



Natural disturbance and stand structure of old-growth northern white-cedar (*Thuja occidentalis*) forests, northern Maine, USA



Shawn Fraver^{a,*}, Laura S. Kenefic^b, Andrew R. Cutko^c, Alan S. White^a

^a School of Forest Resources, University of Maine, Orono, ME 04469, USA

^b U.S. Forest Service, Northern Research Station, Bradley, ME 04411, USA

^c Maine Bureau of Parks and Lands, Augusta, ME 04333, USA

ARTICLE INFO

Keywords:

Dendrochronology
Gap dynamics
Growth releases
Primary forest
Stand dynamics
Thuja occidentalis

ABSTRACT

Natural disturbance histories and stand structures derived from old-growth forests are increasingly used to guide forest management prescriptions. Although such information is readily available for a number of forest types, it is lacking for others, such as northern white-cedar (*Thuja occidentalis*) forests, despite this forest type's wide distribution, ecological value, and economic importance in northeastern North America. We applied standard dendrochronological methods to six old-growth northern white-cedar stands within the Big Reed Forest Reserve of northern Maine, USA, to reconstruct the frequency and severity of past natural disturbances. The prevalence of internal decay (well-known for this species) precluded the construction of robust age-class distributions. Overall, 63% of cedar trees contained internal decay, and the probability of rot increased with increasing diameter. Evidence from growth releases reveals sporadic pulses of low- to moderate-severity canopy disturbances. The mean disturbance rate was 6.4% of canopy area disturbed per decade, and pulses rarely exceeded 25% per decade. Based on the subset of complete cores (i.e., those without internal decay), 44% of current canopy trees showed one growth release before achieving canopy status, 26% showed two releases, and 7% showed three releases. Of the 23% that showed no release, most showed persistent slow growth that eventually placed them in the canopy. However, an apparent hiatus in cedar recruitment in recent decades (albeit based on a subset of complete cores), as well as low cedar abundance in the sapling layer, suggest that cedar may not maintain dominance in the future overstory. Current structure in these stands is similar to that reported from other old-growth conifer forests in the region: mean living tree basal area was 44.3 m² ha⁻¹, density of large (> 40 cm dbh) living trees was 130 trees ha⁻¹, and coarse woody debris volume was 183 m³ ha⁻¹. Taken together, these findings suggest that multi-aged silvicultural treatments incorporating periodic harvests of low to moderate intensity, retention trees or patches, and protection of coarse woody debris would be appropriate for sustaining or restoring lowland northern white-cedar forests.

1. Introduction

A long history of forest harvesting has simplified forest structure and reduced biodiversity in many regions of the world (Bauhus et al., 2009). In an attempt to reverse those trends, managers are increasingly promoting ecological forestry prescriptions as a means of restoring structural complexity and thereby enhancing biodiversity, while still providing sustained flows of forest commodities. Many ecological forestry prescriptions are modelled after the outcomes of natural disturbances, given that disturbances may enhance structural complexity and create opportunities for forest regeneration (Seymour and Hunter, 1999; Palik et al., 2002). For example, natural disturbance

characteristics are used to determine variable density thinning prescriptions (Carey, 2003), establish harvest patch sizes and cutting cycles (Seymour et al., 2002), establish targets for forest restoration (Kuuluvainen, 2002), and guide prescriptions aimed at conferring resistance and resilience to climate change (Nagel et al., 2017). Designing such prescriptions requires an understanding of the frequency and severity of natural disturbances that historically shaped a given forest type, as well as the forest structure that resulted from these disturbances. Although this information is becoming more readily available worldwide (e.g., D'Amato et al., 2008, Svoboda et al., 2014, Sommerfeld et al., 2018), many forest types remain understudied in this regard.

* Corresponding author.

E-mail addresses: shawn.fraver@maine.edu (S. Fraver), laura.kenefic@usda.gov (L.S. Kenefic), andy.cutko@maine.gov (A.R. Cutko), alan.white@maine.edu (A.S. White).

<https://doi.org/10.1016/j.foreco.2019.117680>

Received 23 July 2019; Received in revised form 8 September 2019; Accepted 8 October 2019
0378-1127/ © 2019 Elsevier B.V. All rights reserved.

Northern white-cedar (*Thuja occidentalis*, hereafter cedar) forests represent one forest type for which the natural disturbance regime has not been well explored. In fact, cedar may be one of the least-studied commercial tree species in eastern North America (Hofmeyer et al., 2007), despite its wide distribution, ecological value, and economic importance. Cedar is also the longest lived tree species in northeastern North America, exceeding 1000 years in extreme cases (Kelly et al., 1994). Fraver et al. (2009) report average disturbance rates for cedar stands at the landscape scale; however, variability among stands, temporal details, and forest structure were not addressed. Similarly, Wesely et al. (2018) report mean structural values from several old-growth stands, yet stand-level details were not provided. The lack of detailed stand-level information hampers the development of silvicultural treatments appropriate for restoring structure and promoting cedar regeneration for this community type (Bouffroy et al., 2012).

The history of natural disturbances is best investigated in old-growth (i.e., never harvested) forests, as they provide a long-term record relatively uninfluenced by human activities. Given the widespread forest harvesting that occurred in northeastern North America, few sizeable old-growth forests remain. However, the Big Reed Forest Reserve of northern Maine, USA, a ca. 2000-ha old-growth tract, provides an ideal setting in which to reconstruct the history of natural disturbances and stand structures. The Reserve supports five forest types, two of which are cedar dominated. The Reserve also supports soils, elevation ranges and topographic settings typical of northern Maine and much of New England and adjacent Canada, and is thus considered representative of the larger landscape, except for the absence of past harvesting.

The objectives of this study were to (1) reconstruct the history of natural disturbances in cedar-dominated forests, and (2) provide stand-level structural descriptions of these forests. To address the first objective, we employ dendrochronology methods to assess growth rates that shed light on the timing and severity of past disturbance. We apply these methods to a large number of trees from six cedar-dominated stands within the Big Reed Forest Reserve. The findings from this study will benefit recent concerted efforts to identify appropriate silvicultural prescriptions for this forest type, which has largely been overlooked relative to other types in the region (Bouffroy et al., 2012).

2. Methods

2.1. Study area

We conducted this work in the Big Reed Forest Reserve, owned by The Nature Conservancy, in northern Maine (centered at 46° 20' N and 69° 5' W). This region receives an average of 1058 mm precipitation annually, which is evenly distributed throughout the year (Baron et al., 1980). Mean monthly temperatures range from −10.0 °C (January) to 19.8 °C (July), with an annual mean of 5.3 °C (Baron et al., 1980). Elevations within the Reserve range from 317 to 575 m a.s.l. Field observations and historical records reveal minimal evidence of timber harvesting within the Reserve (Cogbill, 1985; Widoff, 1985) due to its isolation from major rivers for log transport and its protection by owners throughout the 20th century.

The Reserve supports five forest types, including two types dominated by cedar: cedar seepage and cedar swamp forests (Gawler and Cutko, 2010). Seepage forests are dominated by *T. occidentalis*, with *Picea rubens*, *Abies balsamea*, and *Betula alleghaniensis* occasionally abundant; this type occurs on saturated gentle slopes with minerotrophic groundwater drainage. Swamp forests are dominated by *T. occidentalis*; this type occurs on very poorly drained soils with a *Sphagnum* substrate. However, the differences between swamp and seepage forests can be subtle, often characterized by slight topographic changes and understory plant species composition (Gawler and Cutko, 2010).

2.2. Field procedures

The sites used in this study are part of a larger previous investigation of natural disturbance for the entire Reserve (see Fraver et al., 2007, Fraver et al., 2009). Field work for that study was conducted in 2000 and 2001. The study assessed landscape-level disturbance patterns, as well as differences in disturbance histories among the five community types. Plot locations for that study were chosen in a stratified (by forest type) random manner. Randomization was conducted by placing a 100 × 100 m grid over a Reserve base map showing forest types (Widoff, 1985), followed by random selection of grid intersections, denoting the southwest corner of each plot. Plot size was 30 × 50 m. Given the recent interest in managing northern white-cedar under principles of ecological forestry (Bouffroy et al., 2012), we revisited data from this previous study to address these contemporary needs. We thus provide a detailed, stand-level assessment of disturbance history, using dendrochronological and structure data from three northern white-cedar seepage and three northern white-cedar swamp forests.

On each plot we measured diameters of all living and standing dead (snags) trees, and we extracted increment cores (in 2000) at breast height from all living trees ≥10 cm diameter at breast height (dbh = 1.37 m). We conducted a complete tally of saplings (stems < 10 cm dbh but ≥2 m tall) by species in a central 10 × 50 m transect in each plot. We inventoried all downed coarse woody debris (CWD) to better describe stand structure. For each CWD piece originating inside the plot, we recorded length, diameter at each end, decay class (following the five-class system of Sollins, 1982), and species (when not precluded by advanced decay). Only pieces with a diameter at the largest end greater than 10 cm were inventoried. The volume of each CWD piece was calculated as a conic-paraboloid (Fraver et al., 2007), with volumes of decay classes 4 and 5 pieces reduced accordingly to account for gradual collapse through decay (Fraver et al., 2013). We noted if fallen trees had been uprooted or snapped (fracture with splintering), as these suggest evidence of past wind storms; for these we also recorded fall direction. Azimuths of these windthrown trees were analyzed for uniform directionality using Rayleigh's test (Batschelet, 1981), which was conducted using Oriana software (Kovach, 2013).

Northern white-cedar is well known for having internal stem decay, which creates limitations regarding dendrochronological analyses. Specifically, increment cores extracted from hollow trees contain a record of growth only for the outermost, intact portion of the stem, and the absence of internal wood makes tree age determination impossible. To document the prevalence of internal decay, we tallied its presence or absence from all northern white-cedar cores (N = 286, DBH range 10–78 cm) and tested if the probability of decay increased with tree diameter, using logistic regression (PROC LOGISTIC function in SAS; SAS Institute, Inc., 2012).

2.3. Dendrochronological procedures

Increment cores were dried, mounted and sanded to a fine polish using standard methods. For intact cores that missed the pith by less than ca. 15 mm, a pith locator (Appelquist, 1958) was used to estimate the number of rings to the pith. Ring widths were measured on a Velmex sliding-stage stereomicroscope to the nearest 0.01 mm. Cross-dating was conducted using the marker-year method of Yamaguchi (1991), with statistical verification by COFECHA (Grissino-Mayer, 2001). Marker years included those with narrow bands of latewood, false rings, or unusual widths (Schweingruber, 1996). Overall, 5.3% of the cedar cores required dating adjustments due to locally absent rings (one absent ring per core in all but one case of three absent rings).

We used two lines of evidence in the growth patterns of living trees to reconstruct past canopy disturbances: abrupt and sustained increases in radial growth (growth releases) and rapid initial growth (gap recruitments). Growth releases indicate the sudden loss of an overtopping

canopy, and gap recruitment events indicate a tree experienced open, free-to-grow conditions during its transition from seedling to small tree. Each tree-ring series was evaluated for both types of evidence, and both types were treated equally in the reconstruction of disturbance histories. We used the absolute increase method of detecting growth releases, which scales the release thresholds according to the growth rate immediately prior to disturbance, thereby avoiding the false positive and false negative releases common in the standard percent-increase method (Fraver and White, 2005a). The method proceeds by subtracting pre-event 10-year mean growth rates from post-event 10-year rates; if the difference exceeds a predetermined species-specific threshold (e.g., 0.41 mm for cedar), the event is considered a release. The selected thresholds (presented in Fraver and White, 2005a) are meant to screen out minor responses, such as those resulting from nearby canopy gaps, instead focusing on the loss of overhead canopy trees, equivalent to the “major” releases commonly referred to in the literature (e.g., Lorimer and Frelich, 1989, Black and Abrams, 2003). In addition, to be considered valid, a release had to be sustained for at least seven years (Fraver et al., 2009) to screen out recovery from minor growth depressions such as those caused by drought. Finally, following Lorimer and Frelich (1989), we eliminated purported releases occasionally seen in trees judged to have been in the canopy at the time of the event, as these suggest a nearby disturbance, rather than removal of overhead canopy. We assumed trees had been in the canopy in a given year if their back-calculated diameters exceeded a species-specific threshold (e.g., 25 cm for cedar, see Fraver et al., 2009), with thresholds estimated as per Lorimer and Frelich (1989). Gap recruited trees were deemed as such if the mean ring width for the first five years exceeded 1.2 mm (D’Amato and Orwig, 2008) and the subsequent growth pattern was declining, parabolic, or flat (Frelich, 2002).

2.4. Disturbance chronologies and metrics

By convention, growth releases and gap-recruitment events (henceforth releases) were tallied by decade, allowing for the variable lag time between disturbance and a tree’s response (Lorimer and Frelich, 1989). We converted the number of releases in each decade to estimates of canopy area disturbed following Lorimer and Frelich (1989), resulting in an area-based disturbance chronology for each stand. This conversion weights the evidence of disturbance according to the tree’s current (at time of sampling) canopy projection area, which is necessary because the severity of disturbance inferred from small-canopied trees differs from that of large-canopied trees. Current canopy areas were predicted from current tree diameters using regression equations developed from the Reserve (Fraver, 2004). The canopy area disturbed in each decade was expressed as a percent of the total canopy area from trees present in that decade. In forests dominated by shade-tolerant trees, disturbance chronologies may be more informative than age structures, given the weak relationship between tree ages and disturbance events (Lorimer, 1985). As chronologies extend further back in time, they become increasingly uncertain because more trees would have been lost through mortality. To partially overcome this limitation, we truncated chronologies when sample size dropped below 20 trees per plot. By convention, we did not estimate disturbance rates for the most recent decade in our data (1991–2000), because the release-detection method requires a full 10-year post-disturbance period for comparison.

3. Results

Northern white-cedar dominated all stands; however, it had higher relative basal areas in the swamp type (mean 88%) than the seepage type (54%) (Table 1). Common associated species in both types included *Picea* species and *A. balsamea*, with *B. alleghaniensis* being a more common associate in the seepage forest type (Table 1), consistent with the type description (Gawler and Cutko, 2010). Data pooled across all

stands showed a mean living tree basal area of 44.3 m² ha⁻¹, density of 591 trees ha⁻¹, and density of large (> 40 cm dbh) living trees of 130 trees ha⁻¹. Mean CWD volume was 183 m³ ha⁻¹ although this varied markedly among plots (range 120–241 m³ ha⁻¹). Cedar dominated the CWD pool, representing 83% of the total volume (excluding pieces that could not be identified to species), with *P. rubens* representing 12%. Mean sapling density (all species) was 2777 stems ha⁻¹, although density varied among stands and was quite patchy within a stand. Similarly, the density of cedar saplings varied markedly among stands from 0 to 960 stems ha⁻¹. Table 2 lists various structural attributes for each stand.

Windthrow data were pooled because they were too sparse to analyze separately by stand or by species. Uprootings were much more prevalent than stem snaps, accounting for 98% of all windthrown trees ($n = 74$ total observations). Windthrown trees displayed uniform directionality (Rayleigh’s $p < 0.01$, $N = 74$, Oriana software 4.02, Kovach, 2013), with a mean azimuth of 132° (circular SE = 12.4°; Fig. 1). These easterly fall orientations reflect storm winds originating predominantly from the west: winds of gale force or greater (17.2 m s⁻¹) had a mean azimuth of 288° ($p < 0.0001$, $N = 203$, SE = 3.3°; records pooled from the four closest meteorological stations between 1950 and 2000).

The probability of a given cedar tree containing internal decay increased significantly with increasing tree diameter ($\chi^2 p < 0.0001$; Fig. 2). Even for the smallest trees cored, the probability of internal decay was ca. 27%; for the largest trees this increased to ca. 96%. Overall, 63% of cedar cores contained internal decay.

We truncated the early portions of disturbance chronologies at the point where the sample size dropped below 20 trees, meaning that chronologies extended back to 1880 (stands N30 and AK44, shortest chronologies) and as far as 1780 (stand AD27). We found no evidence of stand-replacing disturbance during these periods; in fact, disturbance chronologies revealed that decadal disturbance rates rarely exceeded 25% (Fig. 3). The disturbance chronologies show marked fluctuations through time, with only weak evidence of synchrony among stands. The seepage forests tended to have a higher disturbance rate (9.2% per decade) than did the swamp forests (4.7%). The prevalence of internal decay in cedar precluded the construction of age-class distributions for each stand; however, given the pulses in canopy disturbance (Fig. 3) and the available recruitment age structures (below), we suspect the stands were multi-aged.

Based on the sound cedar cores that hit the pith or passed near the pith ($N = 63$ cores, representing 24% of the total cedar cores), 44% of the current canopy trees showed one growth release before reaching the canopy, 26% showed two releases, and 7% showed three releases (Fig. 4). Of the 23% that showed no release, most showed persistent slow growth with occasional minor increases (not meeting our release criteria) that eventually allowed them to reach the canopy (Fig. 4a). This same subset of cores also allowed us estimate recruitment age (i.e., breast height age) structure; however, the small number of cores required that we pool data from all stands. The resulting age structure, though necessarily sparse, suggests fairly continuous recruitment in the early decades, a recruitment pulse in the late 1800s, and very little recruitment in recent decades (Fig. 5).

4. Discussion

These stands exhibit structural characteristics typical of old-growth conifer forests of the region: abundant snags, high volumes of CWD in various stages of decay, and numerous large (dbh ≥ 40 cm) living and dead trees (Table 2; Cogbill, 1996, Forrester et al., 2005; Fraver and White, 2005b, D’Amato et al., 2008, Wesely et al., 2018). The large trees and abundant CWD serve a particularly important role in maintaining biodiversity (Stokland et al., 2012; Lindenmayer et al., 2012); they are also among the attributes of old-growth requiring considerable time to develop (Jönsson et al., 2009). CWD volumes were on the high

Table 1
Tree species composition, based on relative basal areas, of the six old-growth northern white-cedar stands.

Species	Cedar swamp forest plots			Cedar seepage forest plots		
	AD27	B25	B8	L7	N30	AK44
<i>Thuja occidentalis</i>	83.8	87.2	92.1	60.5	54.5	47.8
<i>Picea rubens</i>	2.7	4.4	3.3	23.5	5.5	22.8
<i>Abies balsamea</i>	2.2	1.1	1.5	2.7	13.6	15.0
<i>Betula alleghaniensis</i>	0.1	2.3	0.1	1.3	23.2	6.6
<i>Picea glauca</i>	5.6	4.6	2.5	10.5	3.0	0.0
<i>Acer saccharum</i>	–	–	–	–	–	5.0
<i>Fraxinus nigra</i>	1.4	–	0.2	–	–	2.8
<i>Pinus strobus</i>	3.7	–	–	–	–	–

Table 2
Structural characteristics of the six old-growth northern white-cedar stands. BA = basal area ($m^2 ha^{-1}$); Density = stems ha^{-1} ; downed CWD volume ($m^3 ha^{-1}$); saplings refer to tree stems < 10 cm dbh but ≥ 2 m tall.

Plot	Live Trees			Snags		Sapling		
	BA	Density	Dens. ≥ 40 cm	BA	Density	Density	% cedar	CWD vol
Swamp forest								
AD27	65.7	707	267	21.2	280	2900	30	127.0
B25	47.7	740	107	11.7	227	4060	24	119.9
B8	50.9	593	140	18.9	233	3300	26	201.9
Seepage forest								
L7	26.6	300	80	16.1	240	2880	4	230.4
N30	38.5	567	113	6.5	53	2120	3	177.4
AK44	36.5	640	73	18.5	180	1400	0	240.5

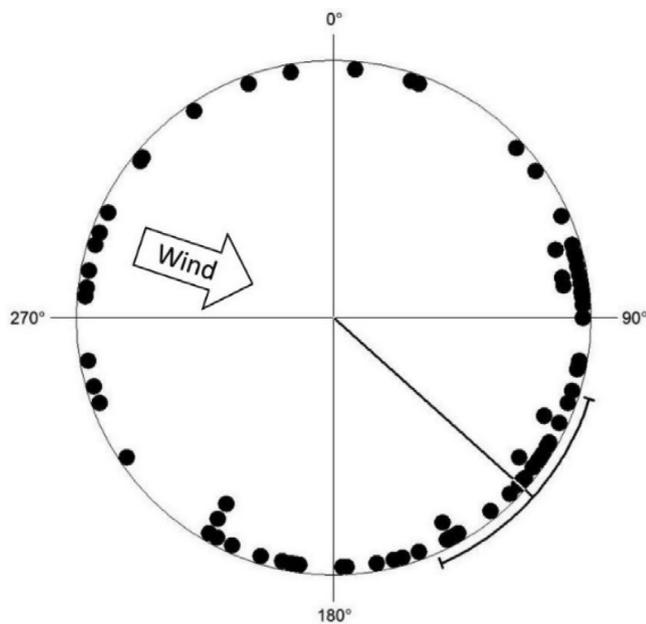


Fig. 1. Circular distributions of fall directions for windthrown trees (uprootings and stem snaps combined), showing a mean of 132° ($SE = 12.4^\circ$). Directional vector represents the mean, with 95% confidence intervals. Each dot represents one windthrown tree. Arrow indicates the direction of gale-force winds in the region.

end of published ranges for this region, which can be explained in part by the slow decomposition (i.e., accumulation) of cedar wood (Wenger, 1984), which is likely further retarded by the excessively moist substrate conditions typical of this forest type.

The prevalence of internal decay in cedar trees precluded the use of robust age structures to infer past disturbance at the stand level (but see below). Overall, 63% of cedar cores contained internal decay, and the probability of decay increased with tree diameter. However, for forests

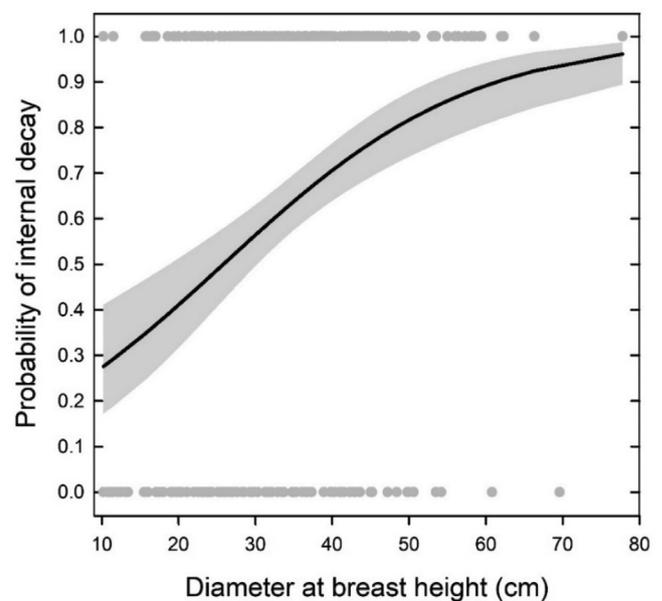


Fig. 2. The probability of internal decay for northern white-cedar increases with increasing tree diameter. Logistic regression based on 286 northern white-cedar cores. Shaded region represents 95% confidence limits.

dominated by shade-tolerant tree species such as these, where small individuals can persist for decades under shade, age structures may be poorly linked to past disturbance (Lorimer, 1985). In these situations, the use of growth releases provides a complementary approach to that of age structures, allowing us to reconstruct past disturbance histories for these stands. Further, growth releases can be evaluated on the intact portions of increment cores from trees with internal decay.

Evidence from growth releases reveals a sporadic sequence of low- to moderate-severity canopy disturbances. The mean disturbance rate was 6.4% of canopy area disturbed per decade, and pulses rarely exceeded 25% per decade. These mean rates are comparable to those of

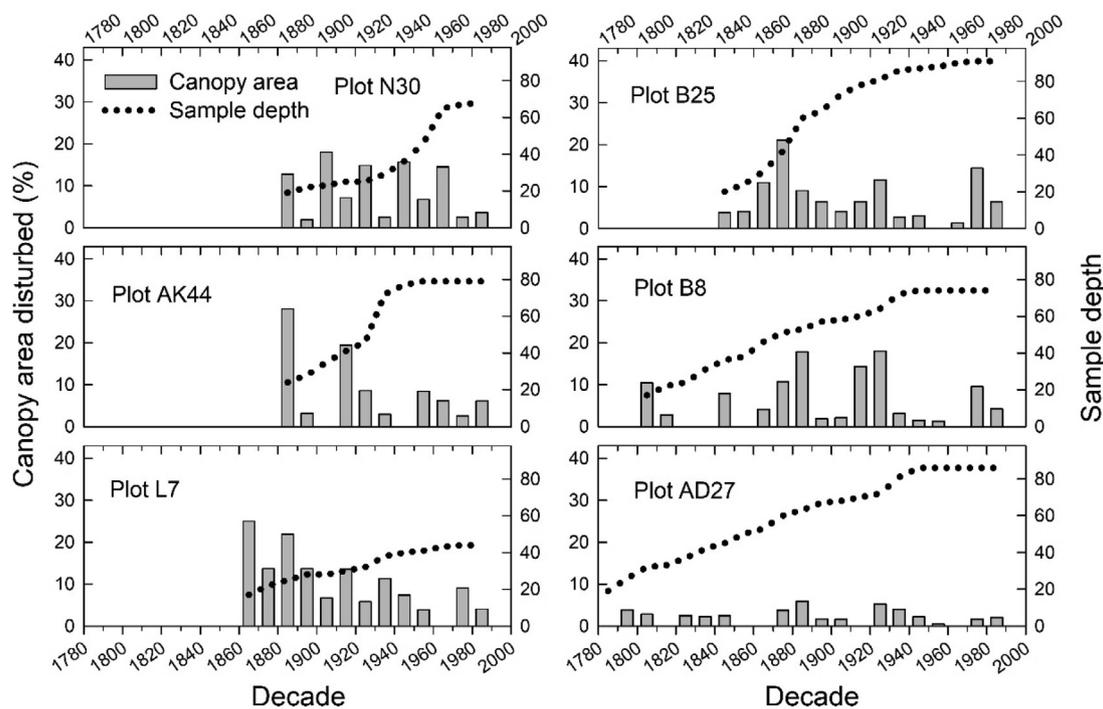


Fig. 3. Disturbance chronologies, expressed as canopy area disturbed per decade, for three old-growth northern white-cedar seepage forests (left panels) and three northern white-cedar swamp forest (right panels). Sample depth refers to the number of canopy trees contributing to the chronology. Chronologies were truncated when sample depth dropped below 20 trees.

old-growth hemlock forests in the region (Ziegler, 2002; D'Amato et al., 2008), yet somewhat lower than those found in red spruce, mixed-wood, or hardwood forests of the region (Fraver and White, 2005b; Fraver et al., 2009). The disturbance pulses influence tree population dynamics by fostering successful recruitment of advance regeneration and releasing formerly suppressed trees that survive the disturbance. The number of releases detected on individual cedar trees point to the importance of canopy gaps for achieving canopy status. Most of the intact (without internal decay) cedar trees required one or more growth releases, following a period of suppression, before reaching the canopy. Similarly, Heitzman et al. (1997), Ruel et al. (2014), and Kincaid (2016) document pronounced positive growth response to release from suppression for this species, even after extended periods of suppression. However, gaps are not the only means of reaching the canopy. In the current study, cedar trees that did not experience growth releases showed persistent slow growth that eventually placed them in the canopy (Fig. 4). Hofmeyer et al. (2010) and Ruel et al. (2014) also report that cedar can maintain steady growth for long time periods, even for large trees. These trees may have benefitted from nearby gaps or from slow forming gaps (Krasny and Whitmore, 1992) that were not detected by release criteria, which rely on abrupt increases in growth.

Contrary to our expectation, these disturbance pulses were not strongly synchronized among stands, even within this small landscape. However, all but one stand showed evidence of moderate-severity disturbances in the late 1800s, possibly from a series of four documented hurricanes that influenced central Maine between 1869 and 1896 (Ludlum, 1963; Neuman et al., 1978). These disturbances coincide with a pulse in cedar recruitment, suggesting cedar benefitted from such disturbances. We acknowledge that the recruitment age structure is necessarily sparse, leaving this relationship admittedly speculative. In contrast to our findings, Ruel et al. (2014) report fairly synchronized cedar growth responses among mixed-species stands, which appeared to be driven by spruce budworm (*Choristoneura fumiferana*) outbreaks that negatively affected co-occurring spruce and balsam fir and hence benefitted cedar. However, the stands studied here had a smaller component of spruce and fir, particularly in the swamp type, and would

thus be less influenced by spruce budworm outbreaks.

The generally low rates of disturbance evident in our results could be attributed in part to the low landscape positions – and accompanying partial protection from wind – occupied by these stands. The three swamp forests in particular occupy low-lying basins protected from wind. Nevertheless, wind appears to be the primary disturbance agent for these cedar stands, where it creates a background of scattered canopy openings and contributes to the pulses of moderate-severity disturbance, which presumably result in larger gaps. Similarly, Pregitzer (1990) found wind to be the primary disturbance agent for lowland cedar stands in the US Lake States. Evidence for past windstorms is seen in the dominant easterly fall direction of windthrow trees (mean azimuth 132°), which corresponds to gale-force or greater winds originating from the west (mean azimuth 288°) in this region (Fig. 1). Although such gusts can occur at any time of the year, the prominence of uprootings (as opposed to stem snaps) suggests seasons other than winter, as uprootings would be less likely in frozen substrates (Everham and Brokaw, 1996).

Previous studies have pointed to regeneration deficiencies for cedar (Heitzman et al., 1997; Palik et al., 2015; Rueling et al., 2019). Though our study was not designed to address this issue, our sapling inventory and recruitment age structure provide some insights. The percent of saplings represented by cedar in the study stands is rather low; however, the swamp forest type consistently had greater densities (840 to 960 saplings ha^{-1}) than did the seepage type (0–100 ha^{-1}). (Table 2). Overall, balsam fir currently dominates the sapling pool (28%), followed by red spruce (21%), then by cedar (17%, stands pooled), although the canopies are currently cedar-dominated. Though we recognize that sapling composition is not a definitive predictor of future overstory composition, these percentages do suggest a risk of losing cedar dominance in the future overstory, particularly considering that cedar is a poor competitor (Larouche et al., 2011). The cedar recruitment deficiencies observed elsewhere have been attributed to browsing by white-tailed deer (*Odocoileus virginianus*) (Heitzman et al., 1999; Cornett et al., 2000a). Though deer populations are not currently high in the study region, historical deer density data are unavailable but

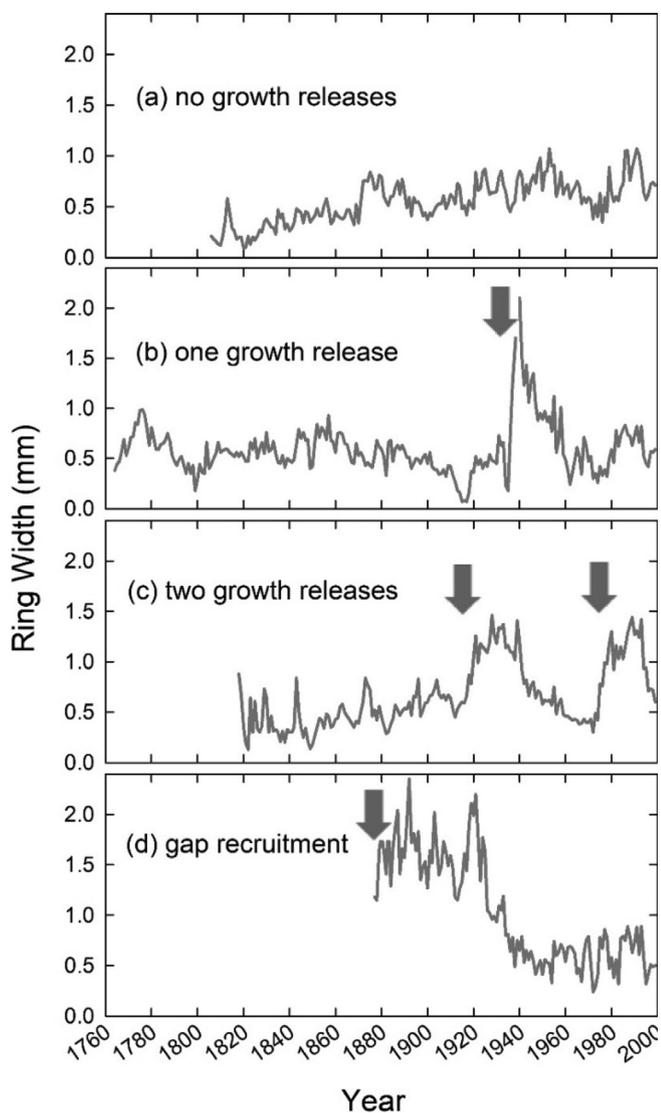


Fig. 4. Radial growth patterns of four northern white-cedar canopy trees, selected to illustrate (a) trees that reached the canopy by persistent slow growth, without requiring a release according to our criteria, (b) trees that reached the canopy after one growth release following a suppressed period, (b) trees that experience two such events, and (c) trees that experienced rapid early growth. Arrows indicate purported canopy disturbances, which presumably caused the growth responses.

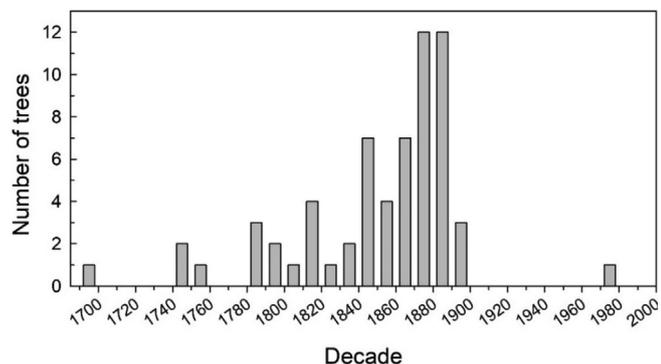


Fig. 5. Recruitment-age (i.e., breast height) based on the sound cedar cores that hit the pith or passed near the pith (24% of the total cedar cores). The small number of such cores required pooling data from all stands.

known to vary over time (Stanton, 1963).

The apparent hiatus in tree recruitment from 1900 onward (Fig. 5) also portends a loss of cedar, despite the relatively constant disturbance rates during this time that seemingly would promote cedar recruitment. However, this age structure should be interpreted with caution, as it is based on only 24% of the cores (i.e., those that were not rotten and hit or passed near the pith). Further, because cedar is slow growing, trees established in this apparent hiatus may not have reached coring size (10 cm dbh) at the time of sampling. Indeed, a regression of recruitment age against dbh ($p < 0.001$, $R^2 = 0.36$) suggests an average age of 81 years for a 10-cm-dbh tree.

Our findings regarding disturbance histories are derived from only six stands in one old-growth reserve, making generalizations to cedar stands in other regions difficult. Unfortunately, no other long-term disturbance histories from old-growth cedar exist for comparison. Limited tree age data from disjunct, hydric old-growth cedar stands in central Manitoba demonstrate the long-term persistence of cedar, also suggesting the lack of stand-replacing disturbances (Grotte et al., 2012). Though conducted in mature upland cedar stands, work from a disjunct population in the southern US revealed a disturbance history similar to that found here: low rates of canopy disturbance occurring in pulses (Kincaid, 2016). Our findings are also consistent with published disturbance chronologies for conifer-dominated forests in the study region, which point to marked temporal fluctuations, with pulses of low- to moderate-severity disturbance occurring every few decades (Ziegler, 2002, Fraver and White, 2005b, D’Amato and Orwig, 2008).

Several considerations suggest the possibility that our methods may have underestimated the amount of past canopy disturbance. First, many trees in cedar stands occur in clumps (Saucier et al., 2018), creating a very patchy canopy when viewed from above. The smaller trees located between clumps may not be limited primarily by light and would thus be less responsive, in terms of radial growth, to the loss of a canopy tree. Given that the growth-release method used here is meant to detect the loss of overhead canopies, its performance may be compromised in such irregularly structured canopies (Frelich, 2002). Second, cedar is the least sensitive (i.e. most complacent, *sensu* Fritts, 1978) of all co-occurring species in this study, meaning that its radial growth is less responsive to surrounding environmental conditions. Cedar had a mean sensitivity of 0.20, while sensitivities of the other species ranged from 0.24 to 0.31. Though our method of detecting growth releases is designed to account for differences in species’ sensitivities (for example, northern white-cedar has the lowest growth-release threshold), this species may simply be a poor registry of disturbance. Third, recent work suggests that release-detection methods may, under the particular conditions examined in two research plots, underestimate past canopy disturbances (Trotsiuk et al., 2018); however, this underestimation arises primarily under high-severity disturbances. Taken together, these caveats suggest that our decadal rates of canopy removal may be underestimates; however, the temporal patterns (pulses) would be little affected.

In summary, the disturbance histories revealed here are typified by a background of low-severity disturbances, punctuated at times by moderate-severity disturbances that rarely exceed 25% canopy removal per decade. Northern white-cedar has likely maintained dominance in the study stands throughout the period covered by this reconstruction. As such, the disturbance dynamics described here consist of structural changes to the forest, with little change in tree species composition. Cedar has persisted historically because of its ability to endure suppression and respond favorably to release, as well as its longevity relative to most co-occurring species. However, the lack of recent recruitment coupled with current low abundance of cedar saplings, relative to red spruce and balsam fir, suggest concern over the future dominance of cedar in these stands, and it suggests the need for further study focused on regeneration.

5. Management implications

Though management guidelines for cedar recommended even-aged regeneration methods until the mid-twentieth century (e.g., Johnston, 1977), research since that time has supported the use of multi-aged silviculture (Van Deelen, 1999, Larouche et al., 2011). Contemporary recommendations are based on experimental manipulations showing that cedar seedling mortality is lower under a partial canopy than in large gaps (Larouche et al., 2011) and observations that cedar can respond to release at advanced ages (Heitzman et al., 1997, Hofmeyer et al., 2010, Ruel et al., 2014). Though some even-aged silvicultural systems are consistent with these growth patterns (i.e. seedling establishment and release over a period of overstory removal in uniform shelterwood followed by thinning to accelerate growth of desired trees), multi-aged silviculture is consistent with these developmental patterns. Specifically, single-tree or group selection and irregular shelterwood have been recommended (Boulfroy et al., 2012).

Our findings add to the body of knowledge supporting the use of multi-aged silviculture for cedar management. Although age structures of cedar stands are rarely known, ages at breast height of cedar trees in the Big Reed Forest Reserve at the time of this study exceeded 300 years, with apparent continuous recruitment over a period of more than 200 years. Canopy disturbance rates averaged 5 to 10% per decade (rarely exceeding 25%). Based on these observations, silvicultural systems that reduce the overstory by roughly 0.5 to 2.5% annually would approximate natural disturbance dynamics observed in the present study. This could be accomplished operationally through the use of selection cutting in which percent removal is equal to cutting cycle length, resulting in a long-term average removal intensity of 1% per year. Alternately, irregular shelterwood or a similar area-based regeneration method could be applied such that area harvested in periodic entries averages 1–2% per year over the long-term, with seldom more than 25% of the stand opened in any decade. An approach similar to this, in which harvesting intensity increases with lengthening return interval and is based on observed natural disturbance rates, has been proposed for other conifer-dominated forest types in the region (Seymour et al., 2002). Finally, because of the sensitivity of these soils, operations in lowland cedar should occur on frozen ground.

Though regeneration methods can be adapted to create disturbance rates and overstory structures comparable to those observed in old-growth stands, long-term sustainability is dependent upon successfully establishing and recruiting regeneration. As mentioned above, results from both our sapling inventory and recruitment age structure suggest a risk of losing cedar dominance in the future overstory. Additional investigation is needed to determine why cedar recruitment and sapling density are low in the study stands, and silvicultural treatments aimed at maintaining cedar dominance should focus on establishing and releasing advance regeneration.

Regardless of silvicultural prescription, the present study supports previous observations in the region that old-growth cedar stands have an abundance of large living and dead trees, as well as downed woody debris (Wesely et al., 2018). Variants of multi-aged silviculture ranging from fairly simplistic shelterwood with reserves to increasingly complex irregular shelterwood or selection systems would facilitate retention of individual trees for two to three rotations of other trees in the stand. This is not only feasible based on cedar's observed potential longevity, but will help to maintain seed sources as well as late-successional characteristics in managed stands. A group of rare Calicoid lichens, for example, have been found on the bark of cedar trees in old-growth stands (Selva, 2003). Finally, consistent with previous work on old-growth cedar in Maine (Wesely et al., 2018), the present study suggests that protection of downed woody debris is warranted in managed cedar stands in light of the high volumes observed in this and other old-growth cedar forests and the recognized role of woody debris as a cedar regeneration substrate (Nelson, 1950, Cornett et al., 2000b).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank the USDA Forest Service Northern Research Station, the Maine Agricultural and Forest Experiment Station, and the U.S. Environmental Protection Agency for providing financial support. We thank R. Dyer, E. Doub, E. Roth, and N. Wesely for assistance in the field and laboratory; we thank J. Allogio and J. Wason for providing comments on an earlier draft of the manuscript; and we thank two anonymous referees for providing valuable comments on the submitted manuscript.

Data accessibility

The data described in the manuscript will be freely available upon request from the corresponding author.

Funding information

USDA Forest Service Northern Research Station (17-JV-11242307-018), the Maine Agricultural and Forest Experiment Station (project ME041605), and the U.S. Environmental Protection Agency (91598801-0, STAR Fellowship to S.F., 2000).

Conflict of Interest

None.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2019.117680>.

References

- Applequist, M.B., 1958. A simple pith locator for using with off-center increment cores. *J. Forest.* 56, 141.
- Baron, W.R., Smith, D.C., Borns Jr., H.W., Fastook, J., Bridges, A.E., 1980. Long-time series temperature and precipitation records for Maine, 1808–1978. Life Sciences and Agricultural Experiment Station. University of Maine, Orono, Maine, USA.
- Batschelet, E., 1981. *Circular Statistics in Biology*. Academic Press, New York, New York, USA.
- Bauhus, J., Puettmann, K., Messier, C., 2009. Silviculture for old-growth attributes. *For. Ecol. Manage.* 258, 525–537.
- Black, B.A., Abrams, M.D., 2003. Use of boundary-line growth patterns as a basis for dendroecological release criteria. *Ecol. Appl.* 13, 1733–1749.
- Boulfroy, E., Forget, E., Hofmeyer, P.V., Kenefic, L.S., Larouche, C., Lessard, G., Lussier, J.-M., Pinto, F., Ruel, J.-C., Weiskittel, A. 2012. *Silvicultural Guide for Northern White-Cedar (Eastern White Cedar)*. General Technical Report NRS-98. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 74 p.
- Carey, A.B., 2003. Biocomplexity and restoration of biodiversity in temperate coniferous forest: inducing spatial heterogeneity with variable-density thinning. *Forestry* 76 (2), 127–136.
- Cogbill, C.V. 1985. Evaluation of forest history and old-growth nature of the Big Reed Pond Reserve, T8 R10 and T8 R11 W.E.L.S., Maine. A report prepared for the Maine Nature Conservancy.
- Cogbill, C.V., 1996. Black growth and fiddlebutts: the nature of old-growth red spruce. In: Davis, M.B. (Ed.), *Eastern Old-growth Forests: Prospects for Rediscovery and Recovery*. Island Press, Washington, D.C., USA, pp. 113–125.
- Cornett, M.W., Frelich, L.E., Puettmann, K.J., Reich, P.B., 2000a. Conservation implications of browsing by *Odocoileus virginianus* in remnant upland *Thuja occidentalis* forests. *Biol. Conserv.* 93 (3), 359–369.
- Cornett, M.W., Reich, P.B., Puettmann, K.J., Frelich, L.E., 2000b. Seedbed and moisture availability determine safe sites for early *Thuja occidentalis* (Cupressaceae) regeneration. *Am. J. Bot.* 87, 1807–1814.
- D'Amato, A.W., Orwig, D.A., 2008. Stand and landscape-level disturbance dynamics in old-growth forests in Western Massachusetts. *Ecol. Monogr.* 78, 507–522.
- D'Amato, A.W., Orwig, D.A., Foster, D.R., 2008. The influence of successional processes

- and disturbance on the structure of *Tsuga canadensis* forests. *Ecol. Appl.* 18 (5), 1182–1199.
- Everham, E.M., Brokaw, N.V., 1996. Forest damage and recovery from catastrophic wind. *Botanical Rev.* 62 (2), 113–185.
- Forrester, J.A., Yorks, T.E., Leopold, D.J., 2005. Arboreal vegetation, coarse woody debris, and disturbance history of mature and old-growth stands in a coniferous forested wetland. *J. Torrey Botanical Soc.* 132 (2), 252–262.
- Fraver, S., 2004. Spatial and Temporal Patterns of Natural Disturbance in Old-growth Forests of Northern Maine, USA. PhD thesis. University of Maine, Orono.
- Fraver, S., White, A.S., 2005a. Identifying growth releases in dendrochronological studies of forest disturbance. *Can. J. For. Res.* 35 (7), 1648–1656.
- Fraver, S., White, A.S., 2005b. Disturbance dynamics of old-growth *Picea rubens* forests of northern Maine. *J. Veg. Sci.* 16, 597–610.
- Fraver, S., Ringvall, A., Jonsson, B.G., 2007. Refining volume estimates of down woody debris. *Can. J. For. Res.* 37, 627–633.
- Fraver, S., White, A.S., Seymour, R.S., 2009. Natural disturbance in an old-growth landscape of northern Maine, USA. *J. Ecol.* 97, 289–298.
- Fraver, S., Milo, A.M., Bradford, J.B., D'Amato, A.W., Kenefic, L., Palik, B.J., Woodall, C.W., Brissette, J., 2013. Woody debris volume depletion through decay: implications for biomass and carbon accounting. *Ecosystems* 16 (7), 1262–1272.
- Frellich, L.E., 2002. *Forest Dynamics and Disturbance Regimes*. Cambridge University Press, Cambridge, UK.
- Fritts, H.C., 1978. *Tree Rings and Climate*. Academic Press, New York, New York, USA.
- Gawler, S., Cutko, A., 2010. *Natural Landscape of Maine: A guide to Natural Communities and Ecosystems*. Maine Natural Areas Program, Maine Department of Conservation, Augusta, Maine.
- Grissino-Mayer, H.D., 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree-ring Res.* 57, 205–221.
- Grotte, K.L., Heinrichs, D.K., Tardif, J.C., 2012. Old-growth characteristics of disjunct *Thuja occidentalis* stands at their northwestern distribution limit, central Canada. *Natural Areas J.* 32 (3), 270–282.
- Heitzman, E., Pregitzer, K.S., Miller, R.O., 1997. Origin and early development of northern white-cedar stands in northern Michigan. *Can. J. For. Res.* 27, 1953–1961.
- Heitzman, E., Pregitzer, K.S., Miller, R.O., Lanasa, M., Zuidema, M., 1999. Establishment and development of northern white-cedar following strip clearcutting. *For. Ecol. Manage.* 123, 97–104.
- Hofmeyer, P.V., Kenefic L.S., Seymour R.S. 2007. Northern White-cedar (*Thuja occidentalis* L.): An Annotated Bibliography. Research Report 07-01. Cooperative Forestry Research Unit, University of Maine. 30 pp.
- Hofmeyer, P.V., Kenefic, L.S., Seymour, R.S., 2010. Historical stem development of northern white-cedar (*Thuja occidentalis* L.) in Maine. *North. J. Appl. For.* 27 (3), 92–96.
- Johnston, W.F. 1977. *Manager's handbook for northern white-cedar in the north central States*. General Technical Report NC-35. St. Paul, MN: North Central Forest Experiment Station, U.S. Department of Agriculture, Forest Service. 18 pp.
- Jönsson, M.T., Fraver, S., Jonsson, B.G., 2009. Forest history and the development of old-growth characteristics in fragmented boreal forests. *J. Veg. Sci.* 20, 91–106.
- Kelly, P.E., Cook, E.R., Larson, D.W., 1994. A 1397-year tree-ring chronology of *Thuja occidentalis* from cliff faces of the Niagara Escarpment, southern Ontario, Canada. *Canadian Journal of Forest Research* 24 (5), 1049–1057.
- Kincaid, J.A., 2016. Structure and dendroecology of *Thuja occidentalis* in disjunct stands south of its contiguous range in the central Appalachian Mountains, USA. *Forest Ecosyst.* 3 (1), 25.
- Kovach, W.L. 2013. *Oriana for Windows, 4.02*. Kovach Computing Services, Pentraeth, Wales, UK.
- Krasny, M.E., Whitmore, M.C., 1992. Gradual and sudden forest canopy gaps in Allegheny northern hardwood forests. *Canadian J. Forest Res.* 22, 139–143.
- Kuuluvainen, T., 2002. Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. *Silva Fennica* 36 (1), 97–125.
- Larouche, C., Ruel, J.C., Lussier, J.M., 2011. Factors affecting northern white-cedar (*Thuja occidentalis*) seedling establishment and early growth in mixedwood stands. *Can. J. For. Res.* 41 (3), 568–582.
- Lindenmayer, D.B., Laurance, W.F., Franklin, J.F., 2012. Global decline in large old trees. *Science* 338 (6112), 1305–1306.
- Lorimer, C.G., 1985. Methodological considerations in the analysis of forest disturbance history. *Can. J. For. Res.* 15, 200–213.
- Lorimer, C.G., Frellich, L.E., 1989. A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. *Can. J. For. Res.* 19, 651–663.
- Ludlum, D.M., 1963. *Early American Hurricanes 1492–1870*. American Meteorological Society, Boston, Massachusetts, USA.
- Nagel, L.M., Palik, B.J., Battaglia, M.A., D'Amato, A.W., Guldin, J.M., Swanston, C.W., Janowiak, M.K., Powers, M.P., Joyce, L.A., Millar, C.I., Peterson, D.L., 2017. Adaptive silviculture for climate change: a national experiment in manager-scientist partnerships to apply an adaptation framework. *J. Forest.* 115 (3), 167–178.
- Nelson, T.C. 1950. *A reproduction study of northern white cedar*. Thesis, Michigan State College of Agriculture and Applied Science, East Lansing, Michigan, USA.
- Neuman, C.J., Cry, G.E., Caso, E.L., Jarvinen, B.R., 1978. Tropical Cyclones of the North Atlantic 1871–1977. National Climatic Center, Asheville, North Carolina, USA.
- Palik, B.J., Mitchell, R.J., Hiern, J.K., 2002. Modeling silviculture after natural disturbance to sustain biodiversity in the longleaf pine (*Pinus palustris*) ecosystem: balancing complexity and implementation. *For. Ecol. Manage.* 155 (1–3), 347–356.
- Palik, B.J., Haworth, B.K., David, A.J., Kolka, R.K., 2015. Survival and growth of northern white-cedar and balsam fir seedlings in riparian management zones in northern Minnesota, USA. *For. Ecol. Manage.* 337, 20–27.
- Pregitzer, K.S. 1990. *The Ecology of Northern White-cedar*. In: *Northern White-cedar in Michigan, Workshop Proceedings*. Agricultural Experiment Station Research Report. Vol. 512, pp. 8–14.
- Ruel, J.-C., Lussier, J.-M., Morissette, S., Rocodeau, N., 2014. Growth response of northern white-cedar (*Thuja occidentalis*) to natural disturbances and partial cuts in mixedwood stands in Quebec, Canada. *Forests* 5, 1194–1211.
- Rueling, L.F., Kern, C.C., Kenefic, L.S., Bronson, D.R., 2019. The northern white-cedar recruitment bottleneck: understanding the effects of substrate, competition, and deer browsing. *Forests* 10, 501. <https://doi.org/10.3390/f10060501>.
- SAS Institute, Inc. 2012. *Base SAS® 9.4 Procedures Guide*. Cary, NC, USA.
- Saucier, L., Ruel, J.C., Larouche, C., 2018. Variations in northern white-cedar (*Thuja occidentalis*) regeneration following operational selection cutting in mixedwood stands of western Quebec. *Can. J. For. Res.* 48 (11), 1311–1319.
- Schweingruber, F.H., 1996. *Tree Rings and Environment: Dendroecology*. Paul Haupt Publishers, Berne, Switzerland.
- Selva, S.B., 2003. Using Calicioid lichens and fungi to assess ecological continuity in the Acadian Forest Ecoregion of the Canadian Maritimes. *Forestry Chronicle* 79, 550–558.
- Seymour, R.S., Hunter Jr., M.L. 1999. *Principles of Ecological Forestry*. In: M.L. Hunter Jr. (ed.), *Managing Biodiversity in Forest Ecosystems*. Cambridge University Press, Cambridge, pp. 21–61.
- Seymour, R.S., White, A.S., deMaynadier, P.G., 2002. Natural disturbance regimes in northeastern North America – evaluating silvicultural systems using natural scales and frequencies. *For. Ecol. Manage.* 155, 357–367.
- Sollins, P., 1982. Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. *Can. J. For. Res.* 12, 18–28.
- Sommerfeld, A., Senf, C., Buma, B., D'Amato, A.W., Després, T., Díaz-Hormazabal, I., Fraver, S., Frellich, L.E., Gutiérrez, Á.G., Hart, S.J., Harvey, B.J., He, H.S., Hlásny, T., Holz, A., Kitzberger, T., Kulakowski, D., Lindenmayer, D., Mori, A.S., Müller, J., Paritsis, J., Perry, G., Stephens, S., Svoboda, M., Turner, M.G., Veblen, T.T., Seidl, R., 2018. Patterns and drivers of recent disturbances across the temperate forest biome. *Nat. Commun.* 9 (1), 4355.
- Stanton, D.C., 1963. *A History of the White-tailed Deer in Maine*. Maine Game Division Bull. No. Augusta, pp. 8.
- Stokland, J.N., Siitonen, J., Jonsson, B.G., 2012. *Biodiversity in Dead Wood*. Cambridge University Press, Cambridge.
- Svoboda, M., Janda, P., Bače, R., Fraver, S., Nagel, T.A., Rejzek, J., Mikoláš, M., Douda, J., Boublik, K., Šamonil, P., Čada, V., 2014. Landscape-level variability in historical disturbance in primary *Picea abies* mountain forests of the Eastern Carpathians, Romania. *J. Veget. Sci.* 25 (2), 386–401.
- Trotsiuk, V., Druckenbrod, D., Martin-Benito, D., Orwig, D., Bishop, D., Barker-Plotkin, A., Fraver, S., Pederson, N., 2018. Testing the efficacy of tree-ring methods for detecting past disturbances. *For. Ecol. Manage.* 425, 59–67.
- Van Deelen, T., 1999. Deer-cedar interactions during a period of mild winters: implications for conservation of conifer swamp deeryards in the Great Lakes region. *Nat. Areas J.* 19, 263–274.
- Wenger, K.F., 1984. *Forestry Handbook*, second ed. John Wiley & Sons, New York, New York, USA.
- Wesely, N., Fraver, S., Kenefic, L.S., Ruel, J.-C., Weiskittel, A., Thompson, M., White, A.S., 2018. Structural attributes of old-growth and partially harvested northern white-cedar stands in Northeastern North America. *Forests* 9, 376.
- Widoff, L. 1985. *The forest communities of Big Reed Pond Reserve, T8 R10, T8 R11, Maine: Results of field work, summer 1985*. Unpublished report.
- Yamaguchi, D.K., 1991. A simple method for cross-dating increment cores from living trees. *Can. J. For. Res.* 21, 414–416.
- Ziegler, S.S., 2002. Disturbance regimes of hemlock-dominated old-growth forests in northern New York, USA. *Can. J. For. Res.* 32, 2106–2115.