

Disturbance dynamics of old-growth *Picea rubens* forests of northern Maine

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Abstract

Question: How have the spatial and temporal aspects of past disturbance shaped the current structure and composition of old-growth *Picea rubens* forests?

Location: Northern Maine, USA.

Methods: We established three 50 m × 50 m plots in old-growth *Picea rubens* forests and mapped the location of trees and saplings. We extracted increment cores from canopy trees, and recorded growth releases indicating past disturbance. By linking spatial data (tree positions) and temporal data (dated growth releases), we reconstructed the location and size of former canopy gaps back to 1920, and determined a more general disturbance chronology extending as far back as 1740.

Results: We found no evidence of stand-replacing disturbances. The disturbance dynamic includes pulses of moderate-severity disturbances caused by wind storms and host-specific disturbance agents (spruce budworm, spruce bark beetle) interposed upon a background of scattered smaller canopy gaps. Consequently, rates of disturbance fluctuated considerably over time. Reconstructed canopy gaps were temporally and spatially scattered; during disturbance peaks, they were both larger and more numerous.

Conclusions: Despite peaks in disturbance, several of which created relatively large gaps, this system has experienced no significant change in species composition. Instead, the shade-tolerant *Picea rubens* has maintained canopy dominance. The patch dynamics described here consist of dramatic structural, not compositional, changes to the forest. The persistence of *Picea rubens* is attributed to a combination of traits: (1) abundance of advance regeneration; (2) ability to endure suppression and respond favourably to release; and (3) longevity relative to ecologically similar species.

Keywords: Canopy gap; Canopy structure; *Choristoneura fumiferana*; Dendrochronology; *Dendroctonus rufipennis*; Dendro-ecology; Patch dynamics; Spruce bark beetle; Spruce budworm.

Nomenclature: Gleason & Cronquist (1991) for vascular plants; Crum (1983) for mosses.

Abbreviation: DWD = Down woody debris.

Introduction

Spatial and temporal patterns of natural disturbance strongly influence forest composition, structure, and function. The interplay between spatial and temporal patterns underlies the concepts of the shifting mosaic steady-state (Bormann & Likens 1979), disturbance patch dynamics (Pickett & White 1985) and landscape equilibrium (Turner et al. 1993). Understanding this interplay in natural forests is vital to the proper interpretation of current forest conditions and provides a benchmark to which current activities can be compared (Foster et al. 1996; Landres et al. 1999).

In the absence of stand-replacing disturbances, forest canopies are opened periodically by the death of single trees or small groups of trees. These smaller-scale disturbances may be patchy in space, creating a mosaic of variously sized gaps in an otherwise unbroken canopy, and variable over time, the result of disturbance peaks and intervening periods of quiescence. Much of the work on canopy gaps has focused on shifts in species composition within recently formed canopy gaps, demonstrating their importance in maintaining tree species of various shade tolerances in the canopies of mature temperate forests (Watt 1947; Forcier 1975; Runkle 1982; White et al. 1985; Clebsch & Busing 1989; Ward & Parker 1989; Payette et al. 1990). Not surprisingly, these studies have documented a range of gap sizes, with shade-intolerant species generally more prevalent in larger gaps, and shade-tolerant species in smaller gaps. However, equal in importance to gap size is the temporal pattern of gap formation. Despite the similarity in *mean* rates of canopy gap formation across diverse regions (Runkle 1985), numerous dendro-ecological studies have demonstrated marked temporal fluctuations at a given site (Veblen et al. 1991; Jonsson & Dynesius 1993; Eisenhart & Veblen 2000; Ziegler 2002; Black & Abrams 2003; but see Frelich & Lorimer 1991).

Field surveys of extant gaps provide much information on the size, shape, and in some cases, the dispersal

of canopy gaps (see Runkle 1982; White et al. 1985; Ward & Parker 1989; Rebertus & Veblen 1993; Battles & Fahey 2000). Such studies, however, are limited to currently visible gaps, that is, gaps that have formed in recent decades. In temperate regions, methods of dendro-ecology can extend the disturbance history much further back in time, yielding detailed information on the timing and temporal variability of disturbance (see Frelich & Lorimer 1991; Eisenhart & Veblen 2000; Ziegler 2002; Black & Abrams 2003). Such studies make use of dated growth releases in surviving trees, taken as evidence of the loss of overtopping canopy trees that formerly constrained growth of the survivors (Lorimer 1985). Dendro-ecological studies, however, typically reveal little about the size and dispersion of canopy gaps. To date, few studies have attempted to link the spatial and long-term temporal aspects of canopy gap formation at the level of the forest stand. However, by linking mapped tree locations with the temporal record of growth releases detected on individual trees, one can estimate the location and area encompassed by particular disturbance events. Linking these spatial and temporal components can expand the inferences provided by typical dendro-ecological studies (e.g. disturbance frequency, severity) to include estimates of historical patch size and patch dispersion (see Payette et al. 1990; Lusk & Ogden 1992; Cherubini et al. 1996; Dahir & Lorimer 1996; Chokkalingam 1998; Parish & Antos 2004).

Surprisingly little is known about patterns of natural disturbance in forests dominated by *Picea rubens* (red spruce), despite the ubiquity and commercial importance of this species in northeastern North America. Such information is scarce simply because so few stands of old-growth *Picea rubens* remain for study, reflecting the harvesting pressure consistently placed on this species since the 1860s. Only 0.02% of the pre-settlement *Picea rubens*-dominated forests remains unharvested in the northeastern USA, most of it occurring as small stands at relatively high elevations (Cogbill 1996). Nevertheless, it is known that outbreaks of the spruce budworm (*Choristoneura fumiferana*) and spruce bark beetle (*Dendroctonus rufipennis*), as well as hurricanes, are important disturbance agents in this region (Seymour 1992; Boose et al. 2001). These disturbance types result in patches of various sizes and degrees of canopy loss. While spruce budworm outbreaks may recur somewhat cyclically (Blais 1983; Royama 1984; Jardon et al. 2003), other disturbances occur quite sporadically. This combination of spatial patchiness and temporal variability has likely created a complex disturbance dynamic in this region, the details of which remain poorly understood.

The general objective of this study was to investigate the effect of past disturbances on the current structure and composition of old-growth mid-elevation *Picea rubens* forests of northern Maine. We linked spatial data (mapped tree positions) and temporal data (dated growth releases) to reconstruct a detailed history of natural disturbance, including the location and area encompassed by particular disturbance events. This level of detail allowed us to address the following specific objectives: (1) estimate historic disturbance patch sizes and patch dispersion; (2) determine the timing, severity, and agents of past disturbances; and (3) assess the importance of canopy disturbance with respect to *Picea rubens* dominance in the canopy.

We conducted this work in the Big Reed Forest Reserve, which at ca. 2000 ha is thought to be the largest remaining tract of old-growth in New England, USA. It escaped harvest originally because of its isolation from major rivers for transporting logs, and later because of deliberate protection by private landowners throughout the 20th century. Many remnant old-growth forests in the eastern USA have escaped harvest simply because they occur on steep slopes, at high elevations, or are otherwise inaccessible. As such, they may not be representative of pre-settlement forests of the surrounding landscape (Lorimer & White 2003). In contrast, the Reserve supports forest communities, soils, elevation ranges, and topographic settings typical of northern Maine. Thus, this study affords a unique glimpse of forest structure, composition, and processes that we take to represent those of pre-settlement forests of this region.

Material and Methods

Picea rubens

The geographic range of *Picea rubens* extends from Nova Scotia and New Brunswick to the southern Appalachian Mountains, where it is found only in the highest elevations. The species is currently quite abundant in the mixed-species secondary forests of New England. For example, among the conifers in Maine, it is first in terms of volume, and second, after *Abies balsamea*, in terms of number (Griffith & Alerich 1996). It forms an important component of several forest community types in the region (Maine Natural Areas Program, Anon. 1991). *Picea rubens* is shade-tolerant, able to remain in the understorey for ca. 100 years before release (Cary 1894), and it has an absolute longevity of ca. 430 years (Cogbill 1996).

Study area

This work was conducted within The Nature Conservancy's Big Reed Forest Reserve of northern Piscataquis County, Maine, USA (46°20' N, 69°5' W). Based on records from Millinocket, the nearest weather station, precipitation is evenly distributed throughout the year, with an average of 1058 mm annually (Baron et al. 1980). Mean monthly temperatures range from -10.0 °C in January to 19.8 °C in July, with an annual mean of 5.3 °C (Baron et al. 1980). Historical records and field observations reveal minimal evidence of timber harvesting in the Reserve (Cogbill 1985; Widoff 1985; Chokkalingam 1998).

The Reserve supports the following five forest community types: *Picea rubens* forest, hardwood forest, mixed-wood forest, *Thuja occidentalis* seepage forest, and *Thuja occidentalis* swamp. Community nomenclature for the latter four communities follows that of the Maine Natural Areas Program (Anon. 1991). Given the relative absence of balsam fir in the overstorey, the spruce-dominated stands do not resemble the spruce slopes or the spruce-fir flats described by the Maine Natural Areas Program (Anon. 1991). We simply refer to this community type as the *P. rubens* forest.

P. rubens forests within the Reserve are found on nutrient-poor sites with thin, rocky soils. They occur in patches, typically not more than a few hectares of nearly pure *Picea*, that grade into other communities. *P. rubens* clearly dominates this community, although *Thuja occidentalis*, *Abies balsamea*, *Pinus strobus*, *Betula alleghaniensis* and *Acer rubrum* may form minor components. The understories, though quite patchy, are dominated by *P. rubens* and *A. balsamea* regeneration, *Vaccinium myrtilloides* and *Maianthemum canadense*. *Hylocomium splendens*, *Pleurozium schreberi* and *Bazzania trilobata* dominate the bryophyte layer, which covers much of the soil surface. In the absence of disturbance, trees form closed-canopy stands. Snags and down woody debris in various states of decay are quite abundant.

Field procedures

The three plots chosen for this study form part of a larger project addressing spatial and temporal patterns of disturbance throughout the Reserve. That project included 37 randomly located plots (30 m × 50 m), four of which occurred in the *P. rubens* community type. One of those four was excluded from this study because the small stand size and its location on a narrow knoll precluded its expansion to the 50 m × 50 m plot size required here for intensive sampling. The remaining three *P. rubens* plots (C20, AB5, AD30) range in eleva-

tion from 412 to 440 m a.s.l. Distances between the three plots range from 2.3 to 3.0 km.

Plots were aligned true north-south and east-west. The *X* and *Y* coordinates were recorded for all living trees – individuals ≥ 10 cm diameter at breast height (DBH = 1.37 m), standing and fallen dead trees, and saplings (individuals ≥ 2 m in height but < 10 cm DBH) within each plot. For each living tree we recorded the DBH and crown class (dominant, co-dominant, intermediate, and overtopped; see Smith et al. 1997). To determine canopy projection area for each tree (see below), we measured the horizontal distance from bole centre to the canopy drip line in four cardinal directions. This was also done for any tree whose canopy extended into the plot. When evident on conifer saplings, the number of elongated internodes above conspicuous branch whorls (indicating release following a period of growth suppression) were recorded. For uprootings and wind snaps, which we take as evidence of wind damage, we recorded the species (when possible), diameter, direction of fall, and decay class, following a four-class system, with class I being least decayed and class IV most decayed (Fraver et al. 2002). To be considered an *uprooting*, a fallen tree had to have a significant portion of its root mass elevated above the now-horizontal stem, with signs of soil upheaval and root tearing (if relatively recent) or pit-and-mound microtopography (if well-decayed). To be considered a *wind snap*, a fallen tree had to show a marked fracture with splintering, in contrast to a brash failure (clean or blunted break, see Panshin & de Zeeuw 1980; Worrall & Harrington 1988), which would suggest the tree had been killed or severely weakened by pathogens before falling.

We conducted an inventory of down woody debris (DWD, including the uprootings and windsnaps mentioned above) to provide a general description of the stands and to shed light on past disturbances. Measurements on each DWD piece included length and diameters at large and small ends. Species were assigned when not precluded by advanced decay. Only pieces with a diameter at the largest end greater than 10 cm were inventoried. Each piece was assigned to one of four decay classes as mentioned above.

We extracted increment cores (one per tree), from all living trees. A total of 526 cores were extracted, 487 of which were from *P. rubens*. Because *P. rubens* seedlings can become established and persist for long periods under shade, we consider an individual to be recruited into the stand only when it surpasses breast height. For this reason we extracted cores at breast height, and all ages are expressed as *recruitment ages*. Because the work was conducted in a strict reserve, we were unable to extract radial cross-sections for dating snags and down woody debris. Instead, we attempted to

extract cores from decay class I and II dead wood. Because of the rapid decomposition of *P. rubens* (Westveld 1931; Foster & Lang 1982), we successfully extracted only 24 deadwood cores, most of which had decayed sapwood. Nevertheless, the sound interior portions of these cores – once cross-dated – provided additional spatially-explicit information on disturbance. Cores were collected in 2001; additional data were collected over the next two field seasons.

Canopy structure

Because canopy structure can reveal much about stand disturbance history (Lorimer 1985; Brokaw & Grear 1991), we recorded vegetation height profiles for the three plots using a modification of Karr's (1971) method. Living vegetation (leaves or woody portions) was recorded as present at a given height interval if it touched a telescoping vertical pole graduated in 1-m increments. The pole was held vertically with the aid of a surveyor's rod level. For distances above the reach of the pole, we used an optical rangefinder to measure the height of vegetation (also in 1-m increments) directly above the pole. The pole was placed at points in a 5 m × 5 m grid (including plot borders), for a total of 121 grid points. Vegetation density was calculated at each height interval as the number of vegetation 'hits' divided by 121. We noted if grid points were located within recent gaps, within recovering (i.e. advancing) former gaps, or intact canopies. In the laboratory, we further separated the intact-canopy grid points: if the point clearly fell in a portion of the plot ultimately determined to have been part of the larger gaps formed during the spruce budworm outbreak of the 1920s (see below), we assigned it to an 'advanced-gap' category. This partitioning produced a chronosequence of vegetation structure: recent gap, advancing gap, advanced gap, and intact canopy.

Laboratory procedures

Cores were mounted and sanded to a fine polish using standard methods. Ring widths were measured on a Velmex sliding-stage stereomicroscope to the nearest 0.01 mm. Cross-dating was conducted using methods of Yamaguchi (1991), with verification by COFECHA (Holmes 1983).

Using the four distances from bole centre to canopy drip line, we estimated the canopy projection area (CPA) for each tree as the sum of the resulting four quarter ellipses (Lorimer & Frelich 1989). We define CPA as the horizontal area (in m²) encompassed by a vertical projection of the canopy drip line. For the purpose of projecting each canopy area onto plot maps, we interpolated six points on each quarter-ellipse arc, using the

formula for an ellipse perimeter. From length and diameter measurements, we calculated the volume of each DWD piece using the formula for a conical frustum. The volumes of pieces in decay class IV were multiplied by the ratio between cross-sectional log height and width (0.575) to account for their elliptical cross-sections resulting from the collapse during decomposition (Fraver et al. 2002).

Detecting growth releases on increment cores

Evidence of disturbance derived from tree-ring widths comes from abrupt increases in radial growth (i.e. *releases*) and rapid growth at the time the tree reached breast height (i.e. *gap-recruited* trees), as both types of evidence suggest the loss of an overtopping canopy tree (Lorimer 1985; Lorimer & Frelich 1989). Each core was evaluated separately for either type of evidence. Gap recruited trees were deemed as such if the mean ring width for the first five years in the series exceeded 1 mm (Lorimer 1980), and the subsequent growth pattern was declining, parabolic, or flat (Frelich 2002).

Growth releases were detected following the absolute-increase method (Fraver & White 2005). Briefly, the method is analogous to the more common percent-increase method (see Henry & Swan 1974; Nowacki & Abrams 1997); however, instead of calculating a percent increase for the comparison of consecutive 10-year intervals, the previous mean 10-year growth is simply subtracted from the subsequent mean 10-year growth. If the difference exceeds a predetermined, species-specific threshold, the event is considered a valid release. The method has the very desirable effect of scaling the release threshold according to the growth rate immediately prior to disturbance. Without adjusting for prior growth, the percentage-increase method becomes too lenient for low rates of prior growth, and too restrictive for higher rates (Lorimer 1980; Glitzenstein et al. 1986; Storaunet et al. 2000; Black & Abrams 2003). The selected absolute-increase thresholds (e.g. 0.58 mm for *P. rubens*) are meant to detect the loss of overhead canopy trees, equivalent to the 'major' releases commonly referred to in the literature. The 10-year temporal window used here is assumed to filter out any short-term growth anomalies resulting from extreme changes in temperature and precipitation (Lorimer & Frelich 1989; Nowacki & Abrams 1997).

Recoveries to previous growth rates following temporary budworm defoliation were not considered valid releases even though they often met arithmetic criteria for release, because they do not indicate the loss of an overtopping canopy. Such events are evident in the tree-ring series as clear budworm 'signals' corresponding to outbreaks from 1810s, 1910s and 1970s (Peirson 1950;

Irland et al. 1988). If, however, the recovery were extreme (i.e. the post-recovery growth rate exceeded the pre-budworm rate by the absolute-increase threshold), it would be considered a valid release. We also discounted purported releases shown on trees determined to have already been in the canopy at the time of the event, because these suggest an adjacent or nearby disturbance rather than the loss of overhead canopy (Lorimer & Frelich 1989). *P. rubens* trees were assumed to have been in the canopy in a given year if their diameters exceeded 22 cm, which was estimated following methods of Lorimer & Frelich (1989). Greater than 95% of trees above this threshold were in the canopy. Diameters were estimated for every year a tree was in the record, following methods of Frelich (2002).

Preparing disturbance chronologies

Using the releases and gap-recruitment events (henceforth *releases*) of canopy trees, we constructed a *disturbance chronology* for each plot. We tallied releases by decade, allowing for the variable delay between a disturbance and a tree's response (Lorimer & Frelich 1989). We converted the number of releases detected in each decade to estimates of canopy area disturbed, generally following the method outlined in Lorimer & Frelich (1989). This method weights the evidence for each release according to the tree's current canopy projection area, simply because the magnitude of disturbance inferred from small trees differs from that inferred from large trees (Lorimer & Frelich 1989; Frelich 2002). We expressed the canopy area disturbed in each decade as a percent of the total canopy area from trees known to be present in that decade. We refer to the proportion of the canopy area disturbed per decade as the *disturbance rate*. We truncated each plot's chronology when number of living trees dropped below 15. Chronologies thus constructed extended back in time to 1820 (shortest) and 1740 (longest).

The disturbance rate calculated as such for recent decades will necessarily underestimate the true rate because many gap-recruited trees will not have achieved the diameter necessary for coring, and insufficient time has passed since disturbance to permit the use of a 10-year post-disturbance window for release detection (Frelich 2002). To overcome this limitation, we measured and dated all recent gaps (1980s and 1990s), and incorporated this information into the disturbance chronologies. Gap areas were obtained from plot maps (not shown) showing current area unoccupied by tree canopies. Gaps were dated following the methods of Dynesius & Jonsson (1991), Hytteborn et al. (1991) and Runkle (1992).

Consequently, we have used two methods of esti-

imating the amount of canopy area lost – one prior to 1980 (canopy area lost expressed as a percent of total canopy area known to be present), and another after 1980 (canopy area lost expressed as a percent of plot area). To determine to what extent these methods differed, we extended the plot-area based chronologies back to 1940; beyond that time too few trees existed to justify expressing canopy area lost as a percent of plot area. For the decades in which the two sets of chronologies overlapped (1940 through 1980), the disturbance rates did not differ by more than 2% for any plot. We feel this similarity justifies the linkage of the two methods for the purpose of better depicting recent disturbances.

Estimating gap sizes and gap dispersion

The disturbance chronology described above depicts only the temporal aspects of disturbance. Here, we link release data with the mapped tree locations to evaluate the spatial aspects of disturbance, focusing on estimated sizes of canopy gaps and their dispersion within the plots. For single-release gaps (i.e. release evident in one tree but none of its neighbours) formed prior to the 1980s, we simply used the current canopy projection area for that tree as an estimate of the former gap area, assuming that the canopy of the released tree came to fully occupy the former gap (Lorimer & Frelich 1989). For multiple-release gaps (i.e. releases evident in several adjacent trees, but not their neighbours) formed prior to the 1980s, we delimited the gap area by encircling on maps the canopy projection areas of adjacent trees showing release. We assume lateral expansion from gap border trees to be minimal, given conifers' limited light-foraging ability (Waller 1986; Muth & Bazzaz 2002). For gaps formed during the 1980s and 1990s, we used the gap areas determined for the disturbance chronologies described above. Because our release criteria are meant to reflect the loss of canopy trees, we felt that only those canopy gaps larger than the median canopy area of intermediate crown-class trees (8.5 m²) should be considered as valid canopy gaps; openings smaller than this may have little effect on tree recruitment and growth.

Reconstructing the area of gaps formed prior to 1980 was problematic because portions of the plot were occupied by current gaps. That is, where a former release event occurred adjacent to a current gap, the former gap would be missing the full set of neighbouring trees with which to delimit the former gap extent. This same limitation existed for gaps adjacent to plot borders. We had intended to overcome this shortcoming by mapping and extracting cores (for release detection) from the dead trees, but wood decay limited our

ability to do so for all but 24 dead trees. These shortcomings hampered our ability to delimit many former gap areas. In these cases, we assumed the former gap did not extend into current gap areas or to areas outside the plot. Consequently, estimated gap areas prior to 1980 are likely underestimates. This situation suggested a division of gap-area data into two groups: *uncertain gap areas*, as just described, and *known gap areas*, which include those gaps reconstructed with an adequate set of neighbouring trees and those measured and dated to the 1980s and 1990s. We use both groups of data for mapping purposes, but use only known gap areas to augment the disturbance chronologies (above) and for calculating mean and median gap area. We reconstructed and mapped gap areas back to the 1920s, a period of active gap formation resulting from a documented spruce budworm outbreak (Irland et al. 1988); beyond that time, too few trees were available for delimiting gaps. Gaps of known area were also used to distinguish between single and multiple tree-fall events, which was aided by using the mapped locations and decay classes of snags and fallen trees (i.e. gap makers).

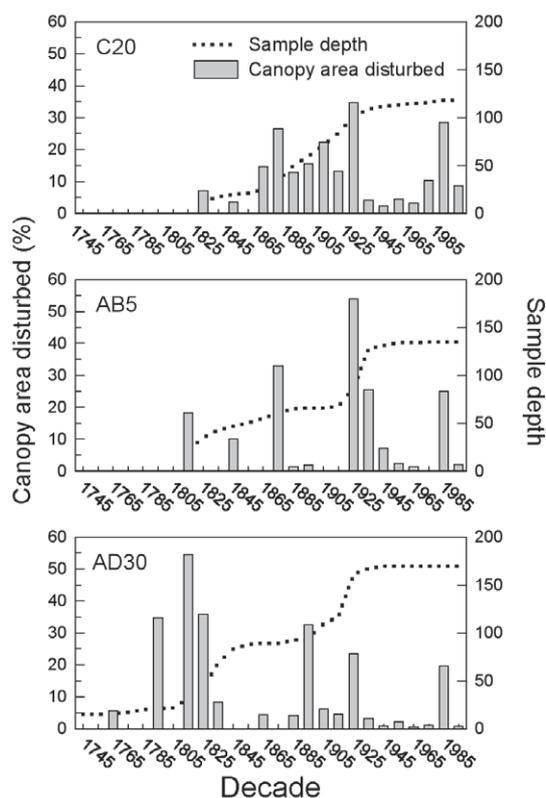


Fig. 1. Disturbance chronologies for three old-growth *Picea rubens* stands. Sample depth refers to the number of canopy trees contributing to the chronology. Chronologies were truncated when sample depth dropped below 15 trees.

Results

Species composition and stand structure

Picea rubens clearly dominates these stands, accounting for 91.7% of relative basal area, all plots pooled. Relative basal areas of associated species were as follows: *Thuja occidentalis* (2.7%), *Pinus strobus* (2.5%), *Acer rubrum* (1.5%), *Betula alleghaniensis* (1.0%), and *Abies balsamea* (1.0%). The mean basal areas ($36.1 \text{ m}^2 \cdot \text{ha}^{-1}$) and stem densities ($701 \text{ ind} \cdot \text{ha}^{-1}$) of these stands are generally within the ranges reported from old-growth conifer forests of the northeastern USA (Cogbill 1996; Foster & Reiners 1983), despite a recent spruce budworm outbreak and the 1983 windstorm that reduced basal areas throughout the Reserve. Mean sapling density was $1628 \text{ ind} \cdot \text{ha}^{-1}$, although density varied markedly between plots, and was quite patchy within a plot. Three species dominated the sapling layer: *P. rubens* (32% of stems), *A. balsamea* (22%), and *B. alleghaniensis* (20%). The mean volume of down woody debris (DWD) was $112 \text{ m}^3 \cdot \text{ha}^{-1}$, although this too varied between plots. DWD volumes were not evenly distributed among decay classes: decay class I contained 16% of the total, class II 43%, class III 28%, and class IV 13%. *P. rubens* dominated the DWD pool, representing 77% of the total volume (excluding pieces that could not be identified to species), with balsam fir second, representing 16%. Table 1 lists various structural attributes for each stand.

Uprootings were more prevalent than windsnaps, accounting for 67% of all wind-thrown trees (55 observations). To analyse directionality of wind-throw, we pooled all data on uprootings and windsnaps because they were too few to analyse separately by plot or decay class. These data displayed uniform directionality (Rayleigh's $p < 0.05$, Oriana software, Kovach 1994), with a mean vector of 96° .

Disturbance rates

We found no evidence of stand-replacing disturbance during the period covered by this investigation. Only rarely did decadal disturbance rates exceed 35% (Fig. 1), and no single-cohort age structure was seen in any of the three stands (Fig. 2, based on complete cores, i.e. those passing through or very near the pith).

Mean decadal disturbance rates for the three plots were 9.3% (plot AD30, SD = 14.7), 9.6% (AB5, SD = 14.9), and 11.8% (C20, SD = 10.3). The overall mean rate was 10.1% (median 4.1%), all plots pooled. Mean rates did not differ among plots (ANOVA: $F_{2, 60} = 0.98, p = 0.38$, after arcsine transformations, Zar 1999). The distribution of decadal disturbance rates was

strongly skewed, with higher rates being increasingly uncommon: 67% of all decadal rates were less than 10% canopy loss, 13% between 10 and 20%, 9% between 20 and 30%, 8% between 30 and 40%, 0% between 40 and 50%, and 3% greater than 50%. Given this skewed distribution, the mean decadal rate (or any disturbance metrics calculated from the mean) may not adequately characterize these disturbance dynamics. Fig. 1 clearly shows the marked and sporadic decade-to-decade fluctuations in disturbance, with peaks in the 1810s, 1920s, 1980s common to all plots (Fig. 1). Further evidence for the sporadic pattern is provided by the absence of temporal autocorrelation in the three chronologies: none had first-, second-, or third-order autocorrelation (p values >0.74 , $|t|$ values <1.0 ; Minitab statistical software (Anon. 2003).

Gap formation, canopy structure, and canopy access

Results from the vegetation height profiles depict a chronosequence – recent gap, advancing gap, advanced gap, and intact canopy — showing the typical restructuring of the canopy following gap formation (Fig. 3). Median gap area was 34 m² (mean 66 m²), with the maximum of 432 m². The majority of gaps (66%) were smaller than 50 m², and 40% of gaps consisted of single-tree events. Closely linked with the issue of gap area is that of gap dispersion. Fig. 4 shows the locations in which gaps were formed for each decade back to the 1920s (note that gaps formed in one decade may persist into subsequent decades, but such overlap is not depicted in Fig. 4). The scattered formation of gaps is quite evident, even during the two decades of peak disturbance. During these decades gaps are both larger and more numerous. Gaps of various ages, and defined as above, currently occupy 32% (C20), 26% (AB%), and 20% (AD30) of plot area, the relatively large percentages the result of the 1983 windstorm that affected the entire Reserve.

The number of releases and gap recruitments (henceforth releases) detected on individual canopy trees attest to the importance of canopy gaps in the dynamics of this forest type. After reaching breast height, most trees

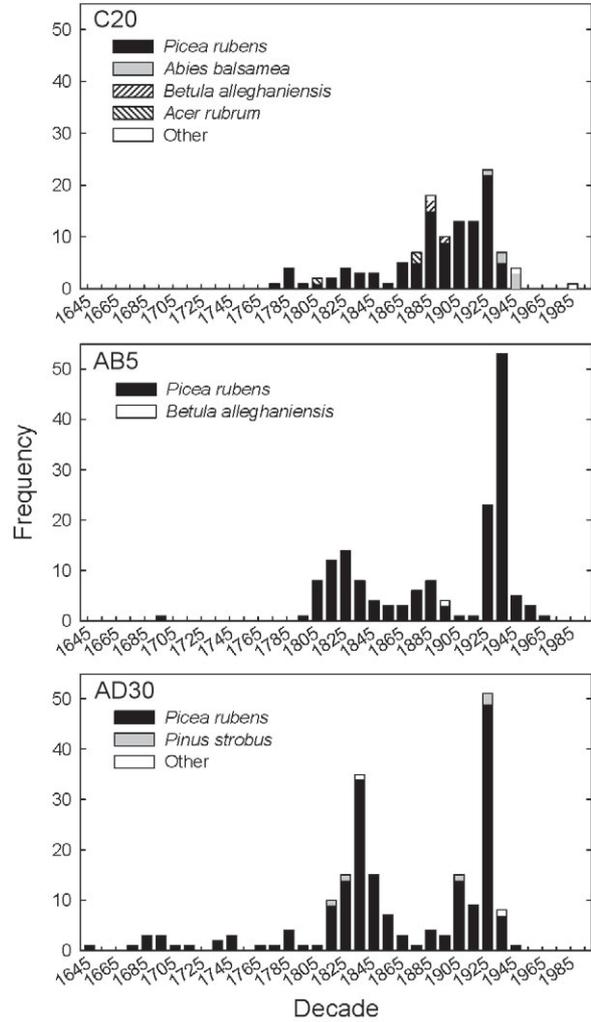


Fig. 2. Recruitment age-class distributions for three old-growth *Picea rubens* stands.

(61.2%) required one release event to accede to the canopy; 17.0% required two events; and 2.4% required three events. 19.4% of trees required no release event. Tree-ring series from this latter group were closely inspected – all showed at least one period of minor growth increase (often corresponding to known peaks in disturbance) yet insufficient to be considered valid releases according to our criteria. Further evidence for the

Table 1. Structural characteristics, including down woody debris (DWD), for the three old-growth red-spruce plots.

Plot	Live trees		Snags		Saplings (ind.ha ⁻¹)	DWD Volume (m ³ .ha ⁻¹)
	Basal area (m ² .ha ⁻¹)	Stems (ind.ha ⁻¹)	Basal area (m ² .ha ⁻¹)	Stems (ind.ha ⁻¹)		
C20	35.6	592	4.7	60	2884	170
AB5	30.6	668	3.7	120	1308	66
AD30	42.1	844	3.1	88	692	99

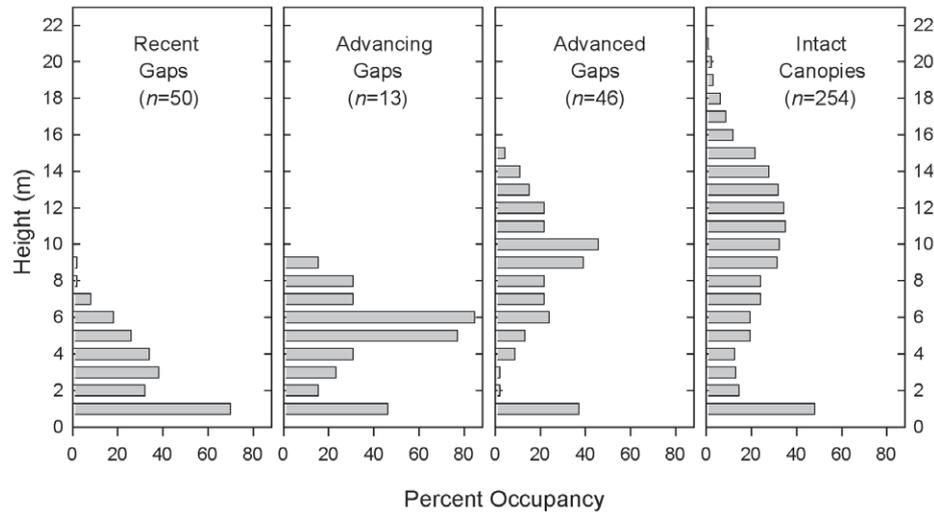


Fig. 3. Vegetation height profiles showing the sequence of canopy restructuring following gap formation. Percent occupancy refers to the number of occupied height intervals expressed as a proportion of sampling grid points assigned to each of the four categories. Number of grid points in each category given by n .

importance of gaps can be seen in the current sapling data: on all three plots, saplings showing marked height-growth releases were 2.7 times more likely to be found directly under recent gaps than outside gaps (χ^2 test, $p < 0.001$); that is, 69% of all released saplings were found under gaps, although gaps represented only 26% of the plot area (all plots pooled). Even saplings not showing growth releases were 1.9 times more likely to be found directly under gaps (χ^2 test, p values < 0.01).

Discussion

Disturbance history

Three peaks in disturbance activity (1810s, 1920s, 1980s; see Fig. 1) correspond to known or suspected spruce budworm outbreaks in the 1810s, late 1910s, and late 1970s (Peirson 1950; Blais 1983; Irland et al. 1988). The percent of canopy area lost during outbreaks ranged from 18.2 to 54.5% per decade. A hurricane suspected to have reached northern interior Maine in 1815 (Boose et al. 2001) may have contributed to the peak in the 1810s, and the severe thunderstorm of 1983 contributed to the peak in that decade.

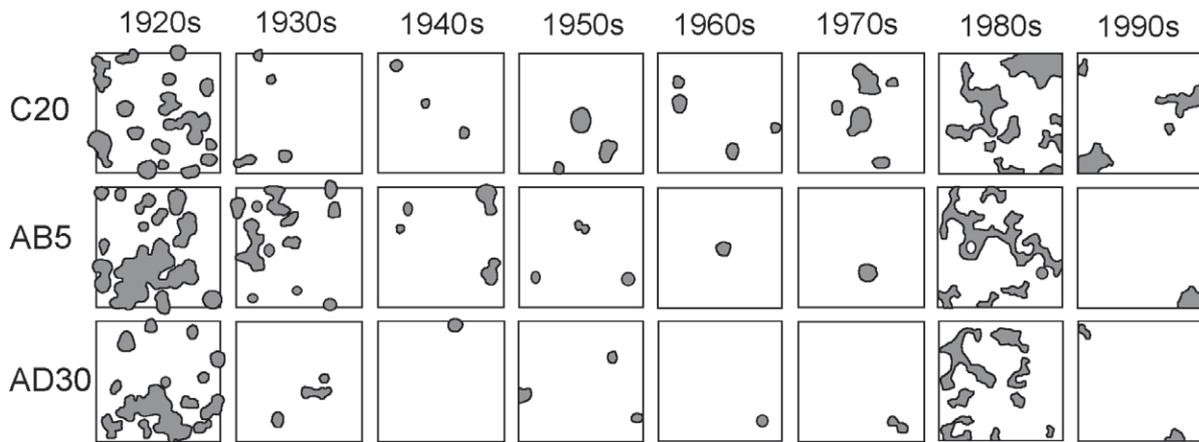


Fig. 4. Estimated size and dispersion of gaps formed in each decade (grey polygons) back to the spruce budworm outbreak of the 1920s. Gap areas prior to 1980 are likely underestimated (see Material and Methods). Gap areas were allowed to extend outside plot borders for earlier decades. Plot size is 50 m \times 50 m; top of page is true north.

The disturbance peak in the 1870s found in two of the three stands is in part the result of a spruce bark beetle outbreak in northern Maine at that time (Packard 1881; Hough 1882; Cary 1900). Its absence on plot AD30 attests to the patchy nature of the outbreaks: though extensive areas were affected, mortality occurred in clumps (Packard 1881; Cary 1900). The hurricanes of 1869 and 1874 (Neumann et al. 1978, Boose et al. 2001) also may have contributed to this peak. The 1790s peak in disturbance on plot AD30 (other plot chronologies did not extend this far) may well reflect the 1788 hurricane thought to have reached northern interior Maine (Boose et al. 2001). The peak in the 1890s on this plot remains unexplained.

Thus, one principle finding is that no stand-replacing disturbances have occurred during the ca. 180 years covered by this investigation: decadal disturbance rates rarely exceeded 35%, and no single-cohort age structure was recorded. The absence of stand-replacing fires in particular may contradict the commonly held view of fire as an important disturbance agent in this region. However, members of our research group have found no fire scars and no shade-intolerant tree species (see below) in the Reserve's *Picea rubens* forests during five field seasons on this and related projects. Further, northern Maine has lowest lightning flash density of any location in the eastern United States (Anon. 2004). Similarly, the absence of stand-replacing wind-throw may seem inconsistent with red spruce's known susceptibility to wind damage (Cary 1896; Canham et al. 2001). The complex canopy structure and stratification of these stands (Fig. 3) may reduce the likelihood of complete wind-throw. The lack of stand-replacing wind-throw is not due to unusual landscape positions of these three plots – none lies in an area protected from wind. In fact, plot AB5 is rather exposed, lying just below the crest of a small ridge.

Though apparently not causing stand-replacing disturbances, wind storms likely create a background of scattered canopy openings, and they may at times contribute to peaks in moderate-severity disturbance. The consistency in fall direction for uprootings and windthrows of all decay classes (overall mean 96°) suggests a number of summer thunderstorms in recent decades: summer storms in this region are typified by westerly winds, while late fall and winter windstorms are typified by northeasterly winds (Wessels 1999).

The lack of stand-replacing disturbances supports early descriptions of the predominantly uneven-aged structure described for pre-settlement spruce forests of Maine (Cary 1896). Similarly, Lorimer & White (2003) estimated quite long point recurrence intervals for large-scale disturbances in the spruce-hardwood forest of this region.

Most previous studies that have produced disturbance chronologies for conifer-dominated forests also show marked temporal fluctuations (Veblen et al. 1991; Jonsson & Dynesius 1993; Eisenhart & Veblen 2000; Ziegler 2002; Black & Abrams 2003; Parish & Antos 2004). Given the large temporal fluctuations found in the present study, the distribution of decadal disturbance rates may be of more use than the mean in characterizing the disturbance history. As pointed out by Jonsson & Dynesius (1993), the reduction of a disturbance history to a mean rate disregards the importance of temporal variability, something we have emphasized in this study. In fact, the range of rates may be more informative than the mean in evaluating historic variability in disturbance (Foster et al. 1996; Landres et al. 1999).

In particular, these disturbance pulses influence tree population dynamics. Although tree recruitment has occurred during most decades, it is clearly not evenly distributed through time. Peaks in recruitment generally follow peaks in disturbance, resulting in multi-aged stand structures (Figs. 1 and 2).

Spatial dispersion and size of canopy gaps

Reconstructed canopy gaps were dispersed spatially as well as temporally. Even during decades of peak disturbance, gaps were dispersed throughout the plots. During these decades gaps were both larger and more numerous. We recognize that the area affected by these openings exceeds the discrete polygons shown in Fig. 4 (Runkle 1982; Lieberman et al. 1989; Battles & Fahey 2000), and at relatively high latitudes it is shifted pole-ward (Parish & Antos 2004). Nevertheless, this finding suggests that even during decades of moderate-severity disturbance, portions of the canopy remain relatively intact, thereby mitigating the effects of such disturbances.

Roughly 40% of canopy gaps consisted of single-tree events, an estimate similar to that found in *Picea jezoensis* forests by Yamamoto (1993) and *Picea-Abies* forests of New Hampshire, USA (Worrall et al. 2005), yet approximately half that found in *Picea-Abies* forests of the southern Appalachian Mountains (White et al. 1985). Gap areas (median 34 m², mean 66 m²), however, are within the ranges of those from other studies of *Picea*-dominated forests (White et al. 1985; Hytteborn et al. 1991; Leemans 1991; Yamamoto 1993; Battles et al. 1995, but see Worrall et al. 2005). We note that direct comparisons to other studies are made difficult because calculations of mean and median gap areas are quite sensitive to the lower cutoff in the definition of a gap. Our cutoff of 8.5 m² (see Material and Methods, *Estimating gap sizes and gap dispersion*) is smaller than that

chosen in most studies, thereby potentially lowering the mean and median. Further, discounting lateral expansion of bordering trees may have resulted in an underestimate. The apparent small gaps encountered here reflect the small size of *P. rubens* canopies: even dominant crown-class trees had a median canopy area of only 24.1 m², with co-dominants at 13.8 m². This finding corroborates several studies demonstrating that forest dominated by trees with small canopies produce gaps of proportionately smaller area (Dahir & Lorimer 1996; Brokaw et al. 2004).

Though relatively small, these gaps are sufficient in size to effect growth releases in understorey *P. rubens*, allowing them, after one to three such events, to accede to the canopy. Nevertheless, 19.4% of current canopy trees showed no major growth releases. The minor growth increases evident in these trees, which often coincided with known peaks in disturbance yet were insufficient to be considered valid releases, suggest that these trees benefited either from nearby gaps or from slow forming gaps (Krasny & Whitmore 1992). Thus, gaps may provide the only means of canopy accession for understorey *P. rubens* in this forest type. The importance of gaps has also been reported for *P. rubens* forests of the southern Appalachian Mountains. Wu et al. (1999) found that *P. rubens* trees require a mean of 1.43 releases prior to canopy recruitment, and White et al. (1985) suggested that 'multiple release events' are necessary for canopy accession.

Up to this point we have largely attributed gap formation during particular decades to single disturbance agents. This is likely an oversimplification, especially considering that our disturbance chronologies (Fig. 1) and reconstructed gap areas (Fig. 4) represent the sum of all events occurring within a given decade. It is likely that various disturbance agents interact, causing gap expansion (the loss of gap border trees) and coalescence over time. For example, the larger gaps formed in the 1920s and 1980s, though initiated by spruce budworm mortality, may have been expanded by subsequent windstorms within those same decades. Our data do not provide the temporal detail required to evaluate gap expansion, and the sequence of gap formation shown in Fig. 4 does not provide conclusive evidence. However, working in the spruce-fir forest of New Hampshire, USA, Worrall et al. (2005), demonstrated that bark beetles, dwarf mistletoe, wind, and various pathogens interact to initiate and expand gaps. In fact, these authors found gap expansion to be more frequent than gap initiation.

Persistence of the shade-tolerant Picea rubens

Although the repeated moderate-severity disturbances documented above have caused dramatic structural changes to these stands (see Figs. 3 and 4), they have caused little or no change in tree species composition. The shade-tolerant *P. rubens* has maintained dominance in the canopy, despite peaks in disturbance that produced gaps considerably larger than the threshold for recruiting shade-intolerant species (see Hibbs 1982; Runkle 1982). This finding is somewhat inconsistent with many studies from temperate regions that emphasize the role of gaps in maintaining tree species of various shade tolerances in the canopy (Watt 1947; Forcier 1975; Runkle 1982; Ward & Parker 1989; Clebsch & Busing 1989; Payette et al. 1990; Woods 2000). In fact, no living or dead intolerant tree species, such as *Betula papyrifera* and *Populus* spp., were found anywhere in these stands (inside or outside plots), despite their abundance in the harvested landscape surrounding the Reserve. Nevertheless, the larger gaps formed during disturbance peaks, while primarily benefiting *P. rubens*, also admit a small number of mid-tolerant species such as *Betula alleghaniensis*, *Acer rubrum* and *Pinus strobus* (Fig. 2). Establishment of *B. alleghaniensis* in particular benefits from the exposed mineral soils of uprooting mounds following windstorms (Hutnik 1952; pers. obs.). Mid-tolerant species currently represent only 3.2% of trees in these forests, and the evidence suggests that they would be virtually absent without such episodic pulses of moderate-severity disturbance.

The persistence of *P. rubens* in the canopy can be explained in part by the abundance of advance regeneration (i.e., seedlings and saplings established prior to gap formation), with gaps acting primarily on the species composition already established. *P. rubens* dominated the sapling layer, and showed marked height-growth releases (as did balsam fir) in response to recent canopy gaps, a finding reported some time ago by Cary (1896) and Westveld (1931). Saplings showing releases were much more likely to be found directly under recent gaps than outside gaps; however, even saplings showing no response were more likely to be found in gaps. The latter finding suggests gaps may increase sapling survival, even in cases where growth appears to be uninfluenced. Fig. 3 clearly shows presence of advance regeneration in recently formed gaps.

Somewhat similar results have been reported from portions of the Great Lakes region of the United States where wind storms dominate as the disturbance agent. Webb (1989) and Webb & Scanga (2001) found that disturbance from a moderate-severity windstorm in Minnesota did not admit shade-intolerant species; how-

ever, the gap sizes reported were smaller than those found here. Webb & Scanga (2001) concluded that rather than set back the successional process, windstorms of that severity accelerate succession by favouring shade-tolerant species. Frelich et al. (1993) and Frelich & Reich (1996) similarly report little change in species composition over long periods in the Great Lakes region despite a known history of moderate-severity windstorms.

By leaving the understorey of advance regeneration intact, outbreaks of the spruce bark beetle and the spruce budworm act much as windstorms. The spruce bark beetle selects only the largest trees, particularly those over 18 inches (46 cm) diameter (Hopkins 1901). Though the budworm is less discriminating with regard to tree diameter, it rarely causes mortality in spruce saplings and small trees (Swaine & Craighead 1924). Canopy openings resulting from bark beetle and budworm outbreaks, like those from moderate severity windstorms, primarily benefit advance regeneration. As a consequence, these natural disturbances appear to secure red spruce's persistence and dominance in the canopy.

One may question why *Abies balsamea*, a shade-tolerant species with similar site requirements to that of *P. rubens*, is not more common in this forest type (it currently accounts for only 1.0% of basal area). In short, the periodic purging of *A. balsamea* by the spruce budworm has maintained this species in low abundance. Despite its name, the spruce budworm causes greatest mortality in this region to *A. balsamea* (Swaine & Craighead 1924). Swaine & Craighead (1924) and Seymour (1992) have proposed that in the absence of stand-replacing disturbances in *Picea-Abies* forests, *A. balsamea* would over time diminish in importance, given *P. rubens*' lower vulnerability to budworm mortality and its greater longevity (to 430 years; Cogbill 1996) relative to *A. balsamea* (to 150 years; Zon 1914). We believe the *P. rubens* stands in this study represent such an outcome. Between budworm outbreaks, however, *A. balsamea* typically increases in abundance, even under the scenario described above. It represented 16% of DWD volume, suggesting its greater importance in these stands prior to the outbreak in the 1970s. It is now somewhat abundant as advance regeneration, accounting for 22% of all saplings. Thus, its presence in the canopy may increase somewhat in coming decades, likely to be reduced once again by the next budworm outbreak. This waxing and waning of balsam fir, however, represents only a minor fluctuation in species composition, not a directional change.

Conclusions

By linking spatial (mapped tree locations) and temporal (dated growth releases) data, we reconstructed a detailed history of natural disturbance in old-growth *Picea rubens* forests. The inclusion of mapped tree locations in particular added spatial resolution not available in typical dendro-ecological studies of stand dynamics. The disturbance history included numerous moderate-severity disturbances, yet none resulting in complete canopy loss. The disturbance history includes a background of scattered canopy-gaps upon which these moderate-severity disturbances are cast, much like the 'nested bicycle' described by Worrall et al. (2005). Despite pulses in disturbance, several of which included gaps seemingly large enough to admit shade-intolerant species, these stands have experienced no significant change in species composition. Instead, *P. rubens*, a shade-tolerant species, has maintained canopy dominance, despite a temporal pattern of disturbance that clearly is not in equilibrium or quasi-equilibrium (*sensu* Frelich & Lorimer 1991). Thus, the patch dynamics described here consists of structural, not compositional, changes to the forest. The persistence of *P. rubens* is attributed to a somewhat unique combination of traits: (1) the abundance of advance regeneration; (2) its ability to endure suppression and respond very favourably to release; and (3) its longevity relative to ecologically similar species.

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