Repeated insect outbreaks promote multi-cohort aspen mixedwood forests in northern Minnesota, USA

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ABSTRACT

Characterizing the timing, severity, and agents of historic forest disturbances is critical to developing management and conservation strategies based on natural processes. Typically such information is derived from retrospective studies of remnant old-growth forests; however, this approach has limited application in regions dominated by secondary forests heavily influenced by past land-use. One striking example is the secondary aspen mixedwood forests of northern Minnesota, which have risen in both abundance and aerial extent, the result of post-settlement harvesting and subsequent land-use changes. Given their recent rise in abundance, as well as their dominance by relatively short-lived aspen, they have not been the focus of retrospective studies examining pre-settlement conditions.

Using methods of dendrochronology, we reconstructed nearly a 90-year history of canopy disturbances and stand development for nine secondary mesic aspen mixedwood forests of northern Minnesota. Results show all stands initiating after near stand-replacing disturbance, presumably harvests, marked by initial recruitment dominated by *Populus tremuloides*. Ensuing development included an extended recruitment period by shade-tolerant species such as *Abies balsamea*, *Acer rubrum*, and *Picea glauca*. However, some stands experienced defoliation by forest tent caterpillar (*Malacosoma disstria*) quite early during the stem exclusion stage (major events occurring as early as 23 years after stand initiation), causing tree mortality and giving rise to a new cohort. Subsequent repeated outbreaks of tent caterpillar and spruce budworm (*Choristoneura fumiferana*) further opened the canopy, resulting in complex mixed-species, multi-cohort stands.

This study is one of the first to link chronic defoliation events with long-term community dynamics for this forest type. Our findings highlight the critical roles these events play in structuring aspen mixedwood forests, particularly within the early stages of stand development, resulting in multi-cohort stands. Moreover, our findings support the growing body of literature suggesting that the range of variability in aspen age structures extends beyond the single-cohort model that has guided forest management in this region. Collectively, these findings have important implications for the design of forest management practices that approximate this range of variability and emulate defoliation disturbances, with early harvest entries aimed at increasing stand structural and compositional complexity.

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1. Introduction

Natural canopy disturbances and tree species' autoecologies, in conjunction with site conditions, largely govern the development of forest composition and structure (age, size and distribution of live and dead trees; Oliver and Larson, 1996; Bergeron, 2000). Correspondingly, knowledge of disturbance and species traits are imperative for predicting and understanding how forest conditions develop over time and in response to disturbance. Understanding these relationships is of particular interest when managing forests

for objectives that include the restoration of historically important and currently underrepresented forest conditions (Engstrom et al., 1999). Typically, information on disturbance regimes is derived from retrospective studies of remnant old-growth forests; this approach has been less often applied in regions dominated by secondary forests heavily influenced by past land-use (Oliver and Stephens, 1977). As a result, such long-term data are rare for many secondary forest types, and when such information exists, it may depict historical reference conditions that no longer apply (White and Walker, 1997). Thus, considerable knowledge gaps impede the development and application of forest management and conservation strategies based on historic patterns of disturbance.

The historic range of variability in successional pathways for a given forest type is often quite large, reflecting differences in

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disturbance regimes and site conditions. For example, a wide range of disturbance and successional patterns has been documented for the mixed aspen (*Populus tremuloides*)-conifer forests (hereafter referred to as 'aspen mixedwoods') of the sub-boreal and boreal regions of North America (cf. McCarthy, 2001; Chen and Popadiouk, 2002), despite general compositional similarities of this community across the continent. Studies of aspen mixedwood forests within northeastern Minnesota, USA have documented relatively frequent stand-replacing fires (70–110 years; Heinselman, 1996) that result in stands and landscapes largely dominated by pioneer species, including *P. tremuloides* and *Betula papyrifera* (paper birch). In contrast, studies of aspen mixedwoods within Quebec, Canada suggest a disturbance regime of less frequent high severity disturbances with conifers dominating the later stages of succession due to species' shade tolerances and gap dynamics driven by insects, fungi, and wind (Bergeron, 2000). Similarly, studies of disturbance in aspen mixedwoods in western Canada also reveal regimes dominated by fine-scale, gap dynamics; however, gaps served to recruit additional cohorts of pioneering hardwoods as opposed to shade tolerant species (Cumming et al., 2000). These findings are part of a growing body of literature that recognizes the role of small-scale disturbances in producing the highly varied patterns of stand structure and composition observed within boreal and sub-boreal landscapes (McCarthy, 2001).

In addition, *P. tremuloides* populations may exhibit a considerable range in age structures within this broad forest type. Nonetheless, single-cohort populations of *P. tremuloides* have served as the model for current forest management; however, recent work has highlighted that multi-cohort aspen populations may develop within these systems (Bergeron, 2000; Cumming et al., 2000; Man and Rice, 2010). The age-cohort structure of this forest type has important implications for understanding the demographics of this species and thus for developing appropriate forest management prescriptions. However, detailed age-structure analyses for this forest type in the US Lake States region have not been undertaken.

The overarching objective of this study was to characterize the link between natural disturbance and patterns of stand development in mature, secondary, aspen mixedwood forests of northern Minnesota, USA. Our specific objectives were to (1) quantify rates of canopy disturbance through the analysis of tree-growth patterns, (2) describe compositional and structural development utilizing tree-age demographics, (3) and to examine the relationships between disturbance history and successional and stand developmental pathways. Our findings identify critical mechanistic relationships between disturbance patterns and community development that can guide management prescriptions meant to emulate the historic successional and forest developmental pathways for this system.

2. Methods

2.1. Study area

Study sites were located in the Laurentian Mixed Forest Province ecoregion of northern Minnesota, USA (Fig. 1), an area typified by a continental climate of short warm summers and long cold winters, with mean annual temperatures of 1.1–4.4 °C and annual precipitation ranging from 53 to 71 cm (Albert, 1995). Sites were underlain by glaciolacustrine deposits, till plains, and stagnation moraines, and they span elevations of 335–488 m. Extensive post-settlement land use in this region has produced an aspen mixedwoods land-base of secondary forests quite different from those of the pre-settlement era (Friedman and Reich, 2005; Schulte et al., 2007).

When compared to pre-settlement forests, contemporary forests of the region are younger on average (Frelich, 1995), and overstory composition is dominated by the pioneer species *P. tremuloides* and *B. papyrifera* (Frelich, 2002; Friedman and Reich, 2005; Schulte et al., 2007). Companion species typical of regional aspen mixedwoods include *Abies balsamea* (balsam fir), *Acer rubrum* (red maple), *Fraxinus nigra* (black ash) and *Picea glauca* (white spruce). Advance regeneration is composed of shade tolerant conifers such as *A. balsamea* and *P. glauca* and the shade tolerant hardwood *A. rubrum*. Typical shrub species include *Acer spicatum* (mountain maple), *Amelanchier* species (Juneberries), and *Corylus cornuta* (beaked hazel).

Study sites were selected from a Geographic Information System (GIS) of mapped and inventoried stands provided by the Minnesota Department of Natural Resources (MNDNR). Sites were selected that were sufficiently large to encompass a minimum of three 0.04 ha plots, contained a *P. tremuloides* cohort older than the regional rotation age of 40–60 years, contained no evidence of recent harvest, and were field-classified as northern wet-mesic boreal hardwood-conifer forest communities based on the state community classification system (MNDNR, 2003). Sites were not randomly selected; instead, we sampled a set of stands that met the aforementioned criteria – a rather small set due to the extensive regional harvest of 40–60 years old aspen mixedwoods. Site indices, tree densities, and basal areas were representative of fully stocked and productive *P. tremuloides* stands (Perala, 1977; Edgar and Burk, 2001). Stands had moderately well to poorly drained aqualf soils originating from clayey glaciolacustrine deposits or fine-textured glacial till.

2.2. Composition, demographics, and structure

Three to six 0.04 ha circular plots (depending on site size) were established at each of the nine sites (site codes A-I), totaling 49 plots. Plots were systematically established every 30–50 m on one or two parallel transects. Transect origins maximized sampling of stand interior conditions and ensured that plot perimeters began at least 30 m from stand boundaries to reduce edge effects (Fraver, 1994). On each plot, all living trees >10.0 cm diameter at breast height (DBH = 1.37 m) were cored at approximately 30 cm above the forest floor. Cores were extracted and processed using standard dendrochronological methods (Stokes and Smiley, 1968). Species, DBH, and crown class (dominant, codominant, intermediate, and suppressed) were determined for all cored trees, and height was measured for one tree in each crown class per plot. Seedlings and saplings were defined as woody stems ⩽0.5 m tall or >0.5 m tall and ⩽1.0 cm DBH, respectively. Both were tallied by species on eight 1.0 m^2 subplots within the main plot. Stems >1.0 cm and ⩽5.0 cm DBH and those >5.0 and ⩽10.0 cm DBH were tallied by species in eight 5.0 m^2 subplots within the main plot. All field work was conducted during the growing season 2009.

2.3. Tree ring analysis and disturbance chronology development

Increment cores were secured in wooden mounts, sanded to a flat, polished surface, and cross-dated using both skeleton plots (Stokes and Smiley, 1968) and marker years (Yamaguchi, 1991). Rings were measured (0.005 mm resolution) using a Velmex micrometer, and dating accuracy of all tentatively cross-dated series were statistically verified using COFECHA (Appendix A; Holmes, 1983). The pith date was taken as the year of recruitment, that is, the year a tree achieved coring height (30 cm). For cores that did not pass directly through the pith, Applequist's (1958) pith locator was used to estimate the number of years required to reach pith. Trees that missed the pith by greater than ten years
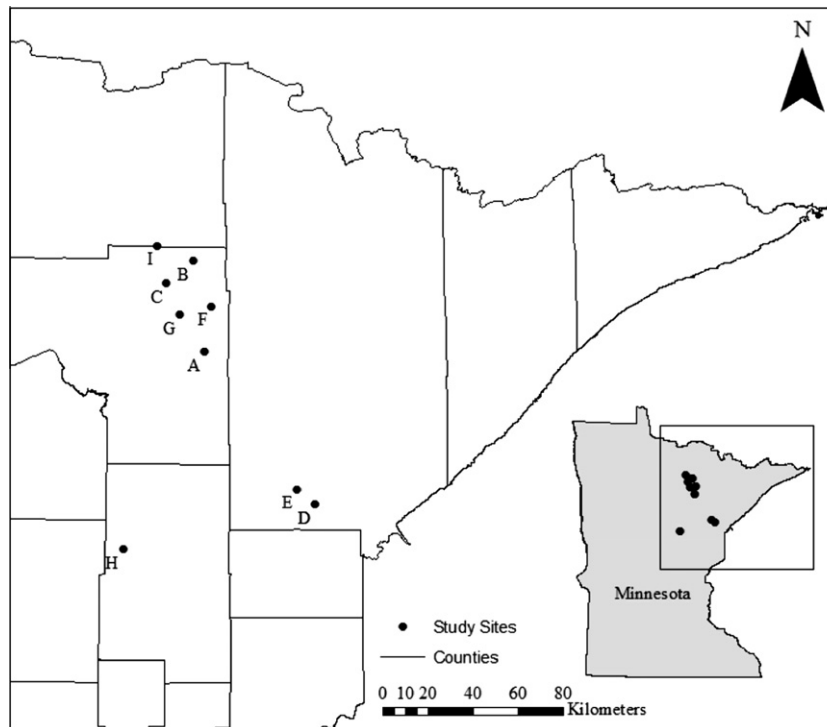
Fig. 1. Location of study sites in northern Minnesota, USA.

(estimated using the Applequist method) were excluded from age-structure analysis.

Tree age data were used to examine stand-level demographics as well as elucidate general patterns of stand development and disturbance across study sites. In order to characterize stand development through time for stands of different ages, calendar years were converted to a standard 'years after stand initiation' scale, and stand-level age data were then pooled across sites to characterize general trends. To this end, tree recruitment age was calculated as the difference between the calendar year of tree recruitment and the median calendar year of recruitment for the oldest *P. tremuloides* cohort (used to estimate stand initiating year). Age-based analyses excluded incomplete cores, which comprised approximately 30% of samples.

Growth patterns seen in surviving trees were used to identify past canopy disturbances (Lorimer and Frelich, 1989) using two lines of evidence: rapid growth responses (i.e., release from suppression or competition in the case of *P. tremuloides*) which suggest the loss of forest canopy, and rapid early growth (i.e., gap recruitment), which suggests the individual was recruited in open conditions (Lorimer, 1985; Lorimer and Frelich, 1989). Releases from suppression were considered valid if they were abrupt, sustained, and of a biologically meaningful magnitude (Frelich, 2002). To this end, releases needed to satisfy (1) the absolute-increase method (Fraver and White, 2005b), (2) the percent-increase method (requiring a 100% growth increase; Henry and Swan, 1974), and (3) a visual examination of the growth trend (Lorimer and Frelich, 1989). Species-specific thresholds for the absolute increase method were determined following Fraver and White (2005b), and genera-specific thresholds were used when species-specific thresholds were unavailable. In both the absolute- and percent-increase method, the average growth rates 10 years before and after a potential disturbance event were compared. While both release criteria demand a sustained increase, the absolute-increase method reduces false negative and false positive releases (resulting from rapid or very slow prior growth, respectively) common in the percent-increase method. The percent-increase method, however, was still necessary because of its ability to estimate the year of disturbance (Fraver and White, 2005b).

Gap-recruited trees also provide a means of detecting past canopy disturbance. Such trees demonstrated rapid initial growth rates exceeding 1.5 mm per year for the first 5 years of growth. Additionally, gap-recruits had to meet the criteria of declining, flat or parabolic growth patterns (Lorimer and Frelich, 1989). The year of gap formation was assigned to the recruitment date. Disturbance data, as with age data (above), were presented on two time-scales: calendar dates and time since initiation dates. Releases and gap recruitments were tallied by stand and translated to decadal canopy disturbance rates using methods established by Lorimer and Frelich (1989) and Frelich (2002). In addition, disturbances events were pooled across all sites and tallied by year following stand initiation (as opposed to calendar dates). This effort best characterized the timing of canopy disturbance relative to stand development.

Each release or gap recruitment revealed the year in which a sample tree began significant ascension to its current canopy position. The percentage of the canopy disturbed in any given decade was assumed to correspond to the proportion of current total exposed crown area (ECA) in intermediate, codominant and dominant crown classes occupied by trees released in that decade (Lorimer and Frelich, 1989). ECA was predicted from DBH using existing regression equations (Frelich, 2002; Ziegler, 2002; D'Amato and Orwig, 2008). Where species-specific equations were lacking, equations for a species with similar form were used (Ziegler, 2002; D'Amato and Orwig, 2008). Following Lorimer and Frelich (1989), a weight was applied to each disturbance event to properly scale inferences for trees of different size. For each site, each observed canopy-disturbance event was thus weighted by:

$$w_i = \frac{ECA_i/ECA_T}{n_i/N} \tag{a}$$

where w_i is the weight for the *i*th 5.0 cm DBH class, ECA_i is the total exposed crown area occupied by the *i*th 5.0 cm DBH class, ECA_T is the total exposed crown area, n_i is the number of stems per *i*th 5.0 cm DBH class, and N is the total number of sampled stems. Therefore, each observed disturbance event represents a proportion of disturbed canopy area equal to w_i. The estimated proportion of canopy area disturbed was summed by decade for each site. Mean decadal disturbance rates were calculated for each site and all sites combined for the decades following stand initiation.

2.4. Direct gap measurements

Owing to methodological constraints, the disturbance reconstruction methods described above exclude information from recent decades because newly established trees have not achieved sufficient diameter for coring. This limitation can be overcome by measuring and dating recent gaps and merging this information into the historical disturbance chronologies (Lorimer and Frelich, 1989; Fraver and White, 2005a). To this end, we focused on recently formed gaps larger than the crown area of a codominant *P. tremuloides*, or roughly 10 m^2, because crown expansion would quickly fill smaller gaps with little effect on understory trees. Gap area was determined by measuring 5–12 radii, depending on gap irregularity, extending from gap center to gap margin (defined as the drip line of gap border trees) and summing the areas of the resulting triangles (Spies et al., 1990). Gap area was then expressed as a proportion of total plot area.

From within each measured gap, basal disks were harvested from three to six of the tallest seedlings and saplings of each tree species present. Disks were processed following the methods detailed above (see Section 2.3), but given the shorter ring-width series, releases from suppression were determined using a 5-year rather than a 10-year running average (requiring a 100% growth increase). Results from these recent gap measurements were merged with those of the historic disturbance chronology to produce a disturbance chronology that extended to the modern decade.

2.5. Disturbance agents

A disturbance etiology was created for the study area to assist in our qualitative interpretation of disturbance histories reconstructed from tree-rings. Published historical records and maps were used to identify the agents potentially responsible for the canopy disturbances determined by methods outlined above. A GIS of digitized disturbances aerially surveyed from 1995 to 2009, as well as non-digitized aerial surveys spanning 1969–1994, provided by MNDNR, yielded qualitative information pertaining to the extent and severity of wind damage and defoliation by eastern spruce budworm (SBW: *Choristoneura fumiferana*) and forest tent caterpillar (FTC: *Malacosoma disstria*) – two insects known to affect aspen mixedwood systems (Sturtevant et al., 2004; Cooke and Roland, 2007). Other defoliating insects are known to affect aspen mixedwoods, such as the large aspen tortrix (*Choristoneura conflictana*) which defoliates *P. tremuloides*; however, we focus on SBW and FTC, both of which are held in the regional literature as the dominant defoliating insects in these forests, acknowledging that other sources of insect defoliation exist. Suspected insect outbreaks were tested by host-non-host analyses (Swetnam and Lynch, 1989) using the OUTBREAK program (Holmes and Swetnam, 1996).

OUTBREAK identifies departures between individual standardized ring-width series of a defoliator host and a standardized series of a non-host species (Holmes and Swetnam, 1996; Speer et al., 2001; Fraver et al., 2007). Departures between the series suggest periods of defoliation, assuming that both species respond similarly to climatic variation, that they do not share a common defoliator, and that neither have periods of overlapping defoliation

events (Bouchard et al., 2007; Fraver et al., 2007). For the purpose of this study, *Populus tremuloides* and *A. balsamea* served as hosts to detect past FTC and SBW events, respectively. Thus, either species served as a non-host in the detection of defoliation events of the other (host) species. Individual *A. balsamea* and *P. tremuloides* ring-width series were standardized in the ARSTAN program (Cook and Holmes, 1997) using a cubic smoothing spline with a 50% frequency response cutoff of 100 years (Speer et al., 2001; Fraver et al., 2007).

OUTBREAK provides users a set of parameters required to define a defoliation event, of which three were manipulated. In selecting appropriate parameter settings for FTC outbreaks, we followed Cooke and Roland (2007), whose work took place roughly 100 km northeast of the study area in Ontario, Canada. Thus, FTC outbreaks had to last at least two years and no more than six, and had to deviate by at least -1.14 standard deviations for at least one year within a period of departure. Other parameters were set to default value when detecting FTC outbreaks.

Given the paucity of studies using *A. balsamea* as a SBW host species (Rauchfuss et al., 2009), program parameters were calibrated to a known defoliation in stand B, where aerial surveys verified that an outbreak occurred between 1995 and 1999. The selected parameters satisfactorily minimized false positives and enhanced known years of defoliation. SBW outbreaks had to last a minimum of 4 years and no longer than 12 years. Growth declines during periods of defoliation had to achieve at least -1.7 standard deviations for one year, and in order to minimize false positives, the entire non-host *P. tremuloides* ring-width index was dampened by raising it to a power of 0.8 (an option within OUTBREAK). For the historical reconstruction of both FTC and SBW outbreaks, interpretation of defoliation events focused on years in which evidence of defoliation was detected in >10% of the host-tree populations.

3. Results

3.1. Composition and structure

P. tremuloides dominated overstory tree composition (35–84% basal area) followed by *A. balsamea* (8–44%) and, to a lesser extent, *A. rubrum* (0–20%), *P. glauca* (0–17%), *B. papyrifera* (0–16%) and *F. nigra* (0–14%, sites pooled; Table 1). Lesser species included *Populus balsamifera*, *Ulmus americana*, and *Tilia americana*. The median year of origin of the oldest *P. tremuloides* cohort served as an estimate for the year of stand initiation (presumably harvest) and ranged from 59 to 84 years with an overall median of 76 years (Table 1). Site indices ranged from 18.3 to 25.0 m (50 years) and stand basal area ranged from 21.0 to 35.8 m^2 ha^{-1}. Average stand density was 613 stems ha^{-1}, but ranged from 367 to 800 stems ha^{-1}. Within-site tree density, as well as seedling and sapling density, varied considerably due to recent canopy disturbance. Across all sites, tree seedling and sapling density averaged 10408 and 8930 stems ha^{-1}, respectively (Appendix B).

3.2. Tree recruitment and growth release

Tree recruitment, or the age at which trees attained sampling height ("Trees" = 30 cm; "Seedlings and saplings" = base of stem), occurred in multiple peaks over the nine decades of stand development. A mix of species dominated initial recruitment, mainly comprised of *P. tremuloides*, but also including *B. papyrifera*, *F. nigra* and *A. rubrum* (Figs. 2 and 3). Recruitment peaks followed at approximately 20, 30, 50, 60 and 75 years after stand initiation (Fig. 2). Following year 10, recruitment was dominated by a mix of species

Table 1
Compositional and physiographic characteristics for aspen mixedwood study sites in northern Minnesota, USA. Standard error for site index is presented in parentheses. Composition is based on the proportion of total stand basal area.

Characteristic	Study site								
	A	B	C	D	E	F	G	H	I
No. plots	6	6	6	3	6	6	6	4	6
Stand area (ha)	7	12	30	3	10	13	13	10	3
Stand age	75	59	72	79	81	84	83	76	68
Tree density (stems ha^{-1})	367	733	588	758	438	563	583	800	688
Site index	20.6 (0.3)	25 (0.7)	24.2 (1.6)	21.1 (0.6)	22.9 (0.6)	19.1 (0.3)	18.3 (0.4)	20.6 (0.6)	23.2 (0.8)
Mean POTR DBH (cm)	31.7	26	36.7	31.5	36.2	33.6	29.3	32.9	34.3
Basal area (m^2 ha^{-1})	23.7	26.3	27.0	35.8	21.0	27.3	22.6	29.2	28.4
Composition (% basal area)	POTR (84)	POTR (53)	POTR (51)	ABBA (44)	ABBA (38)	POTR (69)	POTR (66)	POTR (71)	POTR (49)
	ABBA (14)	ABBA (14)	BEPA (12)	POTR (39)	POTR (35)	ABBA (15)	ACRU (20)	ABBA (13)	ABBA (25)
	PIGL (1)	BEPA (14)	ACRU (11)	PIGL (17)	ACRU (18)	ACRU (9)	ABBA (8)	FRNI (10)	FRNI (14)
		ACRU (13)	ABBA (11)			BEPA (5)	PIGL (4)	OTHER (6)	BEPA (7)

ABBA = *Abies balsamea*; ACRU = *Acer rubrum*; BEPA = *Betula papyrifera*; FRNI = *Fraxinus nigra*; PIGL = *Picea glauca*; POTR = *Populus tremuloides*; OTHER = *Pinus strobus, Populus balsamifera, Tilia americana* and *Ulmus americana*.
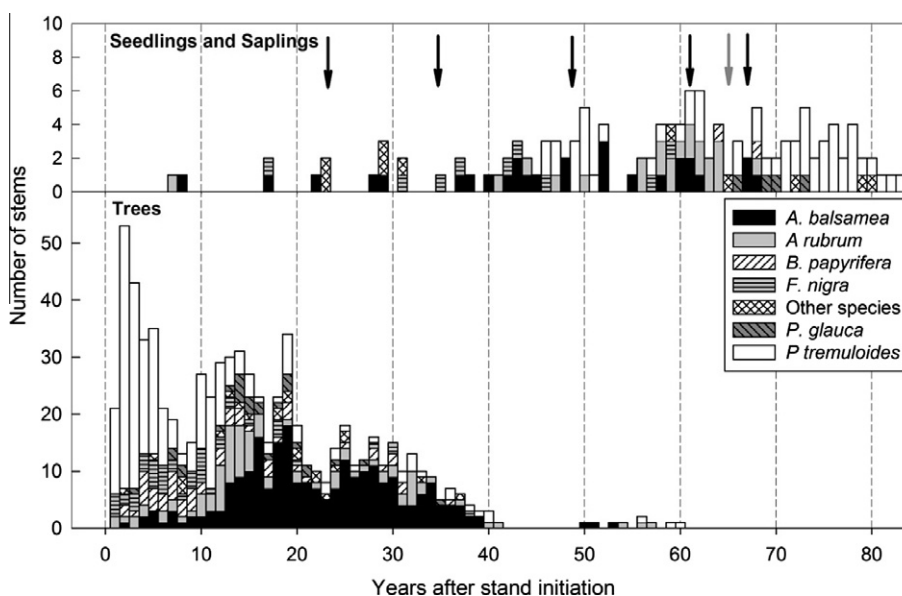

Fig. 2. Recruitment age, or age at sampling height ("Trees" = 30 cm; "Seedlings and saplings" = base of stem), for "Trees" (DBH > 10.0 cm) and "Seedlings and saplings" (DBH ⩽ 10.0 cm) harvested from recently formed gaps within aspen mixedwood systems in northern Minnesota, USA (sites pooled). The horizontal axes of both graphs are temporally scaled to stand initiation. Initial years of defoliation are included for forest tent caterpillar (black arrows) and eastern spruce budworm (gray arrow). 'Other species' include *Pinus strobus, Populus balsamifera, Tilia americana*, and *Ulmus americana*.

primarily composed of *A. balsamea* (year 10–50) and later by *P. tremuloides* (year 50+).

Overstory disturbance, documented as releases from suppression, often coincided with these recruitment periods (Figs. 2 and 3). However, distinct peaks in growth releases lagged behind peaks in recruitment by several years and were most pronounced at stand ages 30, 55, 65 and 75 years (Fig. 4). Early releases from suppression around stand age 30 occurred in a mix of species but were most prominent in shade tolerant species (Fig. 4). Ensuing peaks at 50, 65, and 75 years showed a gradual transition from releases of shade tolerants to gap recruitment of shade intolerants, mainly *P. tremuloides* (Fig. 4).

3.3. Disturbance rates and agents

The prominent initial cohort of the shade intolerant *P. tremuloides* evident at most sites (Fig. 3) suggests stand-initiating disturbance, presumably harvesting between 1924 and 1949. However, the presence of a low density of trees pre-dating *P. tremuloides* cohort establishment indicates less severe harvests at sites B, C, and I.

Excluding decades of stand initiation, mean decadal canopy disturbance rates for all nine sites combined was 6.5% (SD = 2.5; Table 2). Rates of disturbance, however, were highly variable and fluctuated through time, with several peaks synchronized among sites (Fig. 3). Notable peaks in percent canopy area disturbed occurred early in stand development, spanning the third and fourth decade following stand initiation, at sites B, C, D and E (Table 2 and Fig. 3). The majority of sites displayed below-average rates of disturbance during the fifth, sixth, and seventh decades of stand development. Study-wide average rates of disturbance increased substantially from 1.1% at stand age 50–60 to 2.8%, 5.4%, and 9.8% for stand age 60–70, 70–80 and 80+, respectively (Table 2 and Fig. 3). Disturbance peaks were noted again in later decades at all sites. The proportion of canopy opened by recent gaps (see Section 2.4) ranged from 5.5% to 17.8% and included several gaps that had originated more than 20 years ago (sites B, C, E, and I) in which dense shrub layers of *A. spicatum* and *C. cornuta* precluded tree regeneration and/or recruitment (Appendix B).

Host-non-host analyses revealed distinct periods of FTC defoliation that were largely corroborated by published literature and aerial surveys (Fig. 5). The most pronounced and earliest event,
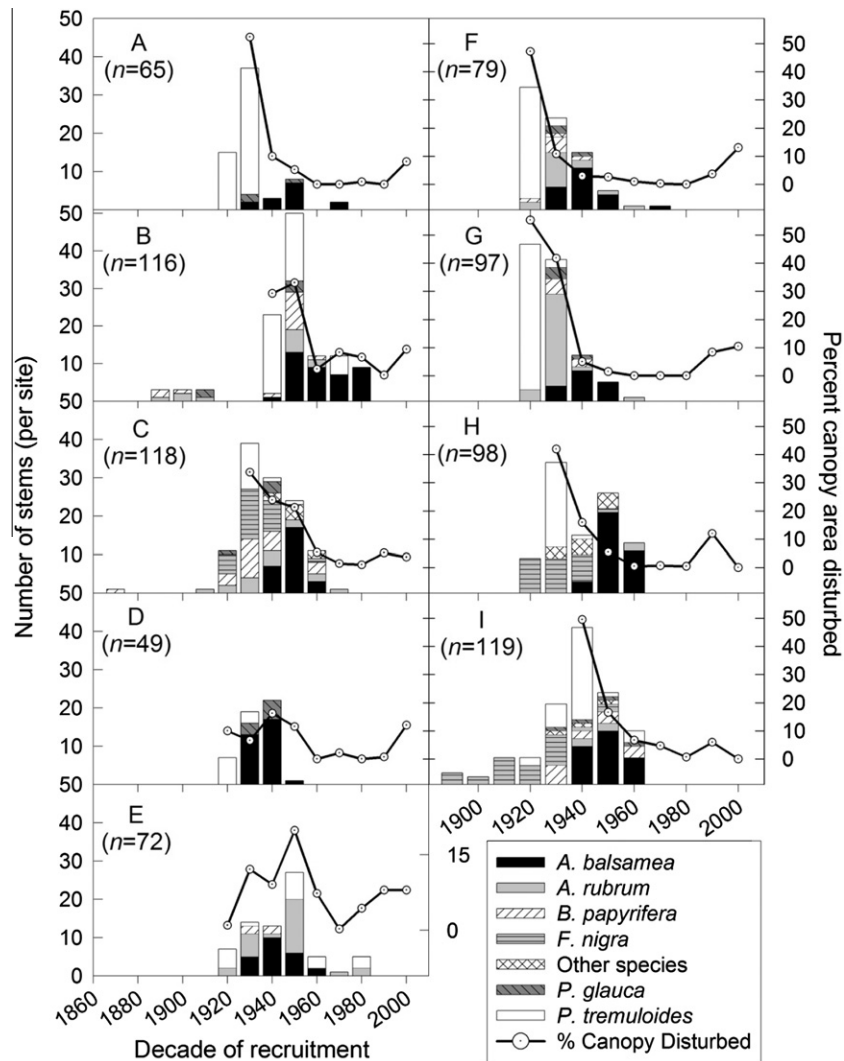
Fig. 3. Decade of tree recruitment, by species, for each of the nine aspen mixedwood study sites (A–I). 'Other species' includes *Pinus strobus*, *Populus balsamifera*, *Tilia americana*, and *Ulmus americana*. The right-hand vertical axis represents the percent canopy area disturbed per decade, plotted with a straight line. Sample size (*n*) refers to the number of trees. Percent canopy area disturbed is presented beginning with the decade of stand initiation, determined to be the decade including the median year of recruitment for the oldest *P. tremuloides* cohort (see Table 1).

confirmed by Churchill et al. (1964) and Witter (1979) spanned 1951–1959 and varied in length from 2 years at sites B and H to 8 years at site E (Fig. 5). Sites D, E, F and G registered significant defoliation during this period, which began an average of 23 ± 2 years after stand initiation (Fig. 5). Initial defoliation coincided with pronounced peaks in recruitment (Fig. 2) and release from suppression at approximately stand age 30 (Figs. 3 and 4).

Examination of the ring-width indices revealed a severe compound defoliation at sites D and E that occurred for 6 and 8 consecutive years, respectively. This event was the longest and most severe FTC defoliation documented across sites and began an average of 23 ± 2 years after stand initiation (Fig. 5). The initial outbreak peaked in 1952, and before the trees completely recovered, a second outbreak occurred in 1957. Unlike the majority of sites, D and E lack a pronounced initial peak in disturbance and recruitment; instead, a second disturbance and recruitment peak occurred 20–40 years after stand initiation (Fig. 3). The second defoliation in site E during the 1950s appears to have fostered recruitment of a second cohort of *P. tremuloides*, *A. balsamea* and *A. rubrum* (Fig. 3).

Following the FTC outbreak of the 1950s, several sites shared defoliation events in the late 1960s, late 1970s, late 1980s and early 1990s (Fig. 5), including a documented FTC defoliation that peaked regionally from 1964 to 1972 (Witter, 1979). Major FTC defoliation was observed at most sites, with the exception of D, F, and I, from roughly 1989 to 1995. This event was moderate in severity; a maximum of 70% of *P. tremuloides* trees showed defoliation (Fig. 5). Average stand age at the onset of this event was 61 ± 3 years for defoliated sites (Fig. 5). This defoliation corresponded to increases in recruitment (Fig. 2), releases from suppression (Fig. 4), and corresponding increases in canopy disturbance (Fig. 3). The most recent FTC defoliation spanned 2000–2006. Defoliation severity was highly variable, with some sites appearing unaffected and others showing dramatic growth reductions (Fig. 5). The average age of defoliated sites at the onset of this defoliation was 67 ± 5 years (Fig. 5). This defoliation corresponded to increases in recruitment and releases for *A. balsamea*, *P. tremuloides*, *B. papyrifera*, *A. rubrum* and *F. nigra* (Figs. 2 and 4).

SBW defoliation began immediately after the 1989–1995 FTC outbreaks, and lasted from roughly 5 years at all sites except H (Fig. 6). This event was severe; at sites A, B, C, F, and G, defoliation occurred in 67–100% of host trees for 4–6 years. At the onset of this SBW defoliation, affected stands had a mean age of 65 years (Fig. 6). Prolonged, severe defoliation combined with two severe windstorms in the region (1995 and 1999, documented by MN DNR aerial surveys) accelerated gap formation and increased
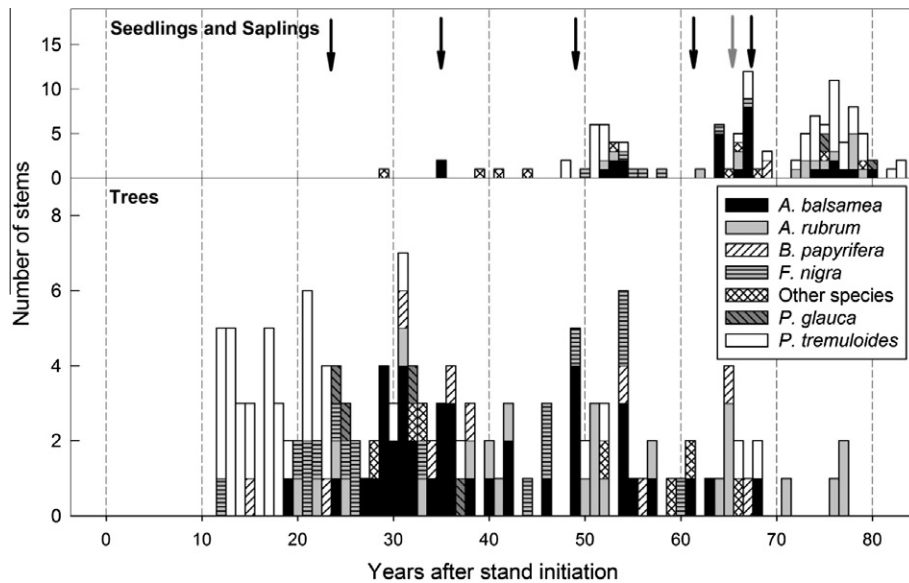
Fig. 4. Age at release from suppression or gap-recruitment within aspen mixedwood systems (sites pooled). "Trees" include only release events from stems with DBH >10.0 cm from the main sample plots. "Seedlings and saplings" include both growth-release and gap-recruitment events for stems with DBH ⩽10.0 cm harvested from recently formed gaps. The horizontal axes of both graphs are temporally scaled to stand initiation. Initial years of defoliation are included for forest tent caterpillar (black arrows) and eastern spruce budworm (gray arrow). 'Other species' include *Pinus strobus*, *Populus balsamifera*, *Tilia americana*, and *Ulmus americana*.

Table 2
Disturbance chronology expressed as cumulative percent canopy area disturbed per decade of stand development for aspen mixedwood sites in northern Minnesota, USA. Stand initiation year is approximated as the median calendar year of recruitment for the oldest *Populus tremuloides* cohort. Mean decadal disturbance rate was calculated excluding the stand initiating decade.

Sites	Stand initiation year	Percent canopy area disturbed per decade of stand development									
		0–10	10–20	20–30	30–40	40–50	50–60	60–70	70–80	80+	Mean
A	1933	52.3	10.0	5.2	0.0	0.0	0.9	0.0	8.0	–	3.4
B	1949	29.2	33.1	2.3	8.3	6.6	0.2	9.4	–	–	10.0
C	1936	33.7	23.8	21.2	5.3	1.4	1.0	5.2	3.1	–	8.7
D	1929	10.0	6.6	16.2	11.5	0.6	2.1	0.0	0.7	12.0	5.4
E	1927	1.0	12.1	9.1	19.8	7.3	0.3	4.4	8.0	8.0	8.7
F	1924	47.2	10.8	2.9	2.6	1.0	0.3	1.6	8.0	8.7	3.9
G	1925	55.3	41.8	5.0	1.5	0.0	0.0	0.0	8.4	10.4	8.1
H	1932	41.9	15.8	5.4	0.5	0.7	0.4	4.5	1.4	–	4.1
I	1940	49.5	16.5	6.7	4.7	1.5	5.1	0.0	–	–	5.8
	Mean	35.6	18.9	8.2	6.0	2.1	1.1	2.8	5.4	9.8	6.5
	Std. dev.	19.1	11.8	6.4	6.4	2.8	1.6	3.3	3.5	1.8	2.5

recruitment and/or release of *P. tremuloides*, *A. balsamea* and *A. rubrum* after stand age 70 (Figs. 2–4).

4. Discussion

The role of insect defoliators in affecting forest community development is widely recognized (e.g., Muzika and Liebhold, 1999); however, the importance of multiple defoliation events on long-term forest successional and structural development has received little attention. This study links reconstructed defoliation histories with long-term community dynamics, documenting that these defoliations gave rise to multi-cohort aspen stands. This finding highlights the critical roles these events play in structuring aspen mixedwood systems, particularly within the early stages of stand development. Moreover, the multi-cohort aspen populations we documented support the growing body of literature that suggests the range of variability in aspen age structures extends beyond the even-aged model that has guided forest management in the region. Collectively, these findings have important implications for the design of forest management regimes that approximate this range in age structures and emulate defoliation disturbances with early harvest entries.

4.1. Stand developmental patterns in aspen mixedwoods

Here we examine the nature and impact of canopy disturbance on species abundance through the course of stand development, including details of individual species performance, within aspen mixedwoods. We borrow from Oliver and Larson (1996) and Frelich (2002) in defining stand developmental stages and include the stages of *stand initiation*, *stem exclusion* and *demographic transition*.

4.1.1. Stand initiation, years 0–10

Several lines of evidence support the contention that these stands originated following stand replacing disturbances, likely clearcutting. First, the oldest and most abundant trees sampled were cohorts of shade intolerant *P. tremuloides*, and very few trees (2% of all sampled trees) predated these cohorts. Second, initial cohorts became established during an active period of forest harvesting that gave rise to *P. tremuloides* forests region-wide (Friedman and Reich, 2005). Although the evidence for stand initiating disturbance could be interpreted as representing a heavy partial harvest, the complete record of initiating disturbance has undoubtedly been eroded due to mortality events within the original even-aged
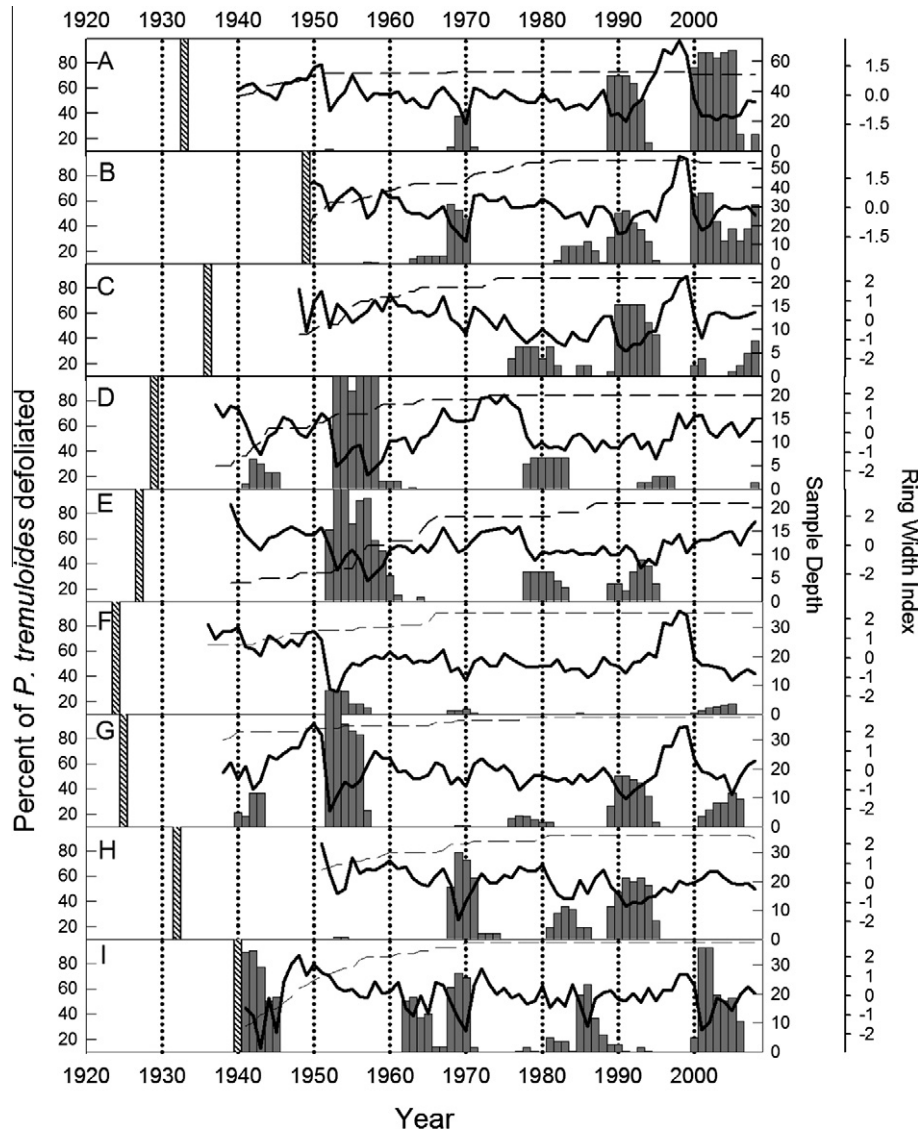
Fig. 5. Forest tent caterpillar host-non-host results presented as the proportion of *Populus tremuloides* trees showing evidence of defoliation (gray bars). The first vertical axis representing percent of host-trees defoliated ranges from 10% to 100%. Sample depth (dashed line) and ring width index (solid line) are presented on the second and third vertical axes, respectively. Year of stand initiation, calculated as median recruitment year of the oldest *P. tremuloides* cohort is shown as hatched bars.

cohort of shade intolerants (Lorimer and Frelich, 1989). Thus, it seem reasonable to assume that these stands became established following harvesting, likely clearcuts, in the early part of the 20th century.

An examination of early recruitment patterns overlaid by deca-dal canopy disturbance rates (Fig. 3) highlight the relationship be-tween severe initiating disturbances and the recruitment of predominantly *P. tremuloides*, *A. rubrum* and *B. papyrifera*, but also *F. nigra*, *A. balsamea* and *P. glauca*. Pre-harvest advance regeneration likely contributed to the diversity of the post-disturbance cohort, and the initial presence of such advance regeneration may have been underestimated because many were likely seedlings less than 30 cm in height at the time of harvest. Legacy trees (i.e., mature trees surviving from the pre-disturbance community; Franklin et al., 2000) though present in low numbers, no doubt increased initial tree diversity within sites B, C, and I (Ilisson and Chen, 2009). This increase was most apparent in site B, where pre-disturbance composition clearly influenced composition of the initial cohort (Fig. 3), thus highlighting the role these surviving trees play in contributing to post-disturbance structure and tree species diversity in these systems.

4.1.2. Stem exclusion, years 10–40

Continuous recruitment of primarily shade tolerant species, including *A. balsamea* and *A. rubrum*, persisted for the first 40 years of stand development and peaked at stand ages 20 and 30 as documented in other studies of sub-boreal mixedwoods (Fig. 2; Peters et al., 2006). We attribute these patterns to both species' differential shade tolerances and a gradual increase in understory resources due to self-thinning of the *P. tremuloides* overstory (Bergeron, 2000). While other research has alluded to the potential for FTC defoliation to slow stand development during stem exclusion by diminishing growth of species such as *P. tremuloides* (Chen and Popadiouk, 2002), we propose that the occurrence of prolonged defoliation between stand age 20 and 30 can increase *P. tremuloides* mortality, thereby accelerating stand development.

As evidence, prolonged FTC defoliation of *P. tremuloides* during this stage caused dramatic growth responses of non-host species (both releases and gap recruitments), most noticeable at stand age 30 (Figs. 4 and 5). Increased mortality of less vigorous *P. tremu-loides* stems during this stage would accelerate stand development by increasing growing space and light within the understory (Lieffers et al., 1999), facilitating recruitment and canopy ascension
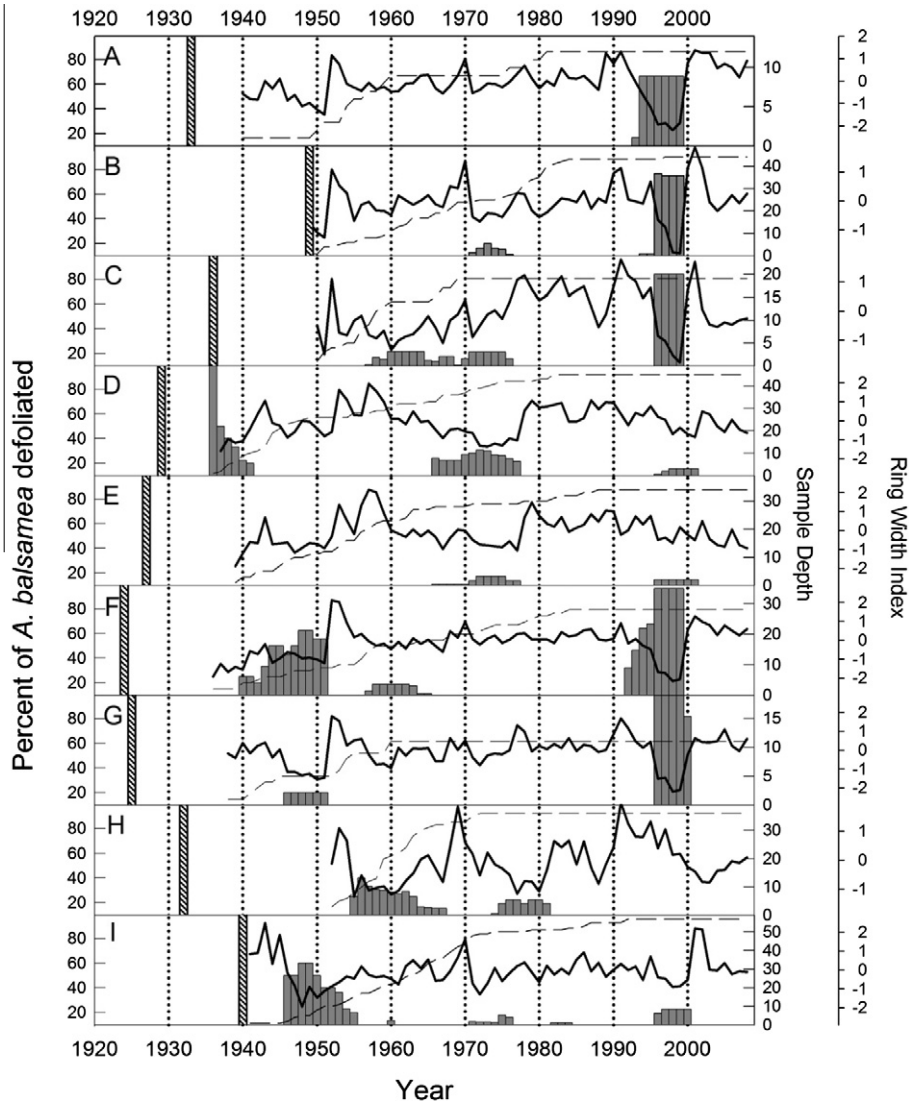
Fig. 6. Eastern spruce budworm host-non-host results presented as the proportion of *Abies balsamea* trees showing signs of defoliation (gray bars). The first vertical axis representing percent of host-trees defoliated ranges from 10% to 100%. Sample depth (dashed line) and ring width index (solid line) are presented on the second and third vertical axes, respectively. Year of stand initiation, calculated as median recruitment year of oldest *Populus tremuloides* cohort, is shown as hatched bars.

of understory stems of shade-tolerant and intolerant species. Similar growth responses were documented in bigtooth aspen (*Populus grandidentata*) forests in northern Lower Michigan (Palik and Pregitzer, 1993), and though the causal agents of such growth increases were unclear, they were generally attributed to density-dependent waves of mortality. Such patterns of natural thinning are known to occur in even-aged stands (Oliver and Larson, 1996), including those dominated by the *Populus* genus (Graham et al., 1963), but the causal agents are often difficult to disentangle. Here, we propose that insect-induced mortality could be responsible for a portion of the compositional and structural variation documented within stem-exclusion aspen mixedwoods.

Past studies have documented multi-cohort age structures for aging aspen mixedwoods (Bergeron, 2000; Cumming et al., 2000; Man and Rice, 2010) and have suggested the potential for significant insect influence in young developing mixedwoods (Frey et al., 2003). However, to our knowledge, ours is the first documented linkage between FTC-induced canopy disturbance and species recruitment during this early developmental stage. Defoliation, tree recruitment, and growth releases showed striking synchronicity among sites D, E, and G, which lie within 100 km of each other (Fig. 1), and corresponded closely to the 1950s FTC

outbreak (Table 2 and Figs. 3 and 5) – one of the most widespread and severe FTC outbreaks of the last century (Churchill et al., 1964; Witter, 1979; Cooke and Lorenzetti, 2006; Cooke and Roland, 2007). Sites D, E, and G experienced severe and prolonged defoliation during this outbreak, which lasted 2–8 years (Fig. 5). Other work has demonstrated that periods of FTC defoliation lasting three or more consecutive years leads to elevated rates of tree mortality in *P. tremuloides* (Duncan and Hodson, 1958; Churchill et al., 1964; Man and Rice, 2010). Though FTC larvae will feed on understory deciduous species during severe outbreaks such as these, intolerant recruitment could be possible during and following severe events because on average only one third of the healthy larvae will translocate from canopy *P. tremuloides* to the understory stratum – where FTC feeding can take place on a number of woody species including *P. tremuloides, C. cornuta, Alnus rugosa, Prunus* spp., and *Salix* spp. (Batzer et al., 1995).

Understory *A. balsamea* showed a clear period of radial growth increase during this early *P. tremuloides* defoliation (Figs. 5 and 6; Duncan and Hodson, 1958; Bergeron, 2000; Bergeron et al., 2002), but it is important to distinguish between short-duration growth increases due to overstory defoliation and sustained increases due to overstory mortality. The stringent release criteria

employed here eliminated the potential 'false positive' releases arising from short-duration growth increases. Thus, prolonged FTC defoliation and enhanced mortality of less vigorous *P. tremuloides* – even in this early stem exclusion stage – are a plausible mechanism that accelerate stand development and contribute to the current varied composition and multi-cohort age structure of these sites.

4.1.3. Demographic transition, years 40–84

Current canopy gaps were largely due to the mortality of older *P. tremuloides* and *A. balsamea* (Figs. 2 and 4). While mortality may be attributed to a variety of factors (e.g., windthrow, fungal infection, climatic stress), the most notable stressor included three nearly consecutive defoliations (FTC, SBW and again FTC) at stand age 61, 65 and 67 that promoted sub-canopy growth responses of not only shade tolerant species (*A. balsamea* and *A. rubrum*), but also intolerant species (*P. tremuloides* and *B. papyrifera*; Figs. 2 and 4). Ghent (1958) documented similar canopy break-up following a comparable defoliation complex in western Ontario and noted increases in the abundance of the understory shrub *A. spicatum* and subsequent decreases in understory tree recruitment following overstory mortality. Similarly, we documented the establishment of dense, recalcitrant *C. cornuta* and *A. spicatum* shrub layers in several sites (e.g., C, E, and I) that occasionally inhibited regeneration. In contrast, increased windfall of recently dead *P. tremuloides* and *A. balsamea* (and the presence of ample advance regeneration) apparently facilitated disruption of the shrub layer and growth of understory trees at sites A and B (Reinikainen *pers. obs.*; Appendix B).

Study-wide, the most recent cohort established during this period was dominated by *P. tremuloides, A. balsamea* and *A. rubrum*, whose median heights (4.0, 4.2, and 3.9 m, respectively; Appendix C) often exceeded those achieved by the dense shrub layer of *C. cornuta* and *A. spicatum* occupying gaps. Over the next few decades, it is likely that continued senescence of the initial *P. tremuloides* cohort will partially open the canopy, leading to recruitment of shade tolerant softwoods and hardwoods, as well as sucker-origin *P. tremuloides* (Cumming et al., 2000; Man and Rice, 2010). These findings align with work demonstrating that aging aspen mixedwoods experience more frequent formation of large gaps (Kneeshaw and Bergeron, 1998), and that such gaps (in excess of 200 m^2) can be large enough to support a contingent of both shade tolerants and intolerants (Groot et al., 2009).

4.2. Disturbance and multi-cohort mixedwoods

Observed decadal disturbance rates were highly variable (Mean = 6.5%, SD = 2.5%; Table 2). Annual rates (0.3–1.0%) were comparable to the global range for boreal forests (McCarthy, 2001). However, these means have little explanatory value relative to the highly variable temporal fluctuations in disturbance, which appear to explain the compositional development of these relatively young forests.

Results clearly show multiple cohorts of *P. tremuloides, A. balsamea*, and associated species. Similar findings have not been reported regionally, where this forest type has substantial commercial and ecological importance. Furthermore, these results are contrary to the current model for aspen mixedwood management that assumes *P. tremuloides* exists as single-cohort populations; however, multi-cohort stands have also been reported for aspen mixedwoods in several Canadian provinces (Bergeron, 2000; Cumming et al., 2000; Man and Rice, 2010).

Prolonged FTC outbreaks, particularly during the 1950s, likely increased *P. tremuloides* mortality and led to additional recruitment of this and other species. Although a clear mechanism for prolonged defoliation events is unknown, Roland (1993) clearly demonstrated the propensity of a highly fragmented landscape in Ontario to experience prolonged FTC defoliation. In such landscapes, increased rates of FTC larval development occur along forest edges due to a loss of connectivity among parasitoid populations, increased insolation and temperature along edges, and the ability of FTC to quickly saturate the demand of predator populations under such conditions (Roland, 1993). Though not quantified in the present study, the landscape studied here is highly fragmented by natural, glacial-shaped features, as well as land use.

Given the opportunistic and shade tolerant nature of *A. balsamea* and *A. rubrum* (Fowells, 1965) and the prolific sprouting ability of *P. tremuloides*, the presence of multiple cohorts of intolerants and tolerants should not be surprising. While the increased presence of *P. tremuloides* root suckers in the understory after stand age 70 is partially a physiological response to the declining *P. tremuloides* overstory, recruitment and releases events earlier in stand development suggest that this species will remain a component of the canopy (Figs. 2 and 4). Diffuse canopies, increased gap formation, expansion of current canopy gaps and the nutrient subsidy provided by the declining parent stem will ensure the presence of *P. tremuloides* in older aspen mixedwoods (Bergeron, 2000; Cumming et al., 2000; Man and Rice, 2010), although perhaps in lower abundance relative to early stand developmental stages.

4.3. Conclusions and management implications

Our findings suggest that the compositional and structural development of secondary, mature aspen mixedwoods of northern Minnesota is influenced by gap-dynamics resulting from insect-induced tree mortality. Interestingly, we identified the presence of multiple cohorts of *P. tremuloides*, as well as *A. balsamea*. These age structures and the general composition of these systems were driven by the processes of recruitment and release due to defoliation and overstory mortality, particularly during the prolonged defoliation of aspen by forest tent caterpillar within the early stages of stand development.

The age structures and developmental patterns documented here have important implications for the conservation and management of aspen mixedwood systems in the region because this forest type is both prevalent and economically important. Current management approaches rely heavily on even-aged regeneration methods using relatively short rotations (40–60 years); however, our findings highlight that multi-cohort systems based on large canopy gaps (>200 m^2) may serve as an alternative approach in cases where approximating long-term developmental dynamics is an objective. In addition, the linkages we documented between tree species recruitment and early canopy disturbance (ages 20–30 years) indicate that efforts to restore and enhance the abundance of species historically important in these forests, including *P. glauca, Pinus strobus*, and *Thuja occidentalis* (Schulte et al., 2007), should be targeted at young stands to emulate this critical, and previously undocumented early recruitment window.

Appendix A. Inter-correlation values for measured tree ring series from the crossdating validation program COFECHA for nine aspen mixedwood sites in northern Minnesota, USA. All major species with adequate sample sizes are displayed except for *Betula papyrifera*, a difficult species to cross-date.

Sites	Abies balsamea	Acer rubrum	Fraxinus nigra	Populus tremuloides
A	0.55	–	–	0.73
B	0.51	0.40	–	0.61
C	0.51	0.40	0.53	0.73
D	0.46	–	–	0.69
E	0.48	0.47	–	0.63
F	0.58	0.47	0.37	0.63
G	0.64	0.54	–	0.67
H	0.54	–	0.57	0.50
I	0.54	0.41	0.53	0.59

Appendix B. Regeneration density (stems ha^{-1}) for seedlings (<0.5 m height), and saplings (>0.5 m height and <1.0 cm DBH) from nine aspen mixedwood sites in northern Minnesota, USA. 'Shrubs' includes non-tree, woody species of the genera *Acer*, *Cornus*, *Corylus, Lonicera, Rosa, Rubus, Salix*, and *Viburnum*.

Site	Abies balsamea	Acer rubrum	Betula papyrifera	Picea glauca	Populus tremuloides	Fraxinus nigra	Shrubs	Total
Seedlings								
A	1612	1000	313	1250	647	0	1033	5855
B	1667	9215	1000	1750	577	1827	1462	17498
C	938	1250	1250	625	625	2679	1949	9316
D	5000	2083	0	1250	329	0	1842	10504
E	1667	4714	0	0	391	0	1104	7876
F	1250	8315	833	625	286	917	1346	13572
G	1111	8049	0	0	223	625	1779	11787
H	3375	1250	0	625	764	5234	1529	12777
I	2500	5893	1250	750	952	5183	2191	18719
Saplings								
A	6480	500	938	417	1552	0	7750	17637
B	458	1366	500	0	2340	962	3750	10626
C	0	0	0	625	1563	2173	3879	8240
D	0	208	0	0	6118	0	1645	7971
E	0	2321	1875	0	4727	2500	5399	16822
F	1094	3696	5417	0	4607	3167	3678	21659
G	694	1433	1250	1250	2321	1250	3418	11616
H	500	0	1250	625	5347	4961	2441	15124
I	37	286	0	250	1845	213	3316	5947

Appendix C. Mean, maximum, and standard deviation (SD) of height (m) and DBH (cm) for gap-recruited seedlings and saplings (DBH <10.0 cm) used to date recently formed gaps in nine aspen mixedwood sites in northern Minnesota, USA.

Species	Height (m)			DBH (cm)		
	Mean	Maximum	SD	Mean	Maximum	SD
Abies balsamea	4.1	8.6	2	4.1	10.0	2.7
Acer rubrum	5	10.3	2.7	3	7.5	2
Betula papyrifera	5.2	5.3	0.1	4.2	5	1.2
Fraxinus nigra	5.1	10.7	2.5	3.2	8.7	2.3
Picea glauca	1.5	1.7	0.1	0.5	0.5	0
Populus balsamifera	3.8	11.3	3.1	2.1	7.4	2.3
Populus tremuloides	4.1	10.6	2.1	2.4	6.7	1.7

References

Albert, D.A., 1995. Regional landscape ecosystems of Michigan, Minnesota, and Wisconsin: a working map and classification. In, General Technical Report NC178. USDA Forest Service North Central Forest Experiment Station, St. Paul, MN, p. 250.

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

Batzer, H.O., Martin, M.P., Mattson, W.J., Miller, W.E., 1995. The forest tent caterpillar in aspen stands – distribution and density-estimation of 4 life stages in 4 vegetation strata. Forest Science 41, 99–121.

Bergeron, Y., 2000. Species and stand dynamics in the mixed woods of Quebec's southern boreal forest. Ecology 81, 1500–1516.

Bergeron, Y., Denneler, B., Charron, D., Girardin, M., 2002. Using dendrochronology to reconstruct disturbance and forest dynamics around Lake Duparquet, northwestern Quebec. Dendrochronologia 20, 175–189.

Bouchard, M., Kneeshaw, D., Messier, C., 2007. Forest dynamics following spruce budworm outbreaks in the northern and southern mixedwoods of central Quebec. Canadian Journal of Forest Research 37, 763–772.

Chen, H.Y., Popadiouk, R.V., 2002. Dynamics of North American boreal mixedwoods. Environmental Reviews 10, 137–166.

Churchill, G.B., John, H.H., Duncan, D.P., Hodson, A.C., 1964. Long-term effects of defoliation of aspen by the forest tent caterpillar. Ecology 45, 630–636.

Cook, E.R., Holmes, R.L., 1997. ARSTAN: chronology development. The International Tree, Ring Data Bank Program.

Cooke, B.J., Lorenzetti, F., 2006. The dynamics of forest tent caterpillar outbreaks in Quebec, Canada. Forest Ecology and Management 226, 110–121.

Cooke, B.J., Roland, J., 2007. Trembling aspen responses to drought and defoliation by forest tent caterpillar and reconstruction of recent outbreaks in Ontario. Canadian Journal of Forest Research 37, 1586–1598.

Cumming, S.G., Schmiegelow, F.K.A., Burton, P.J., 2000. Gap dynamics in boreal aspen stands: is the forest older than we think? Ecological Applications 10, 744–759.

D'Amato, A.W., Orwig, D.A., 2008. Stand and landscape-level disturbance dynamics in old-growth forests in western Massachusetts. Ecological Monographs 78, 507–522.

Duncan, D.P., Hodson, A.C., 1958. Influence of the forest tent caterpillar upon the aspen forests of Minnesota. Forest Science 4, 71–93.

Edgar, C.B., Burk, T.E., 2001. Productivity of aspen forests in northeastern Minnesota, USA, as related to stand composition and canopy structure. Canadian Journal of Forest Research 31, 1019–1029.

Engstrom, T., Gilbert, S., Hunter, M.L., Merriweather, D., Nowicki, G.J., Spencer, P., 1999. Practical applications of disturbance ecology to natural resource management. In: Szaro, R.C., Johnson, N.C., Sexton, W.T., Malk, A.J. (Eds.), Ecological stewardship: a common reference for ecosystem management. Elsevier Science Ltd, Oxford, UK.

Fowells, H.A., 1965. Silvics of forest trees of the United States. US Dept. of Agriculture, Forest Service, Washington, DC.

Franklin, J.F., Lindenmayer, D., MacMahon, J.A., McKee, A., Magnuson, J., Perry, D.A., Waide, R., Foster, D., 2000. Threads of continuity. Conservation in Practice 1, 8–17.

Fraver, S., 1994. Vegetation responses along edge-to-interior gradients in the mixed hardwood forests of the Roanoke River Basin, North Carolina. Conservation Biology 8, 822–832.

Fraver, S., Seymour, R.S., Speer, J.H., White, A.S., 2007. Dendrochronological reconstruction of spruce budworm outbreaks in northern Maine, USA. Canadian Journal of Forest Research 37, 523–529.

Fraver, S., White, A.S., 2005a. Disturbance dynamics of old-growth *Picea rubens* forests of northern Maine. Journal of Vegetation Science 16, 597–610.

Fraver, S., White, A.S., 2005b. Identifying growth releases in dendrochronological studies of forest disturbance. Canadian Journal of Forest Research 35, 1648–1656.

Frelich, L.E., 1995. Old forest in the Lake States today and before European settlement. Natural Areas Journal 15, 157–167.

Frelich, L.E., 2002. Disturbance regimes and forest dynamics. Cambridge University Press, Cambridge, England.

Frey, B.R., Lieffers, V.J., Landhausser, S.M., Comeau, P.G., Greenway, K.J., 2003. An analysis of sucker regeneration of trembling aspen. Canadian Journal of Forest Research 33, 1169–1179.

Friedman, S.K., Reich, P.B., 2005. Regional legacies of logging: departure from presettlement forest conditions in northern Minnesota. Ecological Applications 15, 726–744.

Ghent, A.W., 1958. Mortality of overstory trembling aspen in relation to outbreaks of the forest tent caterpillar and the spruce budworm. Ecology 39, 222–232.

Graham, S.A., Harrison Jr., R.P., Westell Jr., C.E., 1963. Aspens: Phoenix Trees of the Great Lakes Region. The University of Michigan Press, Ann Arbor, Michigan, USA.

Groot, A., Man, R., Wood, J., 2009. Spatial and temporal patterns of *Populus tremuloides* regeneration in small forest openings in northern Ontario. Forestry Chronicle 85, 548–557.

Heinselman, M.L., 1996. The Boundary Waters Wilderness Ecosystem. University of Minnesota Press, Minneapolis.

Henry, J.D., Swan, J.M., 1974. Reconstructing forest history from live and dead plant material – an approach to the study of forest succession in southwest New Hampshire. Ecology 55, 772–783.

Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurements. Tree-Ring Bull 44, 69–75.

Holmes, R.L., Swetnam, T.W., 1996. Program OUTBREAK Users Manual. In. Laboratory of Tree-Ring Research. University of Arizona, Tucson, AZ.

Ilisson, T., Chen, H.Y.H., 2009. Response of six boreal tree species to stand replacing fire and clearcutting. Ecosystems 12, 820–829.

Kneeshaw, D.D., Bergeron, Y., 1998. Canopy gap characteristics and tree replacement in the southeastern boreal forest. Ecology 79, 783–794.

Lieffers, V.J., Messier, C., Stadt, K.J., Gendron, F., Comeau, P.G., 1999. Predicting and managing light in the understory of boreal forests. Canadian Journal of Forest Research 29, 796–811.

Lorimer, C.G., 1985. Methodological considerations in the analysis of forest disturbance history. Canadian Journal of Forest Research 15, 200–213.

Lorimer, C.G., Frelich, L.E., 1989. A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. Canadian Journal of Forest Research 19, 651–663.

Man, R.Z., Rice, J.A., 2010. Response of aspen stands to forest tent caterpillar defoliation and subsequent overstory mortality in northeastern Ontario, Canada. Forest Ecology and Management 260, 1853–1860.

McCarthy, J., 2001. Gap dynamics of forest trees: a review with particular attention to boreal forests. Environmental Review 9, 1–59.

MNDNR, 2003. Field guide to the native plant communities of Minnesota: the Laurentian Mixed Forest Province. Ecological Land Classification Program, Minnesota County Biological Survey, and Natural Heritage and Nongame Research Program. MNDNR, St. Paul, MN.

Muzika, R.M., Liebhold, A.M., 1999. Changes in radial increment of host and nonhost tree species with gypsy moth defoliation. Canadian Journal of Forest Research 29, 1365–1373.

Oliver, C.D., Larson, B.C., 1996. Forest stand dynamics, update edition. John Wiley, New York.

Oliver, C.D., Stephens, E.P., 1977. Reconstruction of a mixed-species forest in central New-England. Ecology 58, 562–572.

Palik, B.J., Pregitzer, K.S., 1993. The repeatability of stem exclusion during even-aged development of bigtooth aspen dominated forests. Canadian Journal of Forest Research 23, 1156–1168.

Perala, D.A., 1977. Manager's handbook for aspen in the north central states. In: General Technical Report NC-36. North Central Forest Experiment Station, Forest Service. US Department of Agriculture, St. Paul, MN, USA, pp. 1–36.

Peters, V.S., Macdonald, S.E., Dale, M.R.T., 2006. Patterns of initial versus delayed regeneration of white spruce in boreal mixedwood succession. Canadian Journal of Forest Research 36, 1597–1609.

Rauchfuss, J., Ziegler, S.S., Speer, J.H., Siegert, N.W., 2009. Dendroecological analysis of spruce budworm outbreaks and their relation to climate near the prairie-forest border in northwestern Minnesota. Physical Geography 30, 185–204.

Roland, J., 1993. Large-scale forest fragmentation increases the duration of tent caterpillar outbreak. Oecologia 93, 25–30.

Schulte, L.A., Mladenoff, D.J., Crow, T.R., Merrick, L.C., Cleland, D.T., 2007. Homogenization of northern US Great Lakes forests due to land use. Landscape Ecology 22, 1089–1103.

Speer, J.H., Swetnam, T.W., Wickman, B.E., Youngblood, A., 2001. Changes in pandora moth outbreak dynamics during the past 622 years. Ecology 82, 679–697.

Spies, T.A., Franklin, J.F., Klopsch, M., 1990. Canopy gaps in douglas-fir forests of the Cascade Mountains. Canadian Journal of Forest Research 20, 649–658.

Stokes, M.A., Smiley, T.L., 1968. An Introduction to Tree-Ring Dating. The University of Chicago Press, Chicago and London.

Sturtevant, B.R., Gustafson, E.J., Li, W., He, H.S., 2004. Modeling biological disturbances in LANDIS: a module description and demonstration using spruce budworm. Ecological Modelling 180, 153–174.

Swetnam, T.W., Lynch, A.M., 1989. A tree-ring reconstruction of western spruce budworm history in the southern Rocky Mountains. Forest Science 35, 962–986.

White, P.S., Walker, J.L., 1997. Approximating nature's variation: selecting and using reference information in restoration ecology. Restoration Ecology 5, 338–349.

Witter, J.A., 1979. The forest tent caterpillar (Lepidoptera: Lasiocampidae) in Minnesota: a case history review. The Great Lakes Entomologist 12, 191–197.

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

Ziegler, S.S., 2002. Disturbance regimes of hemlock-dominated old-growth forests in northern New York, USA. Canadian Journal of Forest Research 32, 2106–2115.