COMPOSITION, STRUCTURE, AND DISTURBANCE HISTORY OF OLD-GROWTH AND SECOND-GROWTH FORESTS IN ADIRONDACK PARK, NEW YORK

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Abstract: Old-growth forests with 300- to 400-year-old trees are uncommon in the eastern United States, but forests that regenerated after anthropogenic disturbance are widespread. I compared patterns of species composition, size structure, and disturbance in old-growth, hemlock-dominated forests with those characteristics of post-fire, second-growth forests in the Adirondack Mountains in northern New York to document the persistence of historical events. The species in the old-growth canopy were shade-tolerant, and the canopy species of the 90-year-old secondary forests were shade-tolerant or shade-intolerant, depending on the stand. The old-growth forests had more larger stems and fewer smaller stems per 0.1 ha than the second-growth forests. From tree-ring widths I reconstructed the disturbance chronology of the stands. The decadal rate of canopy turnover for the 50-yr. period from 1930 to 1979 in old growth (3.1–4.5%) was not significantly different from the disturbance rate in second-growth forest (3.5–4.1%). The composition and structure of old growth were distinctive, but disturbance rates in old growth were similar to patterns in nearby second-growth forest in spite of differences in stand age and past human activity. Together the old growth and the unmanaged secondary forests enhance landscape diversity, and an analysis of natural variability in these forests provides baseline information for conservation efforts elsewhere. [Key words: old growth, disturbance, hemlock-dominated forests, Adirondack Park.]

INTRODUCTION

Old-growth forests—as one form of nature that has not been altered radically by people—are important to scientists and nature enthusiasts alike, in part because they are rare. Old-growth forests developed under former environmental conditions and thus provide a window to the past. These unlogged primary forests also will have value in the future. Botkin (1990, p. 194–195) advocated the protection of wilderness areas "untouched by direct human actions" both to serve as "a baseline from which scientists can measure the effects of human actions elsewhere" and to help maintain biological diversity.

The term *old growth* does not have a single, universal definition (e.g., Franklin et al., 1981; Whitney, 1987; Spies and Franklin, 1988; Hunter, 1989; Oliver and Larson, 1996; Runkle, 1991; Tyrrell, 1992; Vora, 1994; Leverett, 1996; Foster et al., 1996; Frelich, 2002; Frelich and Reich, 2003). Old growth often connotes certain structural characteristics or a uniformity of process (Oliver and Larson, 1996). The structural patterns of old growth include a wide range of tree sizes and ages, a higher proportion of small trees than large trees, more young trees than old trees,

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many standing dead trees and snags, and abundant large logs on the ground (e.g., Whitney, 1987; Oliver and Larson, 1996; Leverett, 1996; Goodburn and Lorimer, 1998; McGee et al., 1999; Ziegler, 2000). The casual observer expects old-growth forests to look impressive in stature compared to younger forests, although stands in intermediate stages of development might have some combination of large-diameter trees and fallen logs, a wide range of tree sizes, and old trees. Forests of eastern white pine (*Pinus strobus* L.) in the Northeast, Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) in the Pacific Northwest, and yellow poplar (*Liriodendron tulipifera* L.) in the Southeast might look like old growth because these long-lived early-successional species grow rapidly following disturbance and can dominate the stands for centuries (Oliver and Larson, 1996). Some definitions of old forests acknowledge that development is ongoing and that canopy trees might not be old or large (Frelich and Reich, 2003).

"Uniformity of process" in old growth means that understory trees, resprouted stems, and newly germinated seedlings grow up into gaps formed when canopy trees die (Oliver and Larson, 1996). Low- to moderate-severity disturbances open up holes in a forest canopy when a single tree or cluster of trees is bent, uprooted, or snapped off (Webb, 1988). Most ideas of old growth assume that the forest persists through time in the absence of large-scale disturbance, but old growth is rarely defined by the frequency and severity of smaller disturbances. Frelich and Reich (2003) recommended, however, that the role of disturbance be recognized when distinguishing primary forests from forests without "a continuous heritage of natural disturbance and regeneration" (p. S12).

It is difficult to predict whether the amount of canopy disturbance in old growth would be more or less than in adjacent second-growth forest because disturbance severity is a product of many factors including tree size, the susceptibility of each species and of individual trees to windthrow, and the age of each tree relative to its natural lifespan. One might expect that the area in gaps (i.e., openings in the tree canopy) would be greater in old growth than in a second-growth forest with smaller trees because the crowns and trunks of large, old trees would create larger holes when the trees fall. Whitney (1986) reported a higher incidence of disturbance in old-growth–hemlock–white pine northern hardwood forests than in other forests, due to the shallow roots of eastern hemlock (*Tsuga canadensis* [L.] Carr.) and the irregular canopy surface of that forest type. Canham et al. (2001) noted for some species, however, that susceptibility to windthrow was lower in old growth than in second growth regardless of stem diameter. They also found that, for small size classes, shade-tolerant species were more resistant to windthrow than were shade-intolerant trees. Tree age also affects its likelihood of falling and creating a gap; if many small, short-lived trees fall in close proximity, then the resulting canopy gap might be larger than the opening caused by the loss of a single large tree.

I characterized the composition, structure, and disturbance history of forests in Adirondack Park in northern New York State (Fig. 1) to search for patterns and processes that old growth had in common with selected younger forests—a research direction recommended by Leopold et al. (1988, p. 184). The objective was to compare selected secondary forests that were burned by logging-related fires about 90 yrs. prior to the study with old-growth forests that originated at least a few hundred

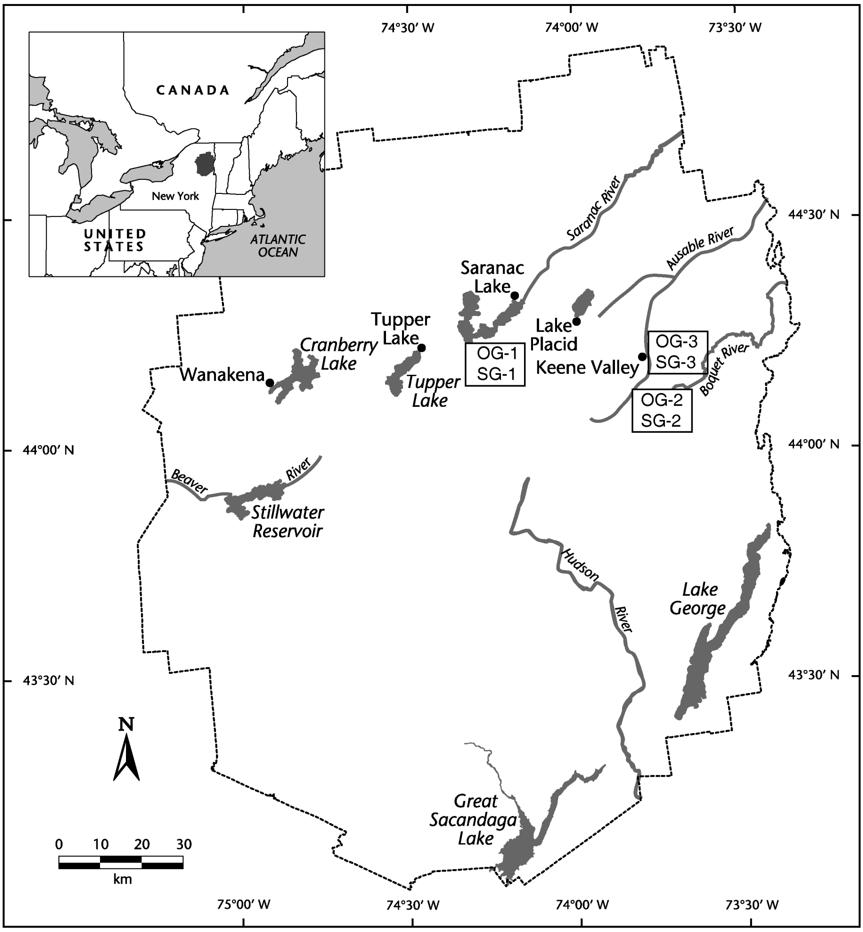

Fig. 1. Old-growth (OG) hemlock-dominated forest and nearby second-growth (SG) forest in Adirondack Park, NY, include sites near Ampersand Mountain (OG-1 and SG-1), Gill Brook in the Adirondack Mountain Reserve (OG-2 and SG-2), and Roaring Brook on Giant Mountain (OG-3 and SG-3).

years before Europeans settled the region. It was not presumed that these younger stands eventually will look like the current old growth. I predicted that the post-fire forests were different from the primary forest due to the legacy of historical events (Foster, 2003). I hypothesized that old growth differed from second growth in terms of the species composition of the overstory, the general form of the diameter distribution of stems and the number of small trees, and the decadal rate of canopy disturbance, as reconstructed from tree rings.

The Adirondack writer Bill McKibben (1995a, 1995b) had an optimistic view of the regenerating forest, which he called the "someday old growth." McKibben (1995a) wrote that "ancient forest is not the real glory of the Adirondacks. It's the new forest merging with the old, the groves thirty and fifty and a hundred years old that are increasingly indistinguishable from old growth" (p. 31). I sought to evaluate whether secondary forests are "increasingly indistinguishable" from old growth, and to identify visual and quantitative similarities and differences between old growth and second growth because a field-based study of this nature had not yet been conducted in the Adirondacks. Studies elsewhere have correlated forest structure and composition with stand age and history (e.g., Hardt and Swank, 1997). I also related the results to *natural variability* concepts, which are used increasingly to address conservation and management issues (e.g., Swanson et al., 1994; Shinneman and Baker, 1997; Landres et al., 1999; Cowell and Parker, 2004). The natural variability of an ecosystem that has been little modified by people refers to the composition, structure, and dynamics of vegetation over space and time (Landres et al., 1999). I incorporated both a pattern-based assessment of species composition and size structure, and a process-based characterization of developmental stages and disturbance chronologies.

Study Area

Adirondack Park (Fig. 1) is the largest publicly protected area in the conterminous United States (New York State Adirondack Park Agency, 2003), at almost three times the size of Yellowstone National Park. Nearly half of the 2.4 million hectares within the park boundary is public and is protected by the New York State constitution, while the remaining property includes private timber lands, settlements, and businesses. The land within the park boundaries is a "wilderness interwoven with human settlement" (McKibben, 1992, p. 60).

Old growth in Adirondack Park is rare today because of logging and logging-related fires in the late 1800s and early 1900s. An estimated 81,000 to 204,000 ha of Adirondack forest (approximately 3 to 8% of the land within the park) is old growth (Leopold et al., 1988; McMartin, 1994). Much of the uncut forest grows in extreme environments avoided by loggers, such as on steep slopes or at elevations above 1200 m. Some old-growth remnants are in less extreme settings, including the 20,000 ha of unlogged old growth in the Five Ponds Wilderness Area (FPWA), and the three smaller areas (60 to 2800 ha) of old growth east of the FPWA that are the subjects of this study. This old growth was not logged because of complex histories of land ownership (Roman, 1980; McMartin, 1994).

I selected three areas of old growth (OG-1, OG-2, OG-3) in the mountainous region of north central Adirondack Park (Fig. 1). The old growth is accessible by hiking trail and is surrounded by younger forest. I collected old-growth data from four 0.1-ha plots near Ampersand Mountain (OG-1), two 0.1-ha plots near Gill Brook (OG-2), and four 0.1-ha plots near Roaring Brook (OG-3). Data from the two or four plots were pooled for each of the three areas of old growth, and results were reported as an average per 0.1 ha unless otherwise specified.

Previous scholars (Leopold et al., 1988; Woods and Cogbill, 1994) had identified these areas of old growth as forests with a wide range of tree diameters, no evidence of logging, clearing, cutting, or planting, and a minimum stand age (200 yrs.) of approximately half the average maximum life span of the dominant tree species.

Eastern hemlock, a species that commonly lives at least 400 yrs. (Godman and Lancaster, 1990), had the highest relative basal area of any species in the old-growth forests selected for this study (Ziegler, 2000). Old-growth hemlock-dominated forest is one of the forest types in middle elevation (400–600 m) upland settings of the northern Adirondacks. 60 to 80% of the canopy trees in each of the three areas of old growth were more than 200 yrs. old (Ziegler, unpublished data, 1996, 1997).

I compared the old-growth forests with three post-fire second-growth forests (SG-1, SG-2, SG-3), and collected data from two 0.1-ha plots in each of these human-disturbed areas. I selected the burned stands using the *Fire Protection Map of the Adirondack Forest* compiled by the state forester Karl Schmitt (1916), and I sampled forests that were disturbed by logging-related fires in 1903 or 1908. Most of the 1903 fires were stand-replacing crown fires rather than surface burns (Suter, 1904), which were fueled by woody debris left behind by loggers and were exacerbated by regional drought. The climate of each area of old growth was similar to that of the associated second growth because the forests were only a few kilometers apart. The environmental settings (e.g., elevation, slope steepness and aspect, topographic position, soil characteristics) of the old growth and corresponding second growth were as similar as possible (Ziegler, 1999).

Second-growth, post-fire forests are common in the Adirondacks. Approximately 344,000 ha (about 14% of the total area currently within the Park, and about 25% of the area of the park at the time of the fires) burned between 1903 and 1913 (Howard, 1914; Jenkins, 1995). Fire is an uncommon and poorly studied disturbance agent in the Adirondacks. Land surveys from 1796 to 1825 indicate that the natural (i.e., before European settlement) return interval for fires in western Adirondack Park may have been on the order of thousands of years (C. V. Cogbill, unpublished data, 1996).

DATA AND METHODS

Establishment of Plots

I used stratified random sampling to create 0.1-ha (20-m x 50-m) permanent plots (10 plots in old growth and 6 plots in second-growth forests) with the long axis oriented parallel to the slope. I selected a stand and then paced a random number of steps from the nearest trail into the forest at a random compass bearing to set the first corner of the rectangular plot.

Species Composition of Canopy Trees

To test the hypothesis that old growth differed from second growth in species composition of the overstory, I recorded the species and diameter at breast height (dbh) of each canopy and understory tree $\geq$2.5 cm dbh on each 0.1-ha plot. Then I compared the shade tolerance of canopy-tree species in old growth to the canopy composition of second-growth forests. If both forest types were dominated by shade-tolerant species that are associated with a lack of recent widespread disturbance then this would suggest that old-growth and second-growth forests were at a similar developmental stage. Conversely, if shorter-lived, shade-intolerant species dominated the canopy of younger forests then it would imply that the impact of major disturbance persists (Bormann and Likens, 1994).

Size Structure of Canopy Trees

I hypothesized that the 300- to 400-year-old trees of the old-growth stands would be larger, and that stands of larger trees would have fewer trees than the second-growth stands. This structure is typical of uneven-aged stands (e.g., Leak, 1964; Quinby, 1991) in which establishment of new trees and mortality are balanced and the stand is self-perpetuating (Whipple and Dix, 1979).

To determine whether the post-fire second-growth forests were structurally similar to old-growth hemlock-dominated forests I analyzed the size distribution of the canopy and understory trees. I plotted the size structure (i.e., average number of trees in each 5-cm category per 0.1 ha) of each area for all canopy and understory trees and saplings $\geq$2.5 cm dbh.

Canopy Disturbance

I predicted that the area in gaps would be greater in old growth than in second growth because the large, shallow-rooted hemlocks would create sizeable openings in the tree canopy when they fall. To test this hypothesis, I reconstructed the disturbance chronology, which describes the pattern of gap formation, or specifically what percentage of the forest canopy is removed each decade. The frequency and severity of canopy disturbance can be determined from the growth-rate patterns of trees (Lorimer, 1985; Lorimer and Frelich, 1989; Frelich, 2002). Each canopy tree that originated in a gap shows rapid early growth in its innermost tree rings. Resources such as space, light, water, and nutrients are freed when a canopy tree falls over. Neighboring trees respond to the increase in resources by growing more quickly, and sometimes growing up into the canopy gap. The growth spurt shows up as a sequence of wider tree rings. A graph of a tree's ring widths over time shows periods of increased, sustained growth when resources became available and the tree was able to "capture" the canopy gap. This event is called canopy accession, and some trees require multiple disturbance events to maintain their canopy status (Canham, 1985, 1989, 1990; Lorimer and Frelich, 1989).

I extracted one increment core at a height of 1 m from each canopy tree on each plot, for a total of 544 cores. The number of canopy trees per 0.1 ha ranged from 26 to 42. In the lab, cores were air dried, mounted in wooden holders, sanded, visually inspected, and dated. I counted rings with a binocular microscope and measured them with a stage micrometer to the nearest 0.01 mm using standard dendrochronological procedures (Stokes and Smiley, 1968; Phipps, 1985). For increment cores missing the pith, I used the ring curvature to estimate the distance to the center of the tree, assuming that growth rings were concentric (Applequist, 1958). I divided this distance by the average growth rate of the innermost 10 yrs. of the core to estimate the number of rings between the end of the core and the pith.

Table 1. Regression Equations[a] to Predict Exposed Crown Area (ECA) in Square Meters from Tree Diameter (dbh) in Centimeters

Species	Equation
Tsuga canadensis (L.) Carrière	ECA = $0.1451(\text{dbh})^{1.3362}$
Picea rubens Sarg.[b]	
Abies balsamea (L.) Miller[b]	
Thuja occidentalis L.[b]	
Acer saccharum Marshall	ECA = $0.377(\text{dbh})^{1.223}$
Acer pensylvanicum L.[b]	
Betula alleghaniensis Britton	ECA = $200.9(e)^{(-65.84/\text{dbh})}$
Betula papyrifera Marshall[b]	
Fagus grandifolia Ehrh.[b]	
Ostrya virginiana (Miller) K. Koch[b]	
Fraxinus americana L.[b]	
Populus grandidentata Michx.[b]	
Prunus serotina Ehrh.[b]	

[a] Equations developed by Lorimer and Frelich, 1989.

[b] Equation adopted for species with lifeform similar to species for which equation was originally determined (Lee E. Frelich, research associate, University of Minnesota, pers. comm., January 25, 2001).

The radial-growth patterns indicated the decade in which each tree reached the canopy. I estimated the proportion of the canopy removed per decade from the number of canopy trees showing either gap origin or significant growth release in a given decade, following methods adapted from Lorimer (1985), Lorimer and Frelich (1989), and Frelich and Lorimer (1991). When a tree falls over or its top is snapped off by wind, the size of the resulting hole in the canopy is a function of the size of the tree's crown. To account for the fact that the crown size of each tree differs with the tree's size, I weighted each release event by the exposed crown area (ECA) of the tree, estimating ECA from the tree's current dbh using regression equations (Table 1) developed by Lorimer and Frelich (1989). This method was based on the assumption that the current canopy trees occupy former canopy gaps. It yielded an estimate of the area of canopy disturbed rather than a real value because crown sizes and stand size-structure change over time (Lorimer and Frelich, 1989; for a discussion of assumptions and biases of this method see Ziegler, 2002).

First, I screened cores for evidence of rapid early growth, which indicated that the tree either germinated following canopy disturbance or was a sapling <1 m tall when the canopy opening occurred. I assumed that a tree originated in a gap if the initial 5 yrs. of growth averaged ≥1.2 mm/yr. (Lorimer et al., 1988; Lorimer and Frelich, 1989; Frelich, 2002), and the date of canopy accession was defined as the year in which the pith formed. All yellow birch (*Betula alleghaniensis* Britton) trees were classified as originating in a gap, regardless of their initial growth rate, because the species is moderately shade tolerant and requires an opening in the canopy for seedlings to become established (Lorimer and Frelich, 1989; Erdmann, 1990).

Second, I analyzed all cores, including those that qualified for rapid early growth, for growth releases (i.e., evidence of entering the canopy). I defined the date of canopy accession as the year in which a growth release began, applying both moderate and conservative criteria. Under moderate criteria (90% confidence level), I defined a growth release as a 50 to 99% increase in growth rate that persisted for 10 to 15 yrs. and was preceded by 10 to 15 yrs. of suppressed growth. Under conservative criteria (95% confidence level), a growth release was an abrupt (within 6 yrs.) increase in growth rate that was more than double the average growth rate of the preceding 15 yrs., and that persisted for at least 15 yrs. The criteria of ≥10 yrs. of suppression followed by ≥10 yrs. of increased growth rate effectively screened out the effects of short-term climate fluctuations on growth rate variability (Lorimer and Frelich, 1989). The moderate and conservative criteria yielded similar results (Ziegler, 2002); I reported the conservative results unless otherwise noted.

The first decade of the disturbance chronology was 1930 to ensure that trees that regenerated following the fires of 1903 and 1908 had reached coring height, and thus were included in the data set. The last decade of the chronology was 1970 to 1979, because saplings in gaps formed in the 1980s might not have been large enough to core in the mid-1990s, and therefore would have been missing from the tree-ring record. Multiple large trees with canopy accession dates in a given decade indicated a major disturbance event. In stands where the amount of the canopy removed was relatively constant each decade, disturbance was frequent but not severe in the stand over 50 yrs.

RESULTS AND DISCUSSION

Species Composition of Canopy Trees

The difference in species composition between old-growth hemlock-dominated forests and the surrounding younger forests was striking. Eastern hemlock, a shade-tolerant tree (Fowells, 1965; Godman and Lancaster, 1990), was the canopy species with the highest basal area in each of the areas of old-growth, while shade-intolerant paper birch (*Betula papyrifera* Marshall) and shade-tolerant sugar maple (*Acer saccharum* Marshall) had the highest basal area in the post-fire forests (Ketchledge, 1996; Ziegler, 2000). Eastern hemlock was also the canopy species in the old-growth stands with the highest relative number of stems (range: 58–85%), while sugar maple and paper birch had the highest relative number of stems in second-growth forests (range: 24–79%; Table 2). The canopy of one of the second-growth

Table 2. Relative Density (%) of Canopy Trees by Species for Each Area of Old-Growth (OG) and Nearby Second-Growth (SG) Forest

Species	OG-1	SG-1	OG-2	SG-2	OG-3	SG-3
Eastern hemlock (*Tsuga canadensis* [L.] Carr)	85.1		58.0	2.5	80.0	14.1
Sugar maple (*Acer saccharum* Marshall)	6.8	23.9	3.4	79.0	6.3	33.3
American beech (*Fagus grandifolia* Ehrh)	3.3	19.7	15.9	13.6	2.1	
Yellow birch (*Betula alleghaniensis* Britton)	3.3	12.7	3.4	2.5	1.1	17.9
Red spruce (*Picea rubens* Sarg.)	1.7		18.2	2.5	1.1	
Paper birch (*Betula papyrifera* Marshall)		29.6			1.1	26.9
Big-toothed aspen (*Populus grandidentata* Michx.)		4.2			1.1	3.8
Hop-hornbeam (*Ostrya virginiana* (Miller) K. Koch)		2.8			2.1	2.6
Balsam fir (*Abies balsamea* (L.) Miller)		4.2			3.9	
Black cherry (*Prunus serotina* Ehrh.)		2.8				
White ash (*Fraxinus americana* L.)					2.1	
Striped maple (*Acer pensylvanicum* L.)	<1		1.1			
Northern white cedar (*Thuja occidentalis* L.)						1.3

forests was dominated by sugar maple. Two of the areas of second-growth forest (SG-1 and SG-3) had sugar maple and paper birch as co-dominant canopy species.

Paper birch seedlings, which establish after intense disturbance, were in only one of the second-growth forests, and no paper birch saplings grew on any of the plots. The lack of birch seedlings and saplings suggests that the impact of human disturbance is lessening, and that future species composition of the canopy might consist of shade-tolerant species such as sugar maple and American beech (*Fagus grandifolia* Ehrh.), which grew in the understory. Sugar maple decline and beech bark disease, two serious concerns in the Northern Forest of the northeastern United States, might limit the canopy accession of maple and beech, but it is not clear what species would take their place. Eastern hemlock faces its own challenges.

Eastern hemlock dominated the canopy of each of the old-growth areas, and the second-growth forests in this study had little hemlock in the canopy. The canopy composition in old growth was not the same as in second-growth forests, but canopy dominance by shade-tolerant species in some of the younger post-fire forests suggests that these were mulitcohort stands in a later developmental stage than might have been predicted based on time since fire (Oliver and Larson, 1996). Eastern hemlock likely will be rare in second-growth forests for the foreseeable future because of the persistent effects of early 20th-century logging and fires and the current direction of forest development. The pattern was similar in hemlock–white pine–northern hardwood forests of Michigan, where logging "permanently altered the species composition" (Whitney, 1987, p. 675). In Michigan, the logged old-growth forests of hemlock, beech, and sugar maple became stands dominated by sugar maple. The hot fires that followed logging promoted further vegetation change.

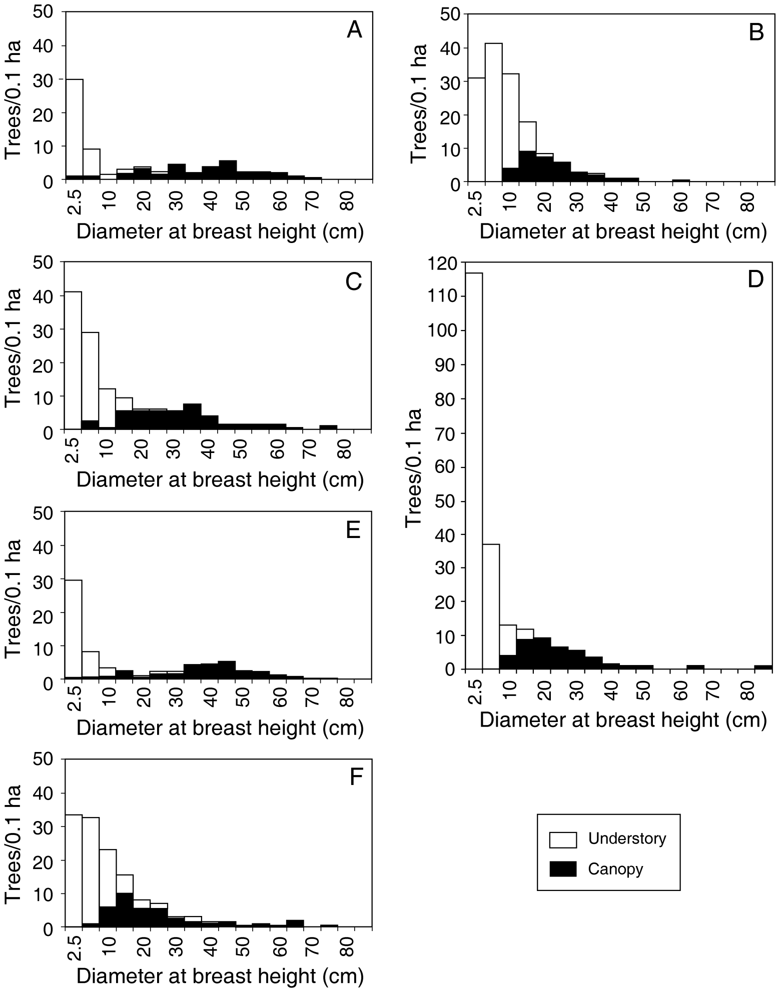

Fig. 2. Size structure (trees/0.1 ha in each diameter class) in each area of old-growth (OG) and nearby second-growth (SG) forest. Compare area A with B, C with D, and E with F. Diameter (cm) is indicated by the lower limit of each size class interval (e.g., 2.5 indicates the 2.5–4.9 cm size class; 10 indicates the 10–14.9 cm size class).

It is unlikely that hemlock will dominate the canopy of the post-fire forests in the Adirondacks, at least in the next century. First, the local conditions have changed since initial hemlock establishment at these sites. Second, hemlock regeneration in both old growth and second growth will be impeded by some combination of factors including regional hemlock decline, browsing by deer and other herbivores on hemlock seedlings and saplings, and the threat of hemlock woolly adelgid (*Adelges tsugae* Annand), a non-native insect that has decimated hemlock forests in southern New York, southern New England and the central Appalachian Mountains.

Table 3. Statistically Significant Differences between Old-Growth and Second-Growth Forests

Characteristic	Old-growth versus second-growth forest
Canopy trees	More species of shade-tolerant trees in old growth.
Size structure	Wider range of sizes and lower density of small stems in old growth.
Canopy gaps[a]	Larger average gap size in old growth.
Coarse woody debris[a]	Greater volume of logs ≥20 cm dbh in old growth.
Structural characteristics[a]	Greater basal area of trees in old growth; lower density of trees (all species) in old growth; higher density of eastern hemlock trees in old growth; lower density of saplings in old growth.
Disturbance chronology	No significant difference between old growth and second-growth forest in proportion of canopy removed per decade over 50-yr. period from 1930 to 1979.

[a]Data are summarized in Ziegler, 2000.

Size Structure

The hemlock-dominated old-growth forests had more larger trees and fewer smaller trees per 0.1 ha than the post-fire stands (Fig. 2). Most stands had a descending monotonic (reverse-J shape) diameter distribution, in which the large number of small trees represents suppressed saplings under the closed canopy (Lorimer, 1985). The second-growth stands had a large cohort of canopy trees that grew up after the fire and also some older trees that survived the fire (Ziegler, 2000), which is not uncommon in second-growth hardwood forests (Cole and Lorimer, 1994). The largest tree (86 cm dbh) of all sampled stands was a hemlock on one of the post-fire plots (Fig. 2D). The large (60–85 cm size classes) canopy trees in the second-growth forests survived the fire, providing evidence of the patchiness of the burn.

The distribution of stems in 5-cm size classes of the SG-2 forest (Fig. 2D) was similar to the size structure of nearby old growth (Fig. 2C), but the very high density of stems (118 per 0.1 ha) in the smallest size class at SG-2 reflected the younger age and different species composition of the second-growth stand. The second-growth stands had an abundance of small-diameter, suppressed stems in the understory compared to the lower density of small trees in the old growth (Fig. 2) because stem exclusion and self thinning (i.e., death from suppression due to limited space and light) still occurred in the understory of the secondary forest (Oliver and Larson, 1996). The size structure, therefore, differed between old-growth and second-growth forest—not in the range of sizes but in the proportion of large versus small stems. This pattern was the opposite of the size structure in old-growth and second-growth forests of the FPWA (Canham et al., 2001), where the older stands had fewer larger trees and more smaller trees, presumably because beech bark disease killed many of the large trees (Charles D. Canham, forest ecologist, Institute of Ecosystem Studies, pers. comm., April 2, 2004). Additional structural properties were characteristic of the old growth in my study (Table 3); canopy gaps were larger and the volume of coarse woody debris was greater in old growth than in second growth (Ziegler, 2000).

Canopy Disturbance

Contrary to the hypothesis that more of the canopy would be disturbed in old growth than in second growth, disturbance patterns were comparable across two stages of forest development, in spite of differences in species composition and structure. The proportion of the canopy removed per decade from 1930–1979 averaged 3.1 to 4.5% (conservative and moderate criteria, respectively) for the old growth, and 3.5 to 4.1% for the second-growth forest. The decadal disturbance rates were similar between areas of old-growth and second-growth forest (Fig. 3). For example, overall disturbance rates at Ampersand Mountain old growth (OG-1) and nearby secondary forest (SG-1) were low for all decades (Fig. 3B), whereas the percentage area in gaps at Gill Brook (OG-2) and nearby second-growth forest (SG-2) was high during the 1970s (Fig. 3C). The disturbance rate of all old-growth stands was similar to that of all second-growth stands (Fig. 3A). The Mann-Whitney test ($p = 0.704$) suggested that there was no significant difference in the amount of disturbance between the old-growth forests and the younger post-fire stands.

The similar area in canopy gaps implies that the amount of space for regeneration was comparable in old growth and second growth, although the types of microsites (i.e., mounds, pits, stumps, and dead boles) for colonization likely differed (Webb, 1988). The life history of the canopy species might help explain the similarity in disturbance patterns across different aged forests. Paper birch in the post-fire stands was near the end of its typical lifespan (Fowells, 1965), so canopy gaps were created as the birch trees died and fell over or snapped off. In second-growth forests, the high density of stumps and snags and the relatively large total area of canopy gaps probably were related to the abundance of aging birch trees (Ziegler, 2000). Shorter-lived, shade-intolerant, post-disturbance species might also have influenced historical patterns of area in gaps, although the secondary forest with the greatest percentage area in gaps in the 1970s (SG-2 in Fig. 3C) had a high density of sugar maple and no paper birch in the canopy in the mid-1990s (Table 2).

A dendrochronological reconstruction of the disturbance regime provides valuable information about forest processes, such as windthrow, that can help guide ecosystem managers (Swanson et al., 1994). The state-owned Adirondack forests are unmanaged due to their protection status as "forever wild," but process-based assessments of forests could help inform conservation decisions at adjacent and nearby privately-owned forests.

Natural Variability Concepts

The species composition, size and age structure, and developmental stage of the younger forests are different from those features of old growth, and so we could conclude that the second-growth forest is outside the range of natural variability in its appearance. The intense fires of the early twentieth century that killed most of

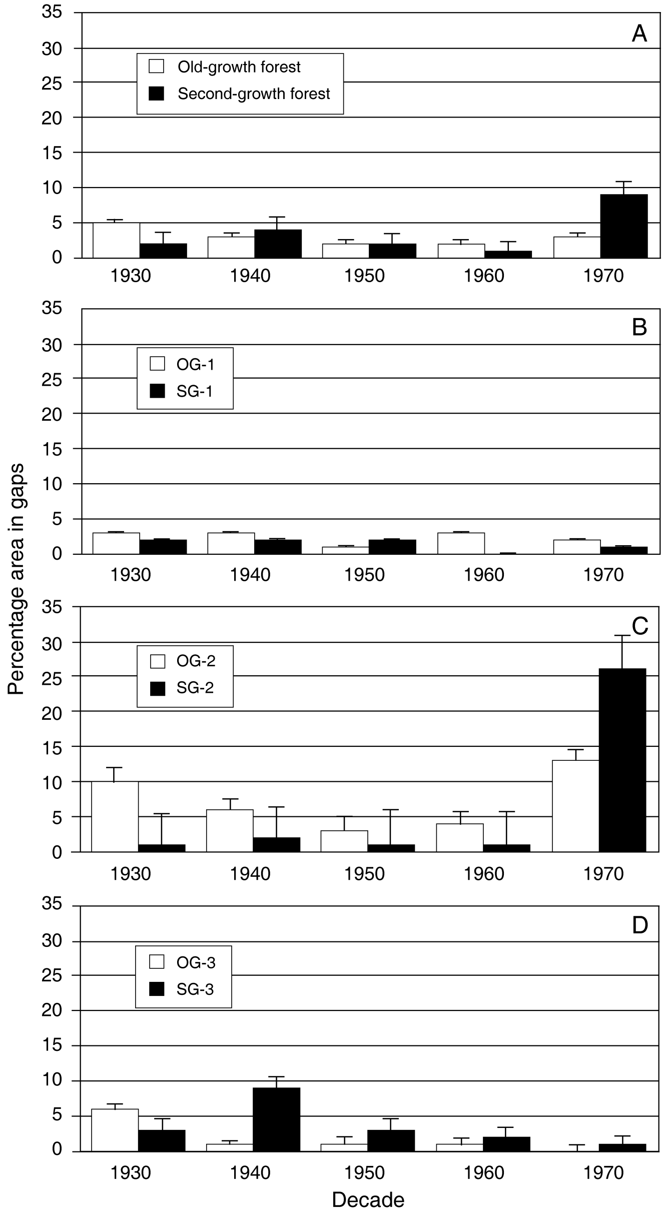

Fig. 3. Estimated percentage (plus one standard error) of study area converted to canopy gaps for each of five decades: (A) all study areas; (B) near Ampersand Mountain (OG-1 and SG-1); (C) near Gill Brook (OG-2 and SG-2); and (D) near Roaring Brook on Giant Mountain (OG-3 and SG-3).

the trees and triggered a large pulse of regeneration (see Fig. 5 in Ziegler, 2000) fell outside the normal range of disturbance of approximately 0 to 50% of the canopy per decade over the 130-yr. period from 1850 to 1979 (Ziegler, 2002). We should not conclude from the natural disturbance regime that catastrophic fires did not occur prior to European settlement, or that intense windstorms do not topple trees over large geographic areas. On the contrary, in 1995 sustained winds of greater than 120 km/hour with gusts exceeding 160 km/hour blew down more than 60% of the trees on 15,000 acres in the western Adirondacks (Jenkins, 1995). The post-fire secondary forest recovered to the point that the disturbance regime fell within the range of natural disturbance of the past 130 yrs. These results illustrate that pattern-based assessments of natural variability can differ from process-based analyses of the same forests, supporting the idea that both types of criteria are necessary for defining old growth and for managing forests of all developmental stages.

SUMMARY AND CONCLUSIONS

The forests of Adirondack Park are diverse even at a particular elevation range and latitude due in part to differences in history of disturbance and land protection. Almost 100 yrs. after anthropogenic disturbance, old-growth stands differed from nearby post-fire forests in species composition, size structure, and developmental stage; the recovering forests are not indistinguishable from old growth. The disturbance chronology over a 50-yr. period was similar in old growth and nearby second-growth forests in spite of stand age, species composition, and lasting effects of human activity. It is difficult to predict how disturbance will affect the forests over the next 50 yrs., in part because we do not know whether a stand-replacing disturbance will initiate the development of a new forest. Even if wind storms were to continue at the present rate and intensity, the effect of disturbance on the percentage area in gaps might change over the next century as species composition changes with stand development—especially in the second-growth stands dominated by paper birch close to its maximum lifespan. Species composition and forest structure do not predetermine the impact of small-scale disturbances, and disturbance frequency and severity are not unique to old growth. These primary forests meet descriptive definitions of old growth, but they cannot necessarily be distinguished from secondary forests by the percentage area in canopy gaps.

Whether old growth is valued for its record of the past, for its present-day aesthetic qualities, or for its significance for future generations, it is an important component of our protected areas in the Adirondacks and elsewhere. At the same time, the post-fire forests, which have regenerated on their own over the past century, add to the landscape's diversity. The fact that regeneration in the unmanaged forests was successful after major human disturbance should give us hope for the future (McKibben, 1995a, 1995b) even if the younger forests are visibly different from old growth and never will return to the pre-logging conditions. These second-growth forests—no longer thought of as *secondary* in a pejorative sense—are an example of what Zimmerer and Young (1998) called "intact-if-not-untouched nature" (p. 8). Second-growth forests are an integral part of the Adirondack wilderness (Ziegler, 1999) because they appear "natural" or "wild" to the uninformed park visitor (Vale, 1987).

Nearly one century after logging-related fires released resources for a new cohort of trees, the species composition and structural characteristics of the forest still reflect the impact of intense disturbance. This land-use legacy is similar to the "persistent imprints on ecosystem structure and function" that Foster et al. (2003, p. 79) described at eight Long Term Ecological Research sites in the eastern United States and the Caribbean. With time the human-disturbed forests in the Adirondacks might develop structural characteristics similar to nearby old growth (Ziegler, 2000), even if species composition is unlikely to return to its predisturbance state (Cowell and Dyer, 2002). Patterns and processes will change in response to disturbance events, pathogens, herbivores, acid deposition, local environmental variations, and global change, but the future Adirondack forests will continue to fill many ecological and aesthetic roles.

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