurricanes and ice storms, had similar effects on these portions of the landscape (e.g., BASH, CRD, HA; Fig. 4). While much of the variation in disturbance history among and within our sites was likely due to the random nature of gap-scale disturbances (Runkle 1982, Frelich and Lorimer 1991), the interactions between disturbance severity, topographic exposure, forest structure, and species composition may have influenced these patterns.

In regions where windstorms are the predominant type of natural disturbance, topographic exposure often controls the patterns of disturbance effects on the landscape (e.g., Foster 1988, Boose et al. 1994, Jenkins 1995, Ruffner and Abrams 2003). In particular, areas situated on windward slopes or exposed ridges often experience higher average rates of disturbance than more protected portions of the landscape (Frelich and Lorimer 1991, Foster and Boose 1992). This relationship was observed in our study, as sites with the highest average levels of canopy disturbance (CRD, HA, HB) were topographically exposed to peak wind gusts for the most destructive, historic hurricane events in western Massachusetts (Appendix C; 1788, 1815, 1846, 1938), whereas topographically protected sites (WB, MO) had some of the lowest observed average disturbance rates. In addition, study areas located on northwest-facing slopes experienced higher rates of disturbance in the 1780s and 1790s than other portions of the landscape (Fig. 4). As a result of these gradients, average canopy residence times for trees across our study areas varied considerably, with protected areas containing residence times at least twice as long (e.g., 294 yr at WB; Table 2) as those observed on more exposed areas (e.g., 123 yr at HA; Table 2). This gradient is consistent with Frelich and Lorimer (1991*b*), who reported canopy residence times ranging from 60 yr to 323 yr across an old-growth landscape in Upper Michigan.

Table 3. Decades significantly correlated (Bonferroni-corrected; $P < 0.05$) with at least one nonmetric multidimensional scaling axis in ordinations of disturbance chronologies for (a) all study areas ($n = 18$) from 1870–1989 and (b) a subset ($n = 11$) of study areas from 1780–1869.

Decade	Axis 1	Axis 2
a) All sites (1870–1989)		
1880		−0.72
1910	0.81	
1920	0.65	
1940	0.74	
1950	0.66	
1980	0.69	
b) Older subset (1780–1869)		
1780	0.81	
1790	0.88	
1820		−0.73
1840	−0.61	

Note: Values shown for axis 1 and axis 2 are Pearson correlation coefficients.

Forest structure and composition often influence the stand and landscape-level impacts of disturbances such as wind (Foster and Boose 1992, Canham et al. 2001), ice (Lemon 1961, Boerner et al. 1988, Rhoads et al. 2002), and insects and diseases (Twery and Patterson 1984, Orwig et al. 2002). While the majority of our study areas were similar in composition and structure, several sites differing in forest composition and structure experienced different disturbance impacts. For example, *P. rubens*-dominated forests tended to have the highest average disturbance rates and greater disturbance peaks during events such as the 1788 hurricane compared to other study areas (Fig. 4). These patterns may be due to the higher susceptibility of *P. rubens* to windthrow relative to other species in these stands, including *T. canadensis* (Canham et al. 2001). In addition, the dominant to emergent canopy positions occupied by *P. rubens* and the high number of snapped and windthrown individuals occurring within these areas corroborates this fact (D'Amato et al. 2008). The high elevations of *P. rubens* stands may have also contributed to the greater rates of disturbances at these areas; however, it is interesting to note that the *P. rubens* stand with the greatest disturbance rate occupied an elevation similar to the majority of other stands examined in this study (CRD; Table 1). Our results suggest that northern hardwood areas tended to have lower overall disturbance rates compared to most conifer-dominated sites. Despite this general trend, the low number of northern hardwood old-growth forests precludes us from making generalities about these systems relative to other forest types in the region.

It is important to note that we did not have a large contiguous old-growth landscape to rigorously evaluate spatial patterns of disturbance, and our study plot locations were dictated by the places on the landscapes in which old-growth forest still remained. As such, this discussion should be viewed as a qualitative evaluation of the regional patterns of disturbance among 18 variously spaced study areas and not a rigorous assessment of historic patterns of landscape-wide disturbance in western Massachusetts. Nonetheless, the synchrony in several disturbance peaks among geographically distant study areas suggests that this spatial arrangement was able to detect broadscale disturbance signals that likely affected many other similar portions of the landscape that we were unable to sample. Conversely, the discordant nature of disturbance patterns at more local spatial scales reinforces our general understanding of the largely random nature of gap-scale disturbances on the landscape.

Conclusions

In many regions of North America, the lack of large, contiguous old-growth landscapes has historically hampered efforts aimed at developing an understanding of the natural landscape-level disturbance dynamics for a given forest type and region. This study sought to address this constraint by integrating the stand-level disturbance dynamics across the 18 largest remaining *Tsuga canadensis*- and northern hardwood-dominated old-growth forests in western Massachusetts. Dynamics at the stand-level were similar to those documented for these forest types in other regions of northeastern North America and were characterized by relatively frequent, low-intensity disturbances that generally operated randomly on the landscape. By using a novel integration of dendroecological reconstructions of disturbance dynamics across sites using ordination techniques, coupled with model simulations of hurricane damage and historical documents, we were able to demonstrate that broadscale disturbances, such as hurricanes and ice storms, likely resulted in peak periods of disturbance on the landscape that were detected at spatial scales >50 km. Likewise, the lack of synchrony in proximate areas during these events highlights the patchy nature of the effects of these disturbances on similar portions of the landscape. While the scale at which these investigations were conducted is constrained by the extent of remaining old-growth forests on the landscape, this study nonetheless provides important insight into the general patterns of natural forest dynamics for a region in which human disturbance has predominated for centuries. As such, information on the rates of disturbance across these areas is critical for guiding the development of natural disturbance-based silvicultural strategies, as well as for guiding conservation and management strategies aimed at maintaining target levels of various forest successional stages on similar portions of the landscape in southern New England.

Acknowledgments

We thank Jessica Butler, Glenn Motzkin, Christian Foster, and Ben Ewing for assistance with fieldwork. We are particularly indebted to Emery Boose for his assistance in using the EXPOS and HURRECON models. 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 David Foster, 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.

Abrams, M. D., S. van de Gevel, R. C. Dodson, and C. Copenheaver. 2000. The dendroecology and climatic impacts for old-growth white pine and hemlock on the extreme slopes of the Berkshire Hills, Massachusetts, USA. Canadian Journal of Botany 78:851–861.

Applequist, M. B. 1958. A simple pith locator for use with off-center increment cores. Journal of Forestry 56:141.

Attiwill, P. M. 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. Forest Ecology and Management 63:247–300.

Battles, J. J., and T. J. Fahey. 2000. Gap dynamics following forest decline: a case study of red spruce forests. Ecological Applications 10:760–774.

Beers, T. W., P. E. Dress, and L. C. Wensel. 1966. Aspect transformation in site productivity research. Journal of Forestry 64:691–692.

Boerner, R. E. J., S. D. Runge, D. Cho, and J. G. Kooser. 1988. Localized ice storm damage in an Appalachian Plateau watershed. American Midland Naturalist 119:199–208.

Boose, E. R., K. E. Chamberlin, and D. R. Foster. 2001. Landscape and regional impacts of hurricanes in New England. Ecological Monographs 71:27–48.

Boose, E. R., D. R. Foster, and M. Fluet. 1994. Hurricane impacts to tropical and temperate forest landscapes. Ecological Monographs 64:369–400.

Bush, R. R. 1995. Northeastern TWIGS variant of the Forest Vegetation Simulator. USDA Forest Service, Forest Management Service Center, Fort Collins, Colorado, USA. ⟨http://www.fs.fed.us/fmsc/fvs/variants/ne.php⟩

Canham, C. D. 1985. Suppression and release during canopy recruitment in *Acer saccharum*. Bulletin of the Torrey Botanical Club 112:134–145.

Canham, C. D. 1990. Suppression and release during canopy recruitment in *Fagus grandifolia*. Bulletin of the Torrey Botanical Club 117:1–7.

Canham, C. D., and O. L. Loucks. 1984. Catastrophic windthrow in the presettlement forests of Wisconsin. Ecology 65:803–809.

Canham, C. D., M. J. Papaik, and E. F. Latty. 2001. Interspecific variation in susceptibility to windthrow as a function of tree size and storm severity for northern temperate tree species. Canadian Journal of Forest Research 31:1–10.

Cook, E. R., and G. C. Jacoby. 1977. Tree ring–drought relationships in the Hudson Valley, New York. Science 198: 399–401.

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.

D'Amato, A. W., D. A. Orwig, and D. R. Foster. 2008. The influence of successional processes and disturbance on the structure of *Tsuga canadensis* forests. Ecological Applications 18:1182–1199.

Davis, M. B. 1996. Eastern old-growth forests: prospects for rediscovery and recovery. Island Press, Washington, D.C., USA.

Dunwiddie, P. W., and R. T. Leverett. 1996. Survey of old-growth forests in Massachusetts. Rhodora 98:419–444.

Egler, F. E. 1940. Berkshire Plateau vegetation, Massachusetts. Ecological Monographs 10:145–192.

Engstrom, R. T., S. Gilbert, M. L. Hunter, Jr., D. Merriwether, G. J. Nowacki, and P. Spencer. 1999. Practical applications of disturbance ecology to natural resource management. Pages 313–330 *in* W. T. Sexton, R. Szaro, N. C. Johnson, and A. J. Malk, editors. Ecological stewardship: a common reference for ecosystem management. Elsevier Science, Oxford, UK.

Field, D. D., and C. Dewey. 1829. A history of the county of Berkshire, Massachusetts, in two parts. S. W. Bush, Pittsfield, Massachusetts, USA.

Foster, D. R. 1988. Disturbance history, community organization and vegetation dynamics of the old-growth Pisgah forest, south-western New Hampshire, USA. Journal of Ecology 76:105–134.

Foster, D. R., and E. R. Boose. 1992. Patterns of forest damage resulting from catastrophic wind in central New England, USA. Journal of Ecology 80:79–98.

Fraver, S. 2004. Spatial and temporal patterns of natural disturbance in old-growth forests of northern Maine. Dissertation. University of Maine, Orono, Maine, USA.

Fraver, S., and A. S. White. 2005. 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. 1991*a*. A simulation of landscape dynamics in old-growth northern hardwood forests. Journal of Ecology 79:223–233.

Frelich, L. E., and C. G. Lorimer. 1991*b*. Natural disturbance regimes in hemlock–hardwood forests of the upper Great Lakes region. Ecological Monographs 61:145–164.

Fujita, T. T. 1971. Proposed characterization of tornadoes and hurricanes by area and intensity. SMRP Paper 91, Department of Geophysical Science, University of Chicago, Chicago, Illinois, USA.

Heinselman, M. O. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. Quaternary Research 3:329–382.

Henry, A. J. 1921. Great ice storm of November 26–29 in Massachusetts. Monthly Weather Review 49:612.

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.

Hough, A. F., and R. D. Forbes. 1943. The ecology and silvics of forests in the High Plateaus of Pennsylvania. Ecological Monographs 13:299–320.

Jenkins, J. 1995. Notes on the Adirondack blowdown of July 15, 1995: scientific background, observations, and policy issues. Wildlife Conservation Society, Bronx, New York, USA.

Lafon, C. W., and J. H. Speer. 2002. Using dendrochronology to identify major ice storm events in oak forests of southwestern Virginia. Climate Research 20:41–54.

Leak, W. B. 1987. Comparisons of standard and actual tree-growth trends for deciduous and coniferous species in New Hampshire. Canadian Journal of Forest Research 17:1297–1300.

Lemon, P. C. 1961. Forest ecology of ice storms. Bulletin of the Torrey Botanical Club 88:21–29.

Leverett, R. T. 1996. Definitions and history. Pages 3–17 *in* M. B. Davis, editor. Eastern old-growth forests: prospects for rediscovery and recovery. Island Press, Washington, D.C., USA.

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., L. E. Frelich, and E. V. Nordheim. 1988. Estimating gap origin probabilities for canopy trees. Ecology 69:778–785.

Lorimer, C. G., and A. S. White. 2003. Scale and frequency of natural disturbances in the northeastern United States: implications for early successional forest habitat and regional age distributions. Forest Ecology and Management 185:41–64.

Ludlum, D. M. 1963. Early American hurricanes. American Meteorological Society, Boston, Massachusetts, USA.

Ludlum, D. M. 1976. The country journal: New England weather book. Houghton Mifflin, Boston, Massachusetts, USA.

Massachusetts Department of Conservation (MDC). 1922. Annual report of the state forester in Massachusetts. Massachusetts Department of Conservation, Boston, Massachusetts, USA.

Massachusetts Department of Conservation (MDC). 1952. Timber sales agreement for Mohawk Trail State Forest: salvage of hurricane blowndown hemlock timber. Massachusetts Department of Conservation, Boston, Massachusetts, USA.

MassGIS. 2006. Insect infestation datalayer for the years 1934–1997. MassGIS, Commonwealth of Massachusetts, Executive Office of Environmental Affairs, Boston, Massachusetts, USA.

McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon, USA.

McCune, B., and M. J. Mefford. 1999. PC-ORD, multivariate analysis of ecological data. Version 4.0. MjM Software Design, Gleneden Beach, Oregon, USA.

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.

Mount Greylock Reservation Commission (MGRC). 1919. Nineteenth annual report of the Greylock Commission. Wright and Potter, Boston, Massachusetts, USA.

MGRC. 1920. Twentieth annual report of the Greylock Commission. Wright and Potter, Boston, Massachusetts, USA.

MGRC. 1922. Twenty second annual report of the Greylock Commission. Wright and Potter, Boston, Massachusetts, USA.

National Climatic Data Center. 2006. ⟨www.ncdc.noaa.gov/oa/ncdc.html⟩

New England Power Service Company. 1942. Western Massachusetts ice storm photographs collection, 1942. University of Massachusetts, Special Collections, Amherst, Massachusetts, USA.

Nowacki, G. J., and M. D. Abrams. 1994. Forest composition, structure, and disturbance history of the Alan Seeger Natural Area, Huntington County, Pennsylvania. Bulletin of the Torrey Botanical Club 121:277–291.

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.

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., and M. D. Abrams. 1994. Contrasting radial growth and canopy recruitment patterns in *Liriodendron tulipifera* and *Nyssa sylvatica*: gap obligate versus gap-facultative tree species. Canadian Journal of Forest Research 24:2141–2149.

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.

Parshall, T. 1995. Canopy mortality and stand-scale change in a northern hemlock–hardwood forest. Canadian Journal of Forest Research 25:1466–1478.

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

Reid, A. C. 1978. A vegetation survey of Mt. Greylock. Honor's thesis. Williams College, Williamstown, Massachusetts, USA.

Rhoads, A. G., S. P. Hamburg, T. J. Fahey, T. G. Siccama, E. N. Hane, J. Battles, C. V. Cogbill, J. Randall, and G. Wilson. 2002. Effects of an intense ice storm on the structure of a northern hardwood forest. Canadian Journal of Forest Research 32:1763–1775.

Ruffner, C. M., and M. D. Abrams. 2003. Disturbance history and stand dynamics along a topographic gradient in old-growth hemlock–northern hardwood forests of the Allegheny Plateau, USA. Natural Areas Journal 23:98–113.

Runkle, J. R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. Ecology 62:1041–1051.

Runkle, J. R. 1985. Disturbance regimes in temperate forests. Pages 17–33 *in* S. T. A. Pickett and P. S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, San Diego, California, USA.

Scanu, R. J. 1988. Soil survey of Berkshire County, Massachusetts. United States Department of Agriculture, Soil Conservation Service, Amherst, Massachusetts, USA.

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.

Siccama, T. G., M. Bliss, and H. W. Vogelmann. 1982. Decline of red spruce on the Green Mountains of Vermont. Bulletin of the Torrey Botanical Club 109:163–168.

Smith, D. M. 1946. Storm damage in New England forests. Thesis. Yale University, New Haven, Connecticut, USA.

Smith, D. M., B. C. Larson, M. J. Kelty, and P. M. S. Ashton. 1997. The practice of silviculture: applied forest ecology. John Wiley and Sons, New York, New York, USA.

Turner, M. G., V. H. Dale, and E. H. Everham, III. 1997. Fires, hurricanes, and volcanoes: comparing large disturbances. Bioscience 47:758–768.

Twery, M. J. 1983. Variations in the effects of beech bark disease with composition and structure of northern hardwood stands in central New England. Thesis. University of Massachusetts, Amherst, Massachusetts, USA.

Twery, M. J., and W. A. Patterson. 1984. Variations in beech bark disease and its effects on species composition and structure of northern hardwood stands in central New England. Canadian Journal of Forest Research 14:565–574.

Ward, J. S., and G. R. Parker. 1989. Spatial dispersion of woody regeneration in an old-growth forest. Ecology 70: 1279–1285.

Webster, C. R., and C. G. Lorimer. 2005. Minimum opening sizes for canopy recruitment of midtolerant species: a retrospective approach. Ecological Applications 15:1245–1262.

White, P. S. 1979. Pattern, process and natural disturbance in vegetation. Botanical Review 45:229–299.

Whitney, G. G. 1990. The history and status of the hemlock–hardwood forests of the Allegheny Plateau. Journal of Ecology 78:443–458.

Winer, H. I. 1955. A history of the Great Mountain Forest, Litchfield County, Connecticut. Dissertation. Yale University, New Haven, Connecticut, USA.

Yamaguchi, D. K. 1991. A simple method for cross-dating increment cores from living trees. Canadian Journal of Forest Research 21:414–416.

Zen, E-an, G. R. Goldsmith, N. L. Ratcliffe, P. Robinson, and R. S. Stanley. 1983. Bedrock geologic map of Massachusetts. United States Geological Survey, Monograph Series, Reston, Virginia, USA.

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.

APPENDIX A

Regression equations for predicting exposed crown area from tree diameter at breast height (*Ecological Archives* M078-020-A1).

APPENDIX B

A summary of canopy accession strategies based on analyses of initial growth rates and identification of release events (*Ecological Archives* M078-020-A2).

APPENDIX C

Hurricane events affecting the old-growth areas in western Massachusetts based on HURRECON simulations (*Ecological Archives* M078-020-A3).

APPENDIX D

Disturbance events known to have affected portions of the Berkshire Hills and Taconic Mountains in which old-growth study areas are located (*Ecological Archives* M078-020-A4).