A 300-Year History of Disturbance and Canopy Recruitment for Co-Occurring White Pine and Hemlock on the Allegheny Plateau, USA

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A 300-year history of disturbance and canopy recruitment for co-occurring white pine and hemlock on the Allegheny Plateau, USA

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Summary

1 Dendroecological techniques were used to examine the patterns of canopy recruitment in relation to disturbance history for two dominant, yet ecologically contrasting, tree species, *Pinus strobus* (white pine; disturbance dependent) and *Tsuga canadensis* (hemlock; late successional), in a 300–year-old primary forest.
2 Most tree recruitment in both species occurred between 1690 and 1810. All of the white pine, which dominated recruitment during the first 40 years due to more rapid height growth, recruited in this period. Low levels of hemlock recruitment continued until 1900. Most of the younger trees comprised several northern hardwood species. No trees were less than 50 years old and the forest was devoid of an understorey due to intense deer browsing.
3 Radial growth chronologies were determined for 27 cores across all species and age classes. These exhibited 1–11 major and/or moderate releases (indicative of disturbance) in most decades between 1730 and 1990. Peak releases were recorded in the 1950s when a series of severe windstorms impacted the site. Species recruitment patterns were related to earlier growth releases observed in the oldest cores.
4 White pine exhibited a degree of plasticity in initial radial growth (1–5 mm year^{-1}) depending on the time of establishment, as well as the ability to survive through prolonged periods of depressed growth (< 0.5 mm year^{-1}) followed by growth releases. Hemlock was less plastic in its initial growth rates but did have dramatic growth releases (up to 8.8 mm year^{-1}) in several older trees. Thus, both species exhibited some unexpected dendroecological as well as successional attributes.
5 The future of this stand is uncertain due to the impacts of deer and insect outbreaks that plague the region, as well as fortuitous natural disturbances, e.g. wind and fire. Nonetheless, the dendroecological approach elucidated disturbance history, stand development and mechanisms of coexistence of two ecologically contrasting tree species, and should be used to further understanding of the complex ecology of other mixed-species forests and the successional role of various tree species.

Keywords: age structure, dendrochronology, Pennsylvania, stand dynamics, succession, tree rings

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Introduction

Forests along the northern tier of the eastern United States have been classified as hemlock (*Tsuga canadensis* (L.) Carr) – white pine (*Pinus strobus* L.) – northern hardwoods (Nichols 1935; Braun 1950). The witness tree record used to describe tree species composition during the period of early European settlement supports this classification of northern forests (Lutz 1930a; Siccama 1971; Finley 1976; Whitney 1986; Nowacki *et al.* 1990; Abrams & Ruffner 1995). The composition of the pre-European settlement as well as present-day forests indicates that all possible

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combinations of these three species or species groups were possible, including relatively pure stands of each (Braun 1950; Whitney 1994). However, the fact that hemlock, a highly shade tolerant, late-successional species, grew in combination with white pine, a relatively shade intolerant, early successional species, in many of the original forests is particularly intriguing.

The coexistence of these two ecologically contrasting species in pre-European settlement forests has been the subject of considerable debate in the early ecological literature (Jennings 1928; Lutz 1930b; Hough 1932; Morey 1936; Maissurow 1941; Hough & Forbes 1943). These studies generally concluded that even-aged cohorts of white pine became established in a forest or region following catastrophic disturbances such as fire or extensive blow-down, whereas hemlock is a climax species that will replace white pine through succession. However, these studies were often based on a limited amount of tree age data and did not use the dendroecological techniques that are now available. Thus, the examination of yearly radial growth in a multitude of tree cores, coupled with species canopy recruitment data, to distinguish small- and large-scale disturbance events within individual stands (cf. Lorimer 1980; Orwig & Abrams 1994; Abrams & Orwig 1995) is lacking for old-growth white pine and hemlock forests (Foster 1988).

We believe that the ecology of white pine in pre-settlement, mixed-species forests is more complicated than that expressed in the early literature, and the mechanisms of its coexistence with later successional species can be elucidated with dendroecological techniques (Foster 1988; Abrams *et al.* 1995). In this study we examined the composition, size-age structure and radial growth dynamics of a relatively undisturbed, pre-European settlement origin hemlock-white pine forest on the Allegheny Plateau in north-western Pennsylvania. The study site is considered by some to be one of the premier old-growth examples of this forest type remaining in the eastern USA (E. R. Cook, personal communication).

We present a 300-year history of disturbance and canopy recruitment patterns in relation to the coexistence of the ecologically contrasting white pine and hemlock, including changes in forest dynamics before and after European settlement (*c.* 1825). Moreover, at the present time the oldest white pine in this forest are approaching their maximum longevity, while hemlock trees, both young and old, are seriously threatened by the exotic insect hemlock woolly adelgid (*Adelges tsugae* Annand) (McClure 1991). The area is also plagued with extremely high white-tailed deer (*Odocoileus virginianus*) densities, which have greatly limited tree recruitment for the last half-century (Marquis 1981; Whitney 1984). This forest therefore represented a rare opportunity to study the dendroecology of this relatively undisturbed primary forest type before it is irrevocably altered by natural and anthropogenic factors.

SITE DESCRIPTION

The study site is called the Forest Cathedral and is located within the Cook Forest State Park of north-eastern Clarion County in north-western Pennsylvania (41°19′22N, 79°09′51W). The region is part of the unglaciated Allegheny Plateau, which consists of level uplands, dissected mountain coves, rolling hills and deep stream valleys (Braun 1950; Patton 1958). The Forest Cathedral stand is $\approx$ 8 ha in area and has an altitude of 450–490 m a.s.l. The forest topography includes a north-east sideslope and mountain-top with a typical slope of 8–10°. Soils on the study area include the Cookport stony silt loam and Leetonia stony sandy loam (Patton 1958). These soils are moderately to well-drained, acidic, and relatively infertile. Annual rainfall of the region averages 117 cm and the mean annual temperature is 8 °C.

The tract exhibits distinct old-growth characteristics, with trees of large diameter and great height (over 53 m), a variety of tree diameter classes and canopy layers, gap formation, abundant woody debris on the forest floor, and large standing dead trees. However, severe storms in the 1950s created significant blow-down in the forest, after which salvage cutting of the fallen trees was conducted to reduce fire danger and insect infestation (Cook Forest, unpublished report). Evidence of fire in the form of scarred trees and soil charcoal were observed, but we could not determine if these fires occurred before or after European settlement, or both.

Methods

On 5 May 1994, 20 fixed-area plots located at 20-m intervals along transects randomly located through the forest interior were used for vegetation sampling. The species, diameter and crown class were recorded for all trees (d.b.h. $\geqslant$ 8 cm at a height of 1.37 m) occurring within 0.02-ha circular plots at each point. For each tree species, a relative importance value was calculated by summing the relative density, relative frequency and relative dominance (basal area) and dividing by 3 (Cottam & Curtis 1956). Classification of tree crowns into four categories (dominant, codominant, intermediate and overtopped) was based on the amount and direction of intercepted light (Smith 1986). At each plot, two to four representative trees across all species and diameter classes were cored at 1.37 m for age determinations and radial growth analysis. Coring location on each tree was determined individually by tree shape and size to facilitate the interception of the pith. All suitable cores ($n = 55$) were returned to the laboratory for examination. Saplings and seedlings were counted in nested circular plots of 9 m^2 and 5 m^2, respectively, located within each of the overstorey plots. Saplings were classified as tree species $\geqslant$ 1.5 m in height but less than 8.0 cm d.b.h. and seedlings were $<$ 1.5 m in height.

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Age determinations for all cores were made using a dissecting microscope. For cores that by-passed the pith we added a few years (based on the early ring curvature and growth rate) to estimate total age. Cores from the five oldest white pine and hemlock trees were used to construct a growth chronology of the site spanning 250–300 years. These cores were dried, mounted and sanded. Annual growth increments were measured to the nearest 0.01 mm with a tree-ring measuring device (Regents Instruments Inc., Quebec, Canada) and recorded using the MACDENDRO microcomputer program. After cross-dating using signature years (Fritts 1976), annual increments were averaged to obtain a mean growth chronology from each core per species. A ring width index was also created for each tree chronology by dividing yearly mean measured growth values by the expected values obtained from linear or negative exponential regression (Fritts & Swetnam 1989). Annual growth increments were measured for an additional 20 of the most suitable tree cores for growth comparisons across other species and age classes. All cores were examined for periods of suppression and release based on conservative and moderate criteria established by Lorimer & Frelich (1989), who defined a major sustained release as a ⩾ 100% average growth increase lasting at least 15 years, and a moderate temporary release as a ⩾ 50% average growth release lasting from 10 to 15 years. These criteria, coupled with tree canopy recruitment dates, were used to distinguish disturbance events from responses attributed to climatic and thinning factors (Lorimer & Frelich 1989).

Results

The Forest Cathedral stand was dominated by hemlock and white pine, followed by beech (*Fagus grandifolia* Ehrh.) and yellow birch (*Betula alleghaniensis* Britton) (Table 1). Hemlock had an extremely high density, averaging over 11 trees per 0.02-ha plot. In contrast, white pine averaged only 2 trees per plot but had a high importance value due to the large size of

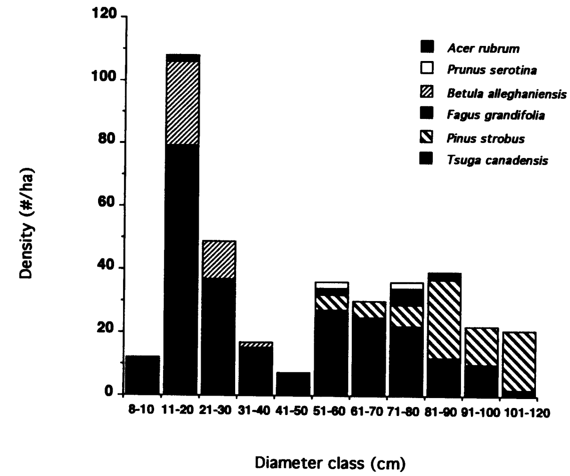

Fig. 1 Diameter (at 1.37 m) distribution of tree species in the Forest Cathedral, Cook Forest State Park, Pennsylvania.

almost all of the existing trees. The total basal area of 78.6 $m^2 ha^{-1}$ on the site is very high but not unprecedented in eastern US forests (Stearns 1950; Baldwin 1951; Rose 1984). Tree regeneration was practically nonexistent within the forest, with only five saplings and three seedlings (mainly hemlock) counted in all 20 plots.

The diameter distribution of 145 trees measured at the site revealed a roughly negative exponential or inverse-J pattern typical of an uneven-aged forest (Fig. 1; Smith 1986). White pine dominated the three largest diameter classes and had no individuals < 51 cm d.b.h. Most white pine grew as an emergent above the dominant canopy class. The diameter distribution of hemlock was negative exponential except for its scarcity in the 8–10 and 31–50 cm classes. Most of the yellow birch occurred in the 11–30 cm classes, whereas beech had a few individuals in most diameter classes from 8 to 90 cm. Relatively few trees of all species occurred in the 8–10, 31–40 and 41–50 cm classes.

The age distribution for all 55 cored trees confirms that this is an uneven-aged forest (Fig. 2). Most trees forming the present overstorey recruited to breast height (1.37 m) between 1690 and 1810, including all of the white pine. Peak recruitment of hemlock also

Table 1 Density, frequency, dominance and importance values for tree species in an old-growth hemlock-white pine forest in north-western Pennsylvania

Species	Density (ha^{-1})	Frequency (# plots)	Dominance ($m^2 ha^{-1}$)	Relative density	Relative frequency	Relative dominance	Relative importance
Tsuga canadensis	222	20	44.9	63.9	38.5	57.5	53.2
Pinus strobus	49	14	29.0	14.1	26.9	37.0	26.0
Betula alleghaniensis	42	6	1.4	12.1	11.5	1.7	8.4
Fagus grandifolia	30	10	2.8	8.6	19.2	3.5	10.4
Prunus serotina	2	1	0.4	0.6	1.9	0.5	1.0
Acer rubrum	2	1	0.1	0.6	1.9	0.1	0.9
Totals	347	52	78.6				

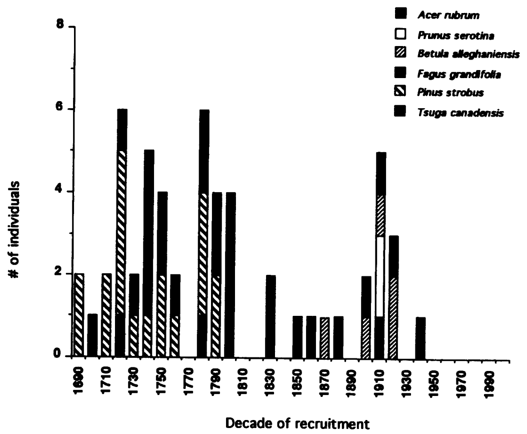

Fig. 2 Age class (at 1.37 m) distribution for tree species in the Forest Cathedral, Cook Forest State Park.

occurred during this early period, but low to moderate levels of recruitment continued from 1830 to 1900. Occasional beech recruitment has occurred throughout most of the 300 year history of the forest, with individuals ranging in age from 67 to 275 years at breast height. The youngest trees were yellow birch, black cherry (*Prunus serotina* Ehrh.), hemlock and red maple (*Acer rubrum* L.), which ranged in age from 51 to 88 years.

Radial growth analysis of the five oldest white pine indicates a period of high initial growth from 1690 to 1715 (Fig. 3). This was followed by generally below average growth punctuated by growth spikes every 15–25 years until 1820. The ring width index for white pine gradually increased between 1820 and 1900, coupled with prolonged releases starting in 1819, 1850 and 1891. Radial growth decreased dramatically from 1900 to 1925, but exhibited additional releases starting in 1926 and 1972. Growth was very low in the 1950s when extensive blow-down was reported in the forest. The mean chronology for the five oldest hemlock exhibited several trends contrasting with the white pine chronology (Fig. 3). The ring width index was initially quite low around 1725, but then increased dramatically, reaching a peak in 1756. Growth decreased until 1820 and then fluctuated about the expected value (ring width index = 1) until 1925. The ring width index was consistently below average from 1925 to 1940, but increased to its maximum value by 1959 and then declined. A period of peak hemlock recruitment was associated with increasing ring width values from 1740 to 1760 (Fig. 3). Similarly, peak white pine recruitment in the early 1700s followed its period of high initial growth. However, frequent hemlock recruitment between 1780 and 1810 occurred when its radial growth was relatively low, although white pine had a distinct growth spike during that period. A pulse of tree recruitment for the hardwood species between 1910 and 1930 coincided with the beginning of increased ring width values in white pine, but not in hemlock. Growth releases in both species after 1940 did not stimulate further tree recruitment at the study site because no tree-size individuals aged at the site were less than 50 years old.

The radial growth chronologies for individual white pine of various ages exhibited contrasting growth patterns and release dates (Fig. 4). A 296-year-old tree had high growth of 3–4 mm $year^{-1}$ for an initial 25-year period, followed by a rapid growth decline from 1725 to 1755 (Fig. 4a). It experienced a moderate release in 1761 and typically grew at a rate of 1.0–1.8 mm $year^{-1}$ until 1915 when its radial growth decreased to 0.2 mm $year^{-1}$ between 1950 and 1975. A white pine established in 1717 obtained peak growth of > 4 mm $year^{-1}$ in 1742, after which growth typically declined with age (Fig. 4c). Moderate growth releases occurred in 1778, 1851 and 1893 and a major release was recorded in 1972, by which time annual growth was < 0.2 mm $year^{-1}$. A similar pattern of decreasing growth with age, as expected from typical radial increment and tree size relationships, was observed in a 266-year-old white pine (Fig. 4e). Several distinct growth peaks throughout the 18th and 19th centuries in this core did not meet the release criteria. A younger white pine of 211 years had low initial growth followed by a series of major and moderate releases (Fig. 4b). This tree is unique for exhibiting much greater average growth in the later years (up to 5 mm $year^{-1}$) compared to earlier years, possibly due to obtaining a dominant canopy position about 1925 (cf. Lorimer & Frelich 1989). A 210-year-old tree had relatively low initial growth of 1–2 mm $year^{-1}$ followed by a moderate release in 1876 and declining growth with age (Fig. 4d). A 192-year-old white pine also had relatively slow early growth, a moderate release in 1829 and major releases in 1955 and 1974 (Fig. 4f).

A hemlock established in 1722 had low initial growth that increased then decreased over a 75-year period (Fig. 5a). Growth remained fairly constant around 1.2 mm $year^{-1}$ until 1954 when a moderate release resulted in peak growth of 4.6 mm $year^{-1}$. Growth then declined precipitously to a low of 0.3 mm $year^{-1}$ in the 1990s. A 256-year-old hemlock had growth rates of 1.5–2.6 mm $year^{-1}$ during its first 100 years (Fig. 5c). Growth declined rapidly between 1848 and 1876, followed by releases in 1878 and 1935. A 198-year-old hemlock averaged about 0.9 mm $year^{-1}$ growth during its initial 80 years, but major releases in 1879 and 1945 elevated the growth rate to 3.6 and 8.8 mm $year^{-1}$, respectively (Fig. 5b). A similarly aged tree had relatively high initial growth around 1800 and a series of major releases in 1842, 1869, 1951, and 1970 (Fig. 5d). A 93-year-old overtopped hemlock had an average growth rate of 0.5 mm $year^{-1}$, despite moderate releases in 1932 and 1954 (Fig. 5e). Another overtopped tree had a moderate release in 1954 producing growth up to 2.0 mm $year^{-1}$, followed by a sharp decline after 1970 (Fig. 5f). Many of the hemlock and white pine chronologies exhibited very low growth in the 1950s, possibly due to injury from a

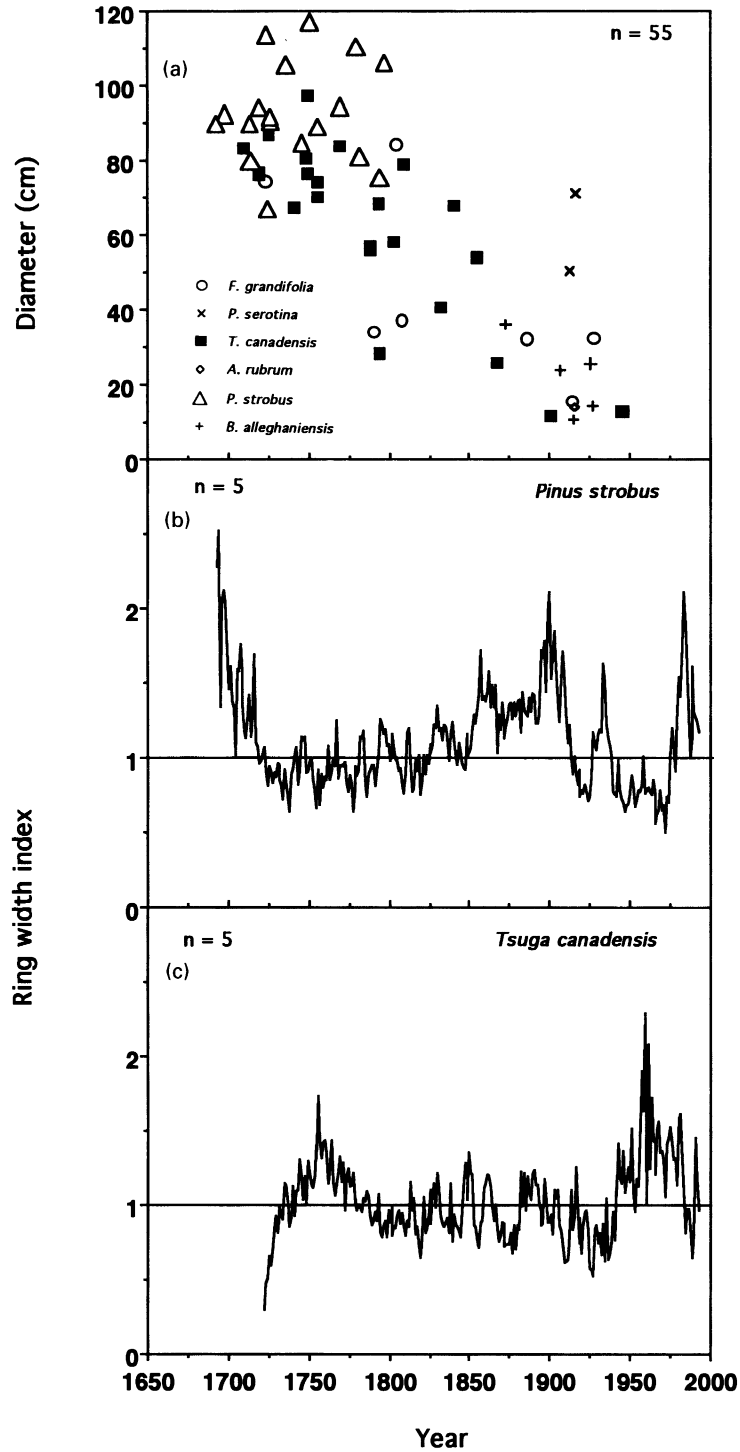

Fig. 3 (a) Age-diameter relationships for all cored trees and the mean ring width index for the five oldest trees of (b) white pine and (c) hemlock in the Forest Cathedral.

series of severe windstorms during that time (cf. Foster 1988), which were followed by releases.

A 275-year-old, codominant beech exhibited a series of major and moderate releases and growth fluctuations between 0.5–2.0 mm year^{-1} (Fig. 6a). An intermediate-sized beech had moderate releases in 1837 and 1872, after which growth reached 4.0 mm year^{-1} (Fig. 6c). An overtopped red maple had relatively high initial growth in the 1920s that declined to < 0.2 mm year^{-1} in the 1950s, which is indicative of gap opening and closure (Fig. 6b). This tree then experienced a major release in 1958 and a moderate release in 1984. A 79-year-old, dominant black cherry had three decades of increasing growth that peaked at > 6.5 mm year^{-1}, after which growth declined rapidly until a moderate release occurred in 1969 (Fig. 6d). A 121-year-old yellow birch had a major release in 1910, whereas a 68-year-old tree had a moderate release in 1957 (Fig. 6e,f).

In the vast majority of decades between 1730 and 1990 a major or moderate release was recorded in one or more trees across all species (Fig. 7). The frequency

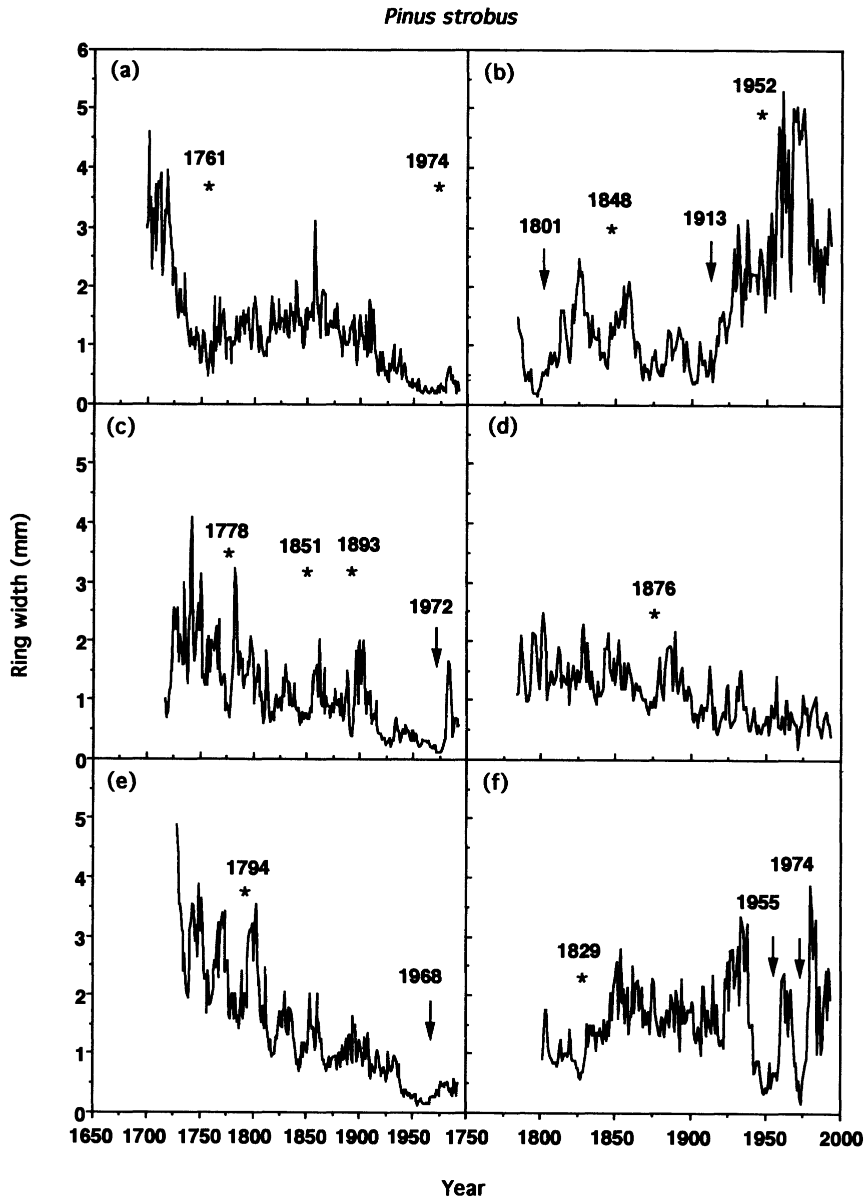

Fig. 4 Radial growth chronologies of selected white pine in the Forest Cathedral. *Moderate release dates; arrows = major release dates (criteria from Lorimer & Frelich 1989).

of releases increased with time, with 49% of the moderate releases and 70% of the major releases occurring during the 20th century, which may be due to the attrition of older trees. Multiple releases following a series of severe windstorms in the 1950s was clearly evident; however, a substantial number of major or moderate releases were also evident in the 1840s, 1870s, 1910s and 1970s.

Discussion

A major finding of this study is that white pine recruitment into the tree-size class occurred throughout the initial 110-year period (1690–1800) of the stand history. We believe that this stand was decimated by a catastrophic disturbance, such as tornado and/or fire, in the 1690s (evidence of more recent disturbances is shown in Fig. 8). Evidence for this is the rapid growth rate of many of the oldest white pine, the pulse of white pine recruitment between 1690 and 1730, and the absence of any hemlock trees older than 284 years. The maximum age of hemlock exceeds 400–500 years, whereas white pine rarely exceeds 300 years (Morey 1936; Hough & Forbes 1943; Rogers 1978; Abrams *et al.* 1995).

Most studies of old-growth white pine, including those using age data, concluded that white pine existed as even-aged cohorts that established soon after large-scale disturbances (Lutz 1930b; Nichols 1935; Morey 1936; Cline & Spurr 1942; Heinselman 1973; Foster 1988). However, white pine can grow as scattered individuals in mixed-species forest, suggesting that it may persist as a gap-phase species (Nichols 1935; Hibbs 1982a). White pine may also

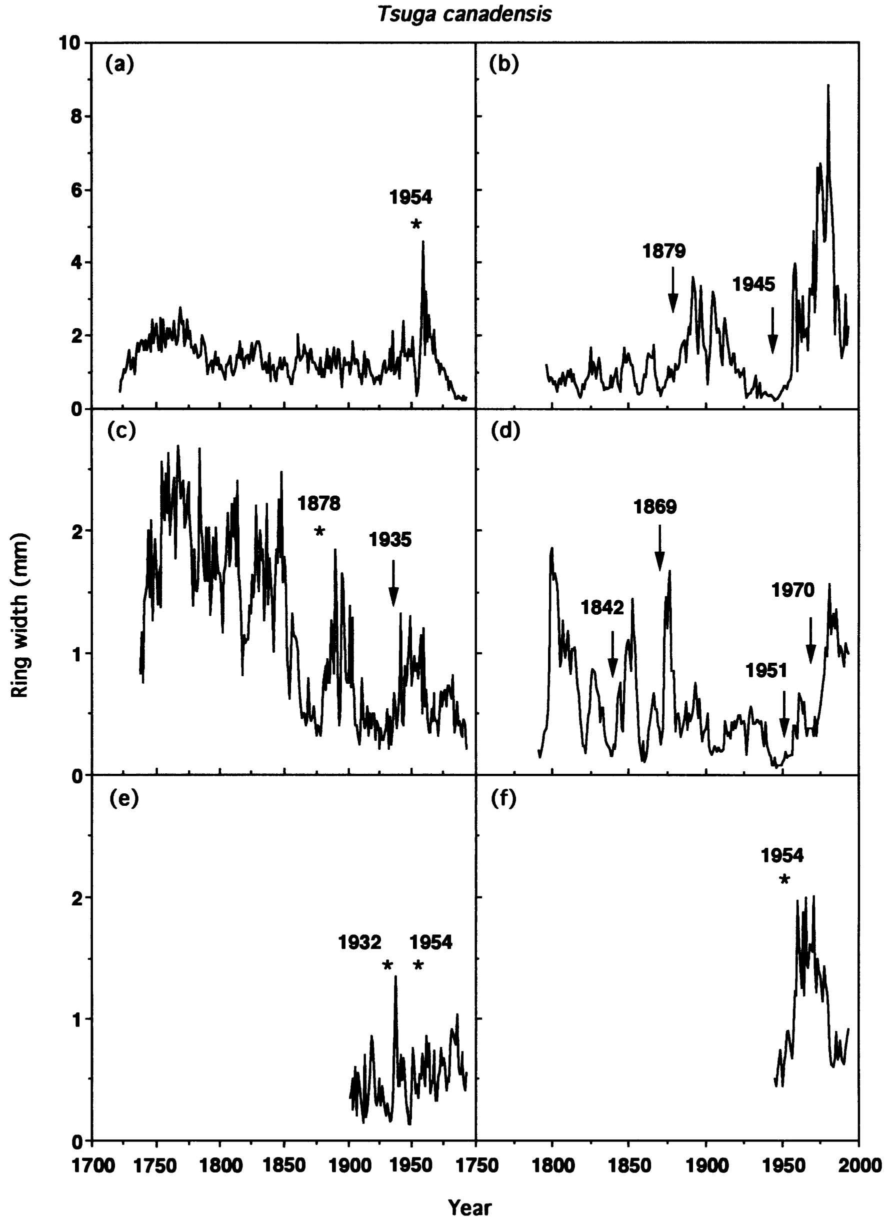

Fig. 5 Radial growth chronologies of selected hemlock in the Forest Cathedral. *Moderate release dates; arrows = major release dates (criteria from Lorimer & Frelich 1989).

represent a physiographic climax on certain higher elevation or sandy sites (Cline & Spurr 1942; Holla & Knowles 1988). Hibbs (1982a) reported that even-aged patches of white pine formed in uneven-aged forests following intermediate-sized canopy disturbances. We arrived at a similar conclusion concerning white pine recruitment in a 300-year-old, uneven-aged mixed-oak forest, where most of the existing white pine canopy became established in two distinct episodes in the 1800 s associated with releases in the tree ring chronologies (Abrams *et al.* 1995).

The recruitment pattern of white pine in this study is not consistent with the idea of strictly early successional, even-aged populations, gap-phase individuals, or a physiographic climax. Rather, white pine dominated tree recruitment for the initial 40-year period, followed by 70 years of concurrent white pine and hemlock recruitment. None of the existing white pine recruited in the forest after 1800. These results are consistent with those reported for a former virgin stand of white pine-hemlock–northern hardwoods in the same region in which white pine recruitment peaked during the initial 80 years of postdisturbance stand development, continued at a lower level for an additional 80 years, and then stopped completely (Hough & Forbes 1943). Thus, white pine can apparently play the role of both early and middle successional species while hemlock recruitment can occur across all successional stages in forests on the Allegheny Plateau. The initial domination of tree recruitment by white pine may reflect its faster height growth relative to hemlock, rather than differential establishment dates between the two species.

In this study, we examined the growth chronologies

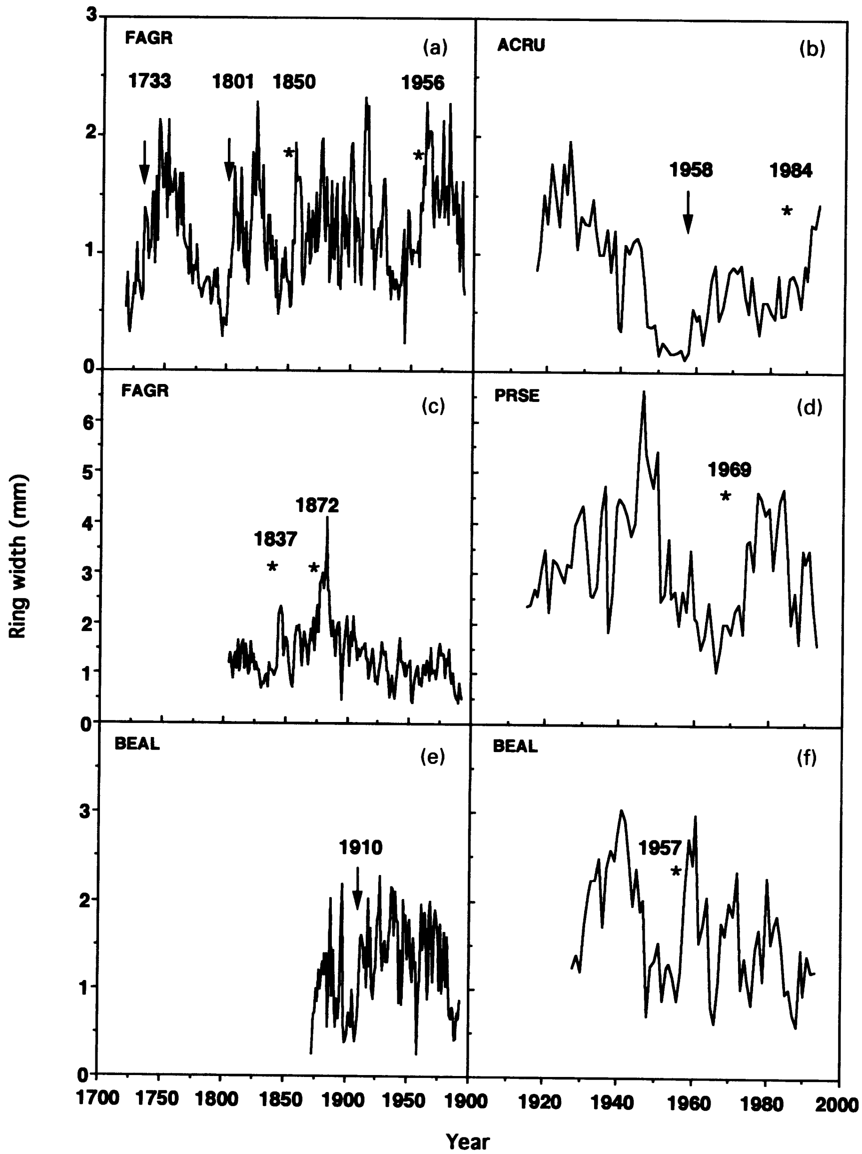

Fig. 6 Radial growth chronologies of selected beech (FAGR), yellow birch (BEAL), red maple (ACRU) and black cherry (PRSE) in the Forest Cathedral. *Moderate release dates; arrows = major release dates (criteria from Lorimer & Frelich 1989).

of white pine and hemlock that became established at different intervals in the stand history. White pine was quite plastic in its initial growth rate, which was typically between 3 and 4 mm $year^{-1}$ for individuals that established early in the stand development and only 1–2 mm $year^{-1}$ for those that established later under less open canopy conditions. Several white pine experienced prolonged periods of slow growth (< 1.0 mm $year^{-1}$) followed by growth releases, which was unexpected from this relatively shade intolerant species (cf. Abrams *et al.* 1995). However, white pine is capable of changes in needle morphology, crown architecture and growth allocation in understorey vs. open-growth saplings (Abrams & Kubiske 1990; O'Connell & Kelty 1994). Hemlock was not very plastic in its early growth, which was typically between 1 and 2 mm $year^{-1}$ regardless of age class. However, dramatic growth releases (4.6–8.8 mm $year^{-1}$) in several older hemlock were very impressive for this late successional, often slow growing species (cf. Abrams & Orwig 1995). Thus, both species exhibited some unexpected dendroecological attributes based on their classification as either early or late successional. Moreover, hemlock is capable of sun-shade plasticity in needle morphology (Abrams & Kubiske 1990), and may produce distinct ecotypes that have differential morphology and radial growth in relation to site, climate and disturbance conditions and so may broaden its ecological range (Kessell 1979).

The cessation of white pine recruitment in mixed-species stands may be due to its relative intolerance of understorey conditions, including increasing shade, root competition and organic seedbed as stands age (Fig. 8; Cline & Spurr 1942). However, if white pine can persist via gap capture in mixed-hardwood forests

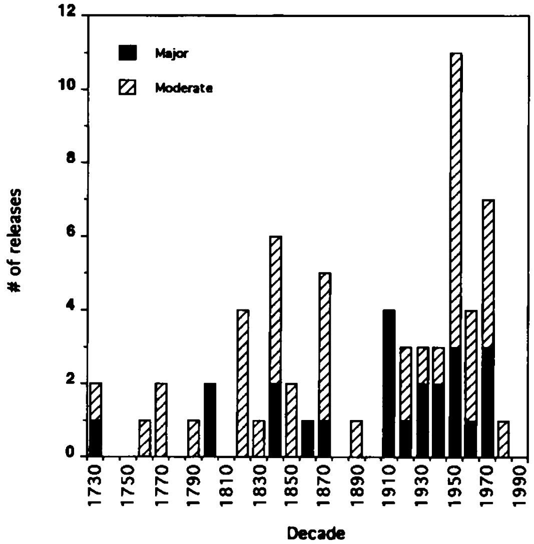

Fig. 7 Decadal distribution of major and moderate releases recorded in 27 cores of all major tree species in the Forest Cathedral.

(Hibbs 1982a; Abrams *et al.* 1995), there may be some unique limitations to white pine recruitment in mature hemlock forests. Hemlock is a highly shade tolerant, evergreen species that produces a very deep shade and a relatively thick organic layer on the forest floor (Rogers 1978; Brown *et al.* 1982; Canham *et al.* 1994). These conditions typically preclude the long term survival of most other northern tree species. Thus in hemlock dominated forests, canopy gaps create opportunities for regeneration of hemlock and a few specialized hardwood species (e.g. beech, yellow birch or sugar maple), but rarely white pine (Woods 1984; Collins 1990; Rogers 1978; Hibbs 1982b). White pine establishment and growth in these forests are dependent on large-scale disturbances, and may require fire-created mineral seedbeds (Maissurow 1941; Heinselman 1973). In old-growth pine-hemlock in New England, Foster (1988) noted that white pine may need a combination of both extensive wind-throw and fire for successful establishment; wind-throw by itself may not be adequate. However, in mixed-hardwood forests, white pine has the advantage of being an evergreen in a deciduous forest and may utilize favorable growth conditions in the nonsummer months when the hardwoods are leafless (cf. Lassoie *et al.* 1983), as well as competing with some tree species of similar or lesser understorey tolerance (e.g. oak, cherry and birch).

In this study, the peak recruitment of hemlock occurred between 1740 and 1800, but after 1870 recruitment of hardwood species exceeded that of hemlock. Thus, despite the apparently high frequency of canopy gaps (based on release dates) occurring in this stand during the last 100 years neither white pine or hemlock had much successful recruitment. The establishment of northern hardwood species between 1870 and 1930 may be due to the degree of canopy openings as well as their ability, relative to hemlock, to grow fast, have less rigorous seedling requirements, have deeper root systems and sprouting ability, and

Fig. 8 Photographs of key ecological features of the Forest Cathedral. (a) large white pine, high density of hemlock in all diameter classes, and forest floor lacking all understorey vegetation; (b) large hemlock with well-developed v-notched fire scar; (c) recent hemlock blow-down and wind-snapped white pine (centre-right); (d) coarse woody debris on forest floor from blow-down.

be less palatable to deer (Rogers 1978; Hibbs 1982b; Mladenoff & Stearns 1993). In addition, these hardwood species may have benefited from the exclusion of fire in this stand (or region) after 1900 (Abrams 1992; Abrams *et al.* 1995). Soil charcoal and fire scarred trees were present in the forest which probably dated from before 1900 (Fig. 8). We attribute the lack of tree recruitment of all species after 1930 and the present day lack of seedlings, saplings and shrubs in the understorey (Fig. 8) primarily to intense deer browsing (Marquis 1981; Whitney 1984). A reconnaissance of the study area in the 1920s reported that 'every old stump and half decayed log is a veritable forest nursery for the birches and hemlock' (Jennings 1928). While we recognized that a multitude of factors can inhibit regeneration of hemlock and other species (cf. Mladenoff & Stearns 1993), we found deer droppings in every one of our sample plots. Without severe deer browsing, hemlock may experience population cycles (recruitment episodes) exceeding 100 years that are expressed through changes in forest structure that perpetuates the species at a site (Hett & Loucks 1976).

Conclusion

The dendroecological approach used in this study elucidated a 300-year history of forest dynamics for two dominant northern conifer species of contrasting ecological status. White pine dynamics in this stand did not fit the characterization of strictly early successional, even-aged cohorts or gap-phase individuals in a mature canopy. Moreover, hemlock did not fit the typical notion of a strictly later successional species. Rather, white pine and hemlock established more-or-less concurrently during a 100-year period, although hemlock recruitment continued at fairly low levels after white pine ceased. The concurrent establishment of both white pine and hemlock after 1690 and their differential speed of obtaining dominance and longevity suggests that succession in this forest is consistent, at least in part, with the initial floristics composition model (Egler 1954). Single- and multiple-tree releases, indicative of small-scale and larger-scale disturbance, were recorded in most decades, although this created few successful opportunities for hemlock or white pine recruitment during the last 100 years. Rather, these disturbances and possibly fire exclusion facilitated increased hardwood invasion. This stand was virtually devoid of an understorey and tree recruitment was practically nonexistent after 1930, despite severe storms in the 1950s, probably due to intensive deer browsing. The future of this stand is highly unpredictable due to the potential impacts of the hemlock woolly adelgid and uncontrollable wildfire due to high fuel loading, as well as the continuation of deer browsing and wind-throw. However, based on current conditions, the long-lived hemlock may continue to dominate this stand well into the future, whereas the existing white pine component will die off in the next century. Regardless of the future scenario, this study provided important documentation of the disturbance history, successional role and mechanisms of coexistence of white pine and hemlock in an old-growth forest of the eastern USA. We believe this dendroecological approach can be used to reconstruct the historical development, dynamics and recruitment patterns in other forests with mixed and ecologically contrasting species, as well as broaden our understanding of the successional role of certain tree species.

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