The dendroecology and climatic impacts for old-growth white pine and hemlock on the extreme slopes of the Berkshire Hills, Massachusetts, U.S.A.

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Abstract: Dendrochronological techniques were used to investigate the dynamics of an old-growth forest on the extreme slope (65%) at Ice Glen Natural Area in southwestern Massachusetts. The site represented a rare opportunity to study the disturbance history, successional development, and responses to climatic variation of an old-growth hemlock (*Tsuga canadensis* (L.) Carr) – white pine (*Pinus strobus* L.) – northern hardwood forest in the northeastern United States. Hemlock is the oldest species in the forest, with maximum tree ages of 305–321 years. The maximum ages for white pine and several hardwood species are 170–200 years. There was continuous recruitment of hemlock trees from 1677 to 1948. All of the existing white pine was recruited in the period between 1800 and 1880, forming an unevenly aged population within an unevenly aged, old-growth hemlock canopy. This was associated with large increases in the Master tree-ring chronologies, indicative of major stand-wide disturbances, for both hemlock and white pine. Nearly all of the hardwood species were also recruited between 1800 and 1880. After 1900, there was a dramatic decline in recruitment for all species, including hemlock, probably as a result of intensive deer browsing. White pine and hemlock tree-ring growth during the 20th century was positively correlated with the annual Palmer drought severity index (r = 0.61 and 0.39, respectively). This included reduced growth during periods of low Palmer drought severity index values, the drought years of 1895–1922, and dramatic increases during periods of high Palmer drought severity index values in the 1970s and 1990s. Significant positive and negative correlations of certain monthly Palmer drought severity index values with 20th century tree-ring chronologies also exist for white pine and hemlock using response function analysis. The results of this study suggest that old-growth forests on extreme sites in the eastern United States may be particularly sensitive to direct and indirect allogenic factors and climatic variations and represent an important resource for studying long-term ecological and climatic history.

Key words: age structure, radial growth analysis, disturbance, climate, fire, tree rings.

Résumé : Les auteurs ont utilisé des techniques dendrochronologiques pour étudier la dynamique d'une forêt surannée venant sur une pente extrême (65 %), dans la réserve naturelle de Ice Glen, au sud-ouest du Massachusetts. Le site présente une rare occasion d'étudier l'histoire des perturbations, le développement de la succession et les réactions aux variations climatiques dans une forêt âgée à pruche (*Tsuga canadensis* (L.) Carr) – pin blanc (*Pinus strobus* L.) – et essences décidues nordiques, dans le nord des États-Unis. La pruche est l'espèce la plus ancienne de la forêt, avec des âges maximum de 305 à 321 ans. Les âges maximum pour le pin blanc et plusieurs espèces décidues sont de 170 à 200 ans. Il y a eu un recrutement continu de nouvelles pruches entre 1677 et 1948. Tous les pins blancs actuels ont été recrutés durant la période de 1800 à 1880, formant une population inéquienne à l'intérieur d'une canopée de pruches surannées inéquienne. Ceci s'accompagne de fortes augmentations dans les chronologies maîtresses des anneaux de croissance, ce qui indique des perturbations majeures dans l'ensemble du peuplement, à la fois pour la pruche et pour le pin blanc. Presque toutes les espèces décidues ont également été recrutées antre 1800 et 1880. Après 1900, il y a eu un déclin rapide dans le recrutement chez toutes les espèces, incluant la pruche, probablement lié à un broutage intensif par les chevreuils. Les anneaux de croissance du pin blanc et de la pruche, au cours du 20ième siècle, montrent une corrélation positive avec l'index de sévérité de sécheresse de Palmer (r = 0,61 et 0,39 respectivement). Ceci inclut une croissance réduite au cours des périodes où l'indice de sévérité de sécheresse de Palmer est faible (les années sèches de 1895 à 1922) et une augmentation spectaculaire au cours des périodes où des valeurs élevées de l'indice de sévérité de sécheresse de Palmer ont été enregistrées, dans les décennies 1970 et 1990. En utilisant l'analyse de fonction de

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réaction (response function analysis), on obtient également des corrélations positives et négatives entre certaines valeurs mensuelles de l'indice de sévérité de sécheresse de Palmer et les données chronologiques des anneaux de croissance, chez le pin blanc et la pruche. Les résultats de ce travail suggèrent que les forêts surannées, venant sur des sites extrêmes de l'est américain, pourraient être particulièrement sensibles aux facteurs allogènes directs et indirects ainsi qu'aux variations climatiques, et constituent une ressource importante pour l'étude à long terme de l'historique écologique et climatique.

Mots clés : structure d'âges, analyse des croissances radiales, perturbation, climat, feu, anneaux de croissance.

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Introduction

Tree-ring analysis, including age structure and dendroecology, has become an important tool in the study of stand dynamics and ecological history (Fritts and Swetnam 1989; Nowacki and Abrams 1994). From tree-ring chronologies, researchers have been able to reconstruct the historical development of forests in terms of species recruitment patterns, the frequency of disturbance factors, populations and successional dynamics, and impacts of climatic variation (Fritts 1976; Cook 1987; Foster 1988*a*; Frelich and Graumlich 1994; Abrams and Orwig 1995; Abrams et al. 1995; Kelly and Larson 1997). Coupling data from tree-ring chronologies, age structure, and land-use history has greatly improved our understanding of the ecology of forests in the eastern United States over long temporal and broad spatial scales (Foster 1988*a*; Abrams and Orwig 1996; Abrams et al. 1997).

The northern forests in the eastern United States are classified as hemlock (*Tsuga canadensis* (L.) Carr) – white pine (*Pinus strobus* L.) – northern hardwood (Nichols 1935; Bromley 1935; Braun 1950). One keystone species of these forests is white pine, which is among the largest in diameter and height of the eastern tree species. Nonetheless, white pine appears to have been a rather minor component of most pre-European forests in the northeast (Lutz 1930*a*; Siccama 1971; Whitney 1994; Abrams and Ruffner 1995). The combination of white pine, an early successional, relatively shade-intolerant species, growing with late successional, shade-tolerant hemlock and northern hardwoods has been the subject of ecological studies throughout the 20th century (Jennings 1928; Lutz 1930*b*; Hough 1932; Maissurow 1941; Hough and Forbes 1943; Abrams and Orwig 1996). Early ecologists concluded that white pine became established following large-scale disturbances, such as fire or wind-throw, and was replaced by shade-tolerant trees during succession. Therefore, hemlock – white pine forests only exist at some intermediate successional stage. However, this does not explain the co-occurrence of white pine and hemlock in eastern old-growth forests that have not been intensively disturbed for 300 or more years.

Recent studies suggest that white pine can form evenly aged populations in intermediate-size gaps in unevenly aged forests (Hibbs 1982*a*; Abrams et al. 1995; Orwig and Abrams 1999). Moreover, a dendroecological study of an old-growth forest on the Allegheny Plataeu in Pennsylvania reported that hemlock and white pine established concurrently following catastrophic disturbance, and that white pine recruitment can last 120 years after stand initiation (Abrams and Orwig 1996). Therefore, more intensive studies are needed to better understand the dynamics and successional role of white pine and hemlock in old-growth forests.

In this study, we investigate the ecological history and dendrochronology of an old-growth, mixed northern conifer – hardwood forest at the Ice Glen Natural Area in southwestern Massachusetts. The site has an average slope of 65% and a very thin soil layer. The extreme nature of this site makes it a good candidate for dendroclimatological investigation (Fritts 1976; Abrams and Orwig 1995). Based on the long tree-ring chronology available for this forest, we designed a study with these specific objectives: (*i*) document the composition and structure of the forest, (*ii*) investigate the long-term patterns of tree-ring variation, (*iii*) document the forest responses to natural and anthropogenic disturbances and climate, and (*iv*) describe the long-term successional dynamics of white pine, hemlock, and northern hardwoods.

Study area

This study was conducted within an 8-ha area of old-growth forest at the Ice Glen Natural Area outside of Stockbridge in Berkshire County, southwestern Massachusetts (42°16′20′′N, 72°18′45′′W). The site lies in a section of Laurel Hill within the Lower Berkshire Hills subregion (Griffith et al. 1994). Ice Glen is located between two ridges of quartzite above the Housatonic River, and it contains a deep ravine (Kirby 1995). Substantial glacial meltwater flow followed by centuries of freezing and thawing of the extreme slopes has resulted in the formation of huge bedrock boulders lining the bottom of the narrow valley. The name Ice Glen comes from the fact that ice and snow trapped in deep crevices between the boulders often remains into the early summer (Kirby 1995). The slope of the old-growth site averages 65% and it primarily has a northwest aspect. This site has an altitude of 420–510 m above sea level. The soil at the study site is Lyman–Tunbridge, a steep, extremely stony, silt-loam formed in glacial till derived from schist, gneiss, and granite and contain surface boulders and scattered rock outcrops (Scanu 1988). The soil is a thin mantle over fractured rock and is excessively drained and medium to strongly acidic. Our measurements of the soil depth to bedrock at the study plots indicate an average soil depth of 11 cm and a range of 4–30 cm. The climate of the region is characteristic of northern temperate-maritime, with long, cold winters and short, mild or cool summers. The annual temperature is 8°C, and average daily summer and winter temperatures are 18.2 and –4.5°C, respectively (Scanu 1988). Average yearly precipitation is 109 cm, which is evenly distributed throughout the year. The average

Table 1. Frequency, density, and dominance information for species from Ice Glen Natural Area in southwestern Massachusetts.

Species	Frequency	Density (stems/ha)	Dominance (m^2/ha)	Relative frequency	Relative density	Relative dominance	Importance value
Acer rubrum	12	35	2.4	19.0	6.2	4.0	9.7
Acer saccharum	1	2	0.2	1.6	0.4	0.4	0.8
Betula alleghaniensis	2	10	0.7	3.2	1.8	1.1	2.0
Betula lenta	6	25	1.5	9.5	4.4	2.5	5.5
Betula papyrifera	4	10	1.1	6.3	1.8	1.8	3.3
Pinus resinosa	2	5	0.7	3.2	0.9	1.2	1.7
Pinus strobus	11	32	6.9	17.5	5.8	11.4	11.5
Quercus rubra	5	22	4.8	7.9	4.0	7.9	6.6
Tsuga canadensis	20	420	42.0	31.7	74.8	69.7	58.8
Totals	63	562	60.2	100	100	100	100

Note: Dominance is based on basal area; frequency is based on presence in plots; and density is based on the number of individuals. Importance value is the average of relative frequency, relative density, and relative dominance.

frost-free season is 144 days. We observed the remains of chestnut (*Castanea dentata* (Marsh.) Borkh.), fire scars on living and dead trees of several species, and the presence of soil charcoal from early fires throughout the study site. A large amount of coarse woody debris was observed in the ravine at the base of the old-growth forest. There was also clear evidence of a recent fire covering approximately 0.5 ha at the upper slopes of the site. We found evidence of deer droppings and intensive deer browsing throughout the stand.

Materials and methods

In the summer of 1998, 20 fixed-area plots, located at 20-m intervals along parallel transects traversing the slope through the forest interior, were used for vegetation and dendroecological sampling. The species, diameter, and crown class were recorded for all trees ≥8.0 cm dbh (diameter at breast height) occurring within 0.02-ha circular plots at each point. Classification of tree crowns into four categories (dominant, codominant, intermediate, and overtopped) was based on the amount and direction of intercepted light (Smith 1986). For each tree species, a relative importance value was calculated as the average of the relative frequency (presence or absence in plots), relative density (number of individuals), and relative dominance (basal area) (Cottam and Curtis 1956). At each plot, two to four live trees were cored for age determination and radial growth analysis. Trees were cored at 0.5 m height, with the exception of the large hemlock trees, which had significant stem taper near the ground; these trees were cored at 1.37 m. Across all 20 plots we obtained cores from all the major stand species over a full range of diameter classes. Additional trees were cored outside the study plots to increase our sampling of older trees for species' tree-ring chronologies. Dead trees were not suitable for dendroecological sampling because of their highly decomposed condition. Saplings and seedlings were counted in nested circular plots of 9 and 5 m^2, respectively, located at the center each of the overstory plots. Saplings were classified as tree species >1.5 m in height but <8.0 cm in dbh, and seedlings were <1.5 m in height. Nomenclature follows Fernald (1950).

Radial-growth analysis

All increment cores (n = 82) from the study area were dried, mounted, and sanded to reveal the cellular structure of the wood (Phipps 1985). To identify missing, partial, or false rings and establish an accurate age chronology, all cores were cross-dated, by species, using the signature year technique (Yamaguchi 1991). On cores where the pith was missed, we used a graphical procedure to estimate the year of origin for the tree (Villalba and Veblen 1997). Twenty hemlock and 18 white pine cores were selected, based on age and quality of the core, and measured to the nearest 0.002 mm with the UniSlide "TA" tree-ring measurement system (Velmex Inc., Bloomfield, N.Y.). To confirm our signature years, we cross-dated our measured cores a second time using the COFECHA program available in the International Tree-Ring Data Bank Program Library (ITRDBL) version 2.1 (Cook et al. 1997). The results from these analyses indicated that older portions of a number of the hemlock cores were suitable for age determination, but not cross-dating, because they were highly fragmented. However, the more recent portions of the older hemlock cores were suitable for dendrochronology. Therefore, we established a hemlock tree-ring chronology starting at 1790, despite that the oldest hemlock trees date back to 1674.

The raw ring widths from the cross-dated hemlock and white pine cores were detrended with a negative exponential curve or negative linear function using the standard chronology from the ARSTAN program in ITRDBL version 2.1. Detrending the raw ring widths removes the effects of tree age and microsite and allows each species to be developed into standardized chronologies (Fritts 1976). We created separate master chronologies for the hemlock and white pine cores. A modified version of the Nowacki and Abrams (1997) method for determining overstory releases was used with the raw ring-width data. A growth increase of greater than 25% sustained for 10 years was identified as a moderate overstory release, and a growth increase of greater than 50% sustained for 15 years was classified as a major overstory release. We examined all 38 hemlock and white pine cores for release dates.

For the dendroclimatology analysis, we used the ARSTAN chronology from the ARSTAN program in the ITRDBL program library version 2.1. The ARSTAN chronology is intended to reveal the strongest climatic signal in the tree-ring data. Palmer drought severity index (PDSI) data for southwestern Massachusetts were obtained from 1895 to 1998 (NOAA 1999). The PDSI value range from +4 (extremely wet) to –4.0 (extremely dry); values less than –1.0 indicate drought conditions (Alley 1984). We calculated Pearson's correlation coefficients between annual PDSI and the ARSTAN ring width index for the hemlock and the white pine chronologies. We performed correlation and response function analysis on the monthly PDSI data using a dendroclimatic year from the previous July to the current August and prior growth with the white pine and hemlock ARSTAN chronologies using the Precon32 program version 5.17B (DendroPower, Tucson, Ariz.).

Results

The forest is comprised of nine tree species and is dominated by hemlock, white pine, and red maple (*Acer rub-*

Fig. 1. Diameter (at 1.37 m) distribution of tree species sampled in plots in an old-growth hemlock – white pine – northern hardwood forest at the Ice Glen Natural Area, southwestern Massachusetts.

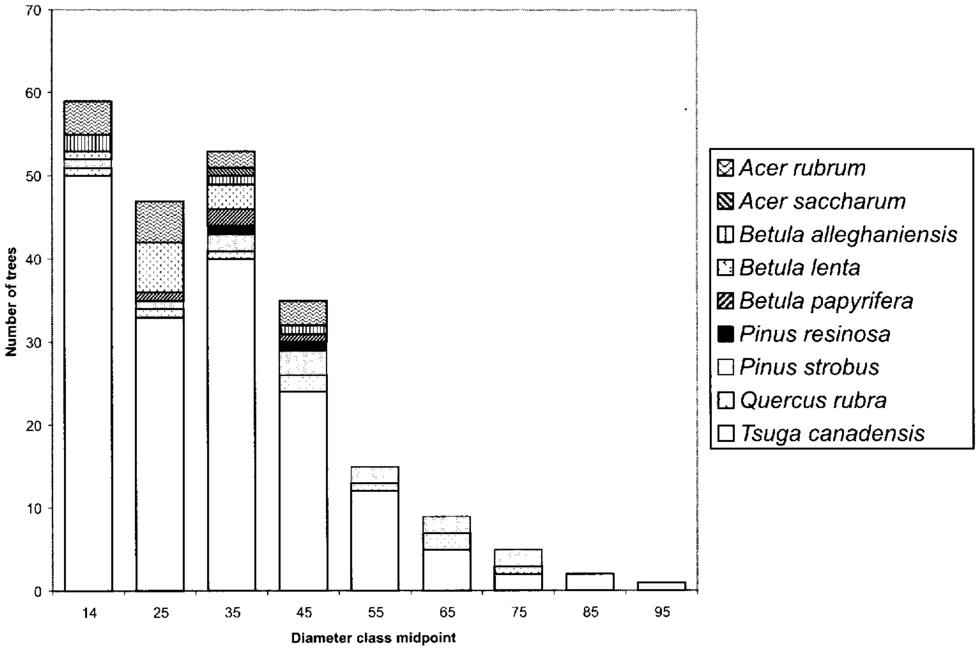
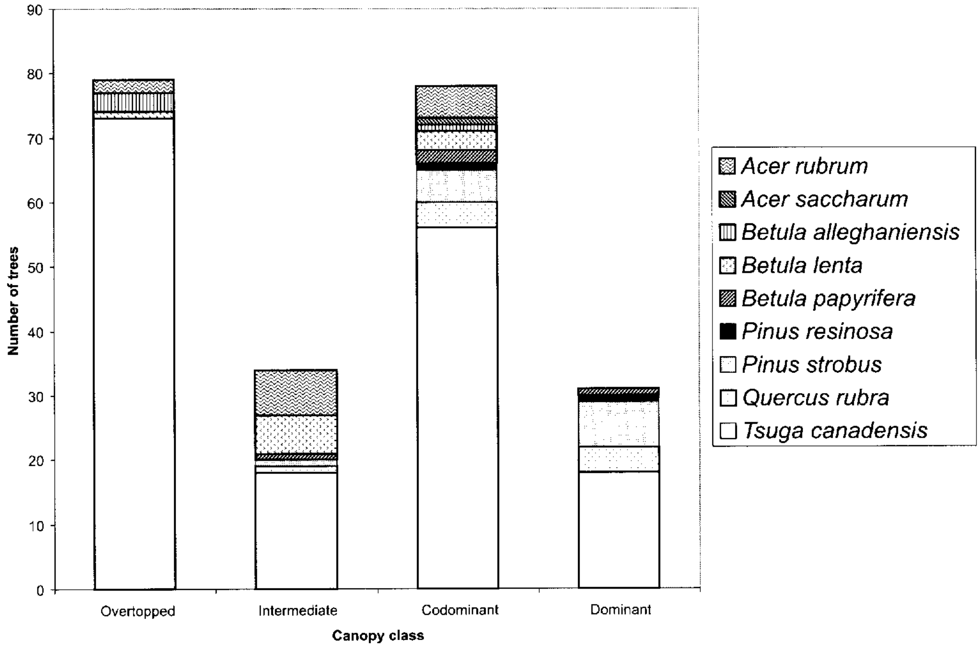


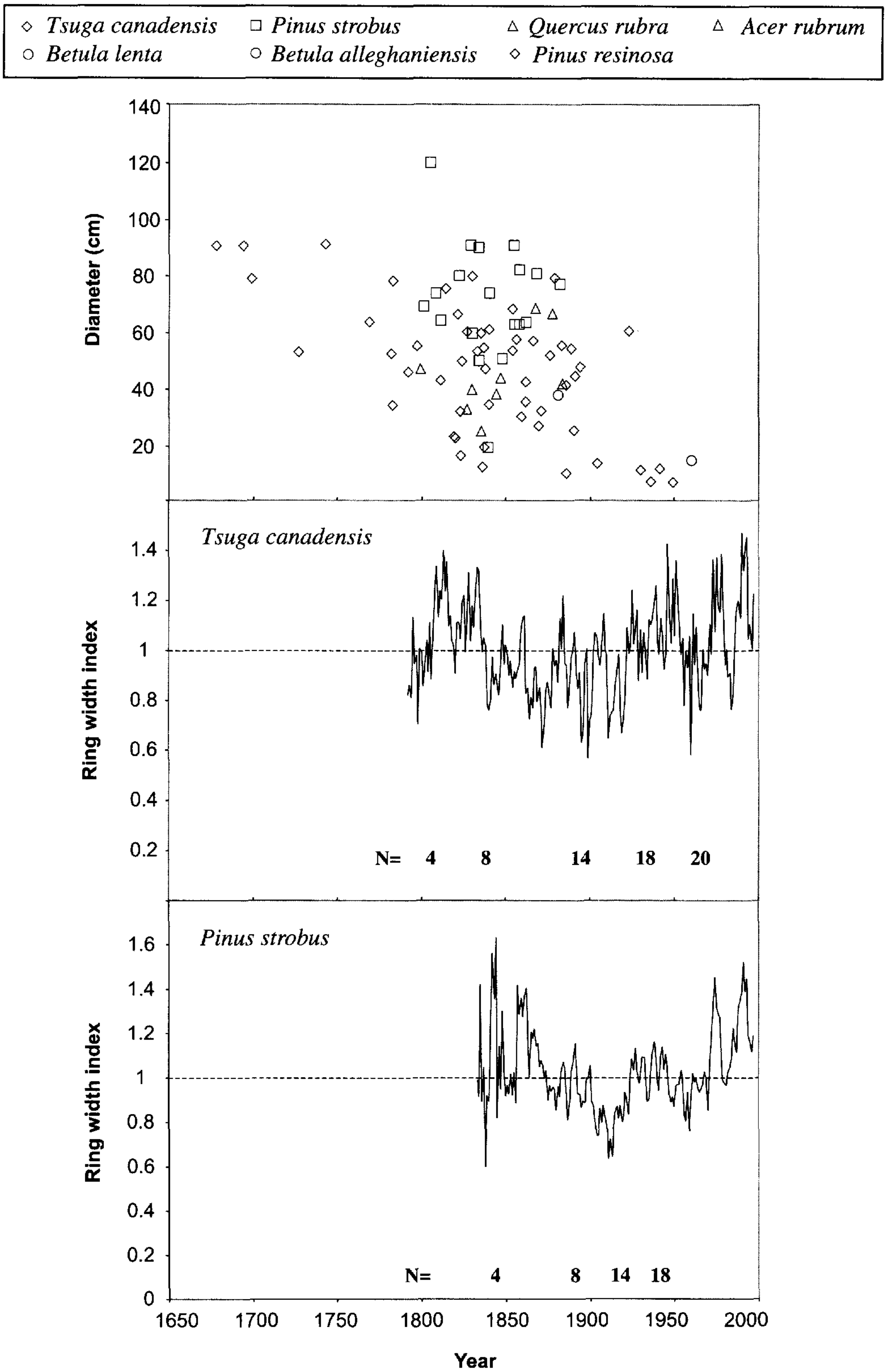
Fig. 2. Canopy class distribution of tree species sampled in plots in an old-growth hemlock – white pine – northern hardwood forest at the Ice Glen Natural Area, southwestern Massachusetts.



rum L.) (Table 1). The six remaining species represent a combined relative importance value of 20%. The high importance value of hemlock is due to a very high score in each of the importance value categories. White pine exhibits relatively high frequency and dominance. Red maple is notable for its high frequency, and, to a lesser extent, its density (Table 1). The total basal area of all trees in the forest is 60.2 m^2 per ha. A high basal area value is typical of many eastern hemlock – white pine forests (cf. Whitney 1994; Abrams and Orwig 1996). The diameter distribution of all measured trees in each plot approximates an inverse-J distribution, typical of an unevenly aged forest, except for the relatively high values in the 35- and 45-cm diameter classes (Fig. 1; Smith 1986). Hemlock dominates every diameter class from 14 to 95 cm. White pine is well represented in the 14- to 75-cm diameter classes. The smallest diameter classes are also dominated by red maple and yellow birch (*Betula alleghaniensis* Britton).

Hemlock dominates each of the canopy classes, followed by white pine and red oak (*Quercus rubra* L.) in the domi-

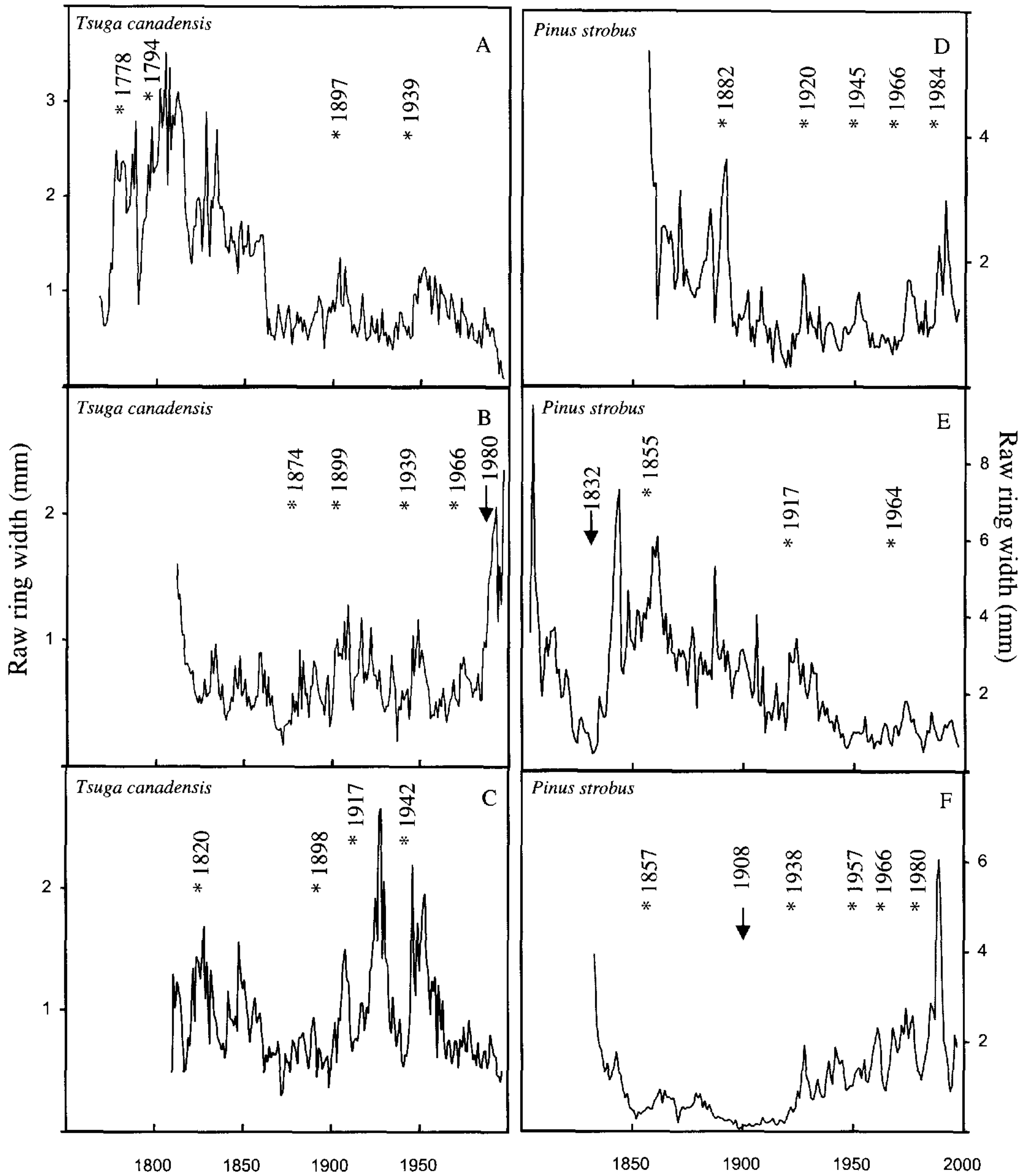
Fig. 3. Age–diameter relationships for all cored trees (A) and the mean standardized ring-width index for the oldest 20 *Tsuga canadensis* (B) and 18 *Pinus strobus* (C) trees in an old-growth hemlock – white pine – northern hardwood forest at the Ice Glen Natural Area, southwestern Massachusetts.



nant class, white pine, red maple, and red oak in the codominant class, and red maple and yellow birch in the intermediate class (Fig. 2). Tree reproduction is very scarce within the forest and is primarily hemlock (222 seedlings and 228 saplings per ha), red maple (56 seedlings per ha), and red oak (56 seedlings per ha).

Based on our sample of 82 cored trees, the forest is distinctly unevenly aged. Hemlock represents all of the trees

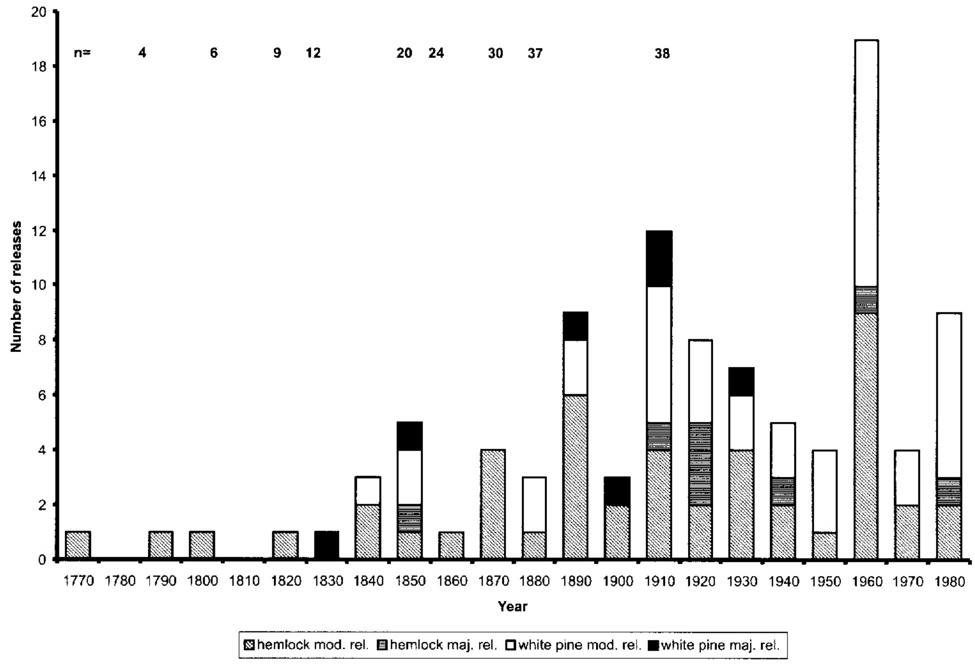
Fig. 4. Individual tree-ring chronologies and release dates for six selected *Tsuga canadensis* (A, B, and C) and *Pinus strobus* (D, E, and F) cores in an old-growth hemlock – white pine – northern hardwood forest at the Ice Glen Natural Area, southwestern Massachusetts. *, moderate release dates; ↓, major release dates (criteria from Nowacki and Abrams 1997).



that were established prior to 1800, and it has a maximum age of 321 years (Fig. 3). Recruitment of this species continued until 1950, albeit at what appears to be a much lower frequency than during the 19th century. White pine ages were restricted to the period from early 1800 to 1880; we sampled no live trees for this species from the 18th or 20th century. There was sporadic recruitment of hardwoods during the 19th century, but almost no tree ages for these species in the 20th century. The Master tree-ring chronology for hemlock indicates a period of generally high growth between 1807 and 1835 (indicative of a major stand-wide disturbance), followed by predominantly low growth from 1862 to 1881 (Fig. 3). Radial growth for hemlock was substantially above average for most years from 1924 to 1953, 1973 to 1981, and 1986 to 1995. The Master tree-ring chronology for white pine exhibits periods of above-average growth from 1857 to 1874, below-average growth from 1901 to 1923, and dramatic growth increases after 1971 and 1982. Many of the same growth variations can be seen in both the hemlock and white pine chronologies.

Radial growth patterns and release dates for individual hemlock and white pine trees are shown in Fig. 4. Hemlock growth ranged from a low of 0.08 mm per year to a high of 3.35 mm per year (Fig. 4A). White pine had a greater range in growth rate from 0.07 to 9.31 mm/year (Figs. 4E and 4F). Both hemlock and white pine exhibited a relatively high number of moderate releases. The timing of these releases reflected some consistency as well as variation among individual trees. For example, releases in 1897–1899, 1917–1920, 1939–1942, and 1964–1966 were recorded in

Fig. 5. Decadal distribution of the total number of trees with major and moderate releases for *Tsuga canadensis* and *Pinus strobus* in an old-growth hemlock – white pine – northern hardwood forest at the Ice Glen Natural Area, southwestern Massachusetts (criteria from Nowacki and Abrams 1997).



three or four of these six trees. Most of the other major and moderate releases are present only in individual cores. The hemlock tree in Fig. 4A had high growth early followed by progressively lower growth over time; this is indicative of a fairly constant growth rate in which the annual wood increments are distributed over an increasingly larger circumference. The hemlock in Fig. 4B had fairly consistent growth for 160 years before a major release in 1980 dramatically increased its growth rate. The white pine in Fig. 4E had high initial growth starting in 1804 followed by a rapid growth decline and then a major release in 1832. This is indicative of its establishment in a small gap followed by gap closure and then gap opening, leading to canopy accession. This tree then had decreasing ring width with age because of the size effect mentioned above. The white pine in Fig. 4F had moderate early growth, followed by decreasing growth for the next 70 years. It then experienced a series of major and moderate growth releases between 1908 and 1980, resulting in growth increases from <0.1 to 6.0 mm per year. Following a peak in 1990, its growth rate declined dramatically.

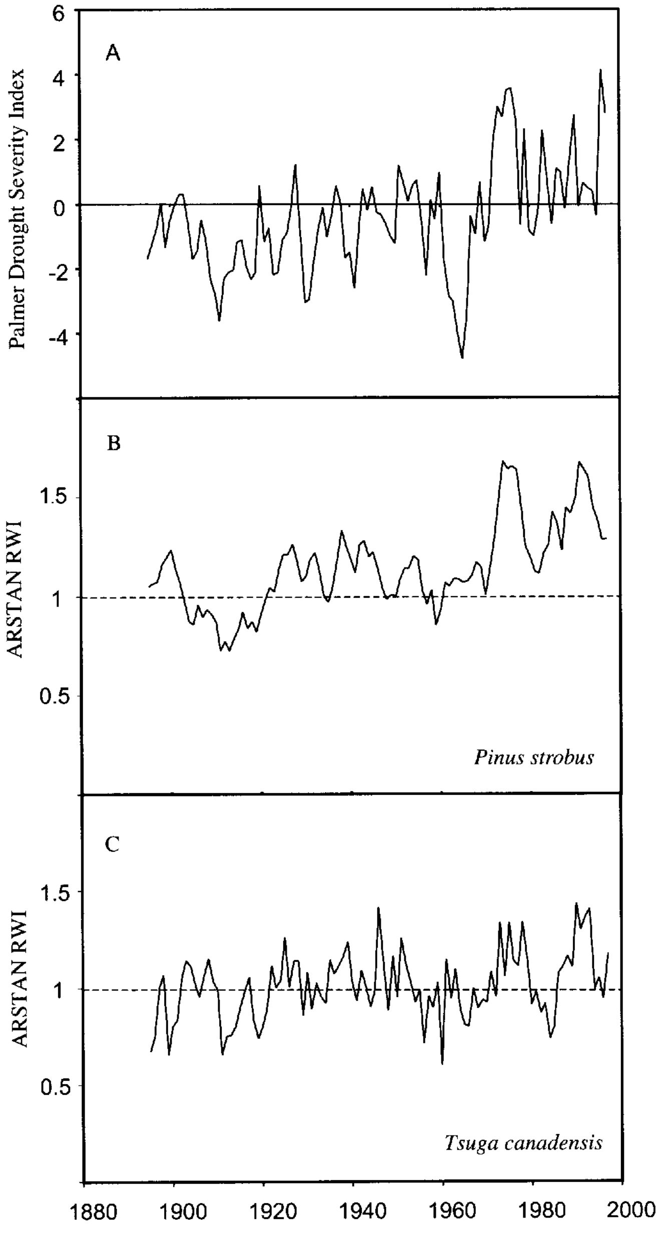
Radial growth releases, of both the major and moderate category, were recorded in hemlock and white pine trees for most decades from 1790 to 1990 (Fig. 5). A relatively large number (25–30%) of releases were recorded in trees during the decades of 1850, 1890, and 1910, but the largest release number (50%) occurred in the 1960s.

The Palmer drought severity index (PDSI) in southwestern Massachusetts was substantially negative (i.e., drought conditions) for most years from 1895 to 1942 and 1961 to 1967, and generally well above average for most years from 1972 to 1998 (Fig. 6). The ARSTAN tree-ring chronology in white pine and hemlock is strongly and positively correlated ($p < 0.001$) with annual PDSI ($r = 0.69$ and 0.39, respectively; Fig. 6). Both species were very reponsive to low PDSI in the early 1900s and high PDSI in the 1970s, 1980s, and 1990s. Hemlock exhibited decreased growth during the severe 1960s drought; this is not apparent in white pine. White pine ARSTAN is negatively related to October PDSI of the previous year, postively related to August PDSI of the current year (Fig. 7), and positively related to the prior 2 years of growth (data not shown). Hemlock ARSTAN is positively related to PDSI of the previous year July, current year January, July, and August (Fig. 7), and the prior 2 years of growth. Hemlock ARSTAN is negatively related to April PDSI of the current year.

Discussion

The results of this study suggest that the existing white pine was recruited in the old-growth forest at Ice Glen between 1800 and 1880. These data suggest a new category for white pine dynamics in eastern old-growth forests; namely, unevenly aged populations of white pine recruiting in an old-growth hemlock canopy. This seems to have been facilitated by a series of major disturbances to the stand in the early to mid-1800s, which is consistent with white pine's reputation of requiring intermediate- to large-sized disturbances for canopy recruitment. Previously documented examples of white pine establishment in old-growth forests include (*i*) an evenly aged population in the initial stand establishment phase following catastrophic disturbance, such as extensive blowdown, land clearing, or fire (Lutz 1930*b*; Morey 1936; Heinselman 1973; Patterson and Foster 1990); (*ii*) an unevenly aged population forming after protracted recruitment in the initial stand establishment phase following catastrophic disturbance, thus playing the role of both early and middle successional species (Hough and Forbes 1943; Abrams and Orwig 1996); (*iii*) evenly aged cohorts recruiting in intermedi-

Fig. 6. Palmer drought severity index for southwestern Massachusetts (A), and ARSTAN ring-width index (RWI) chronologies for white pine (B) and hemlock (C) at the Ice Glen Natural Area, southwestern Massachusetts.



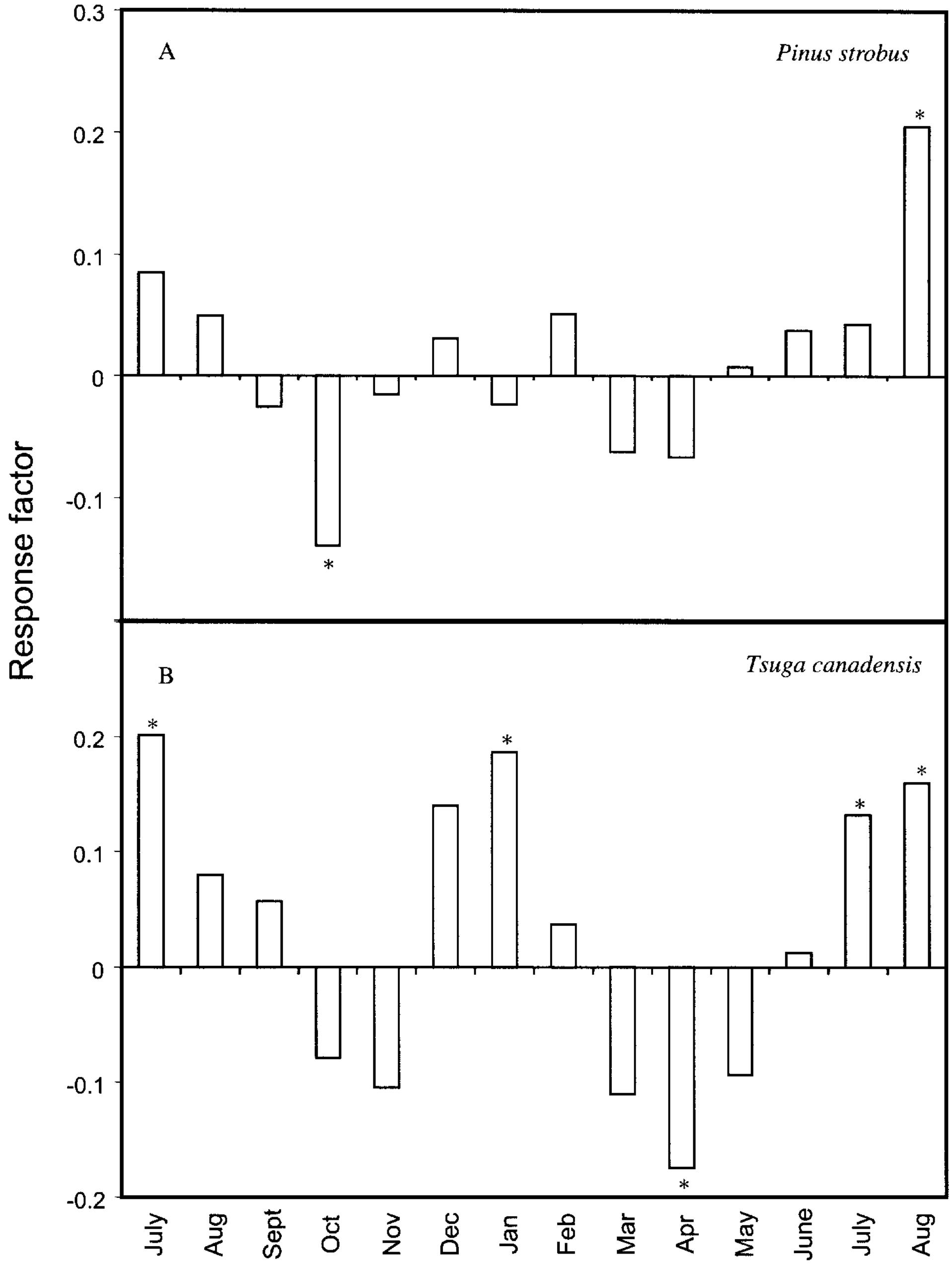
ate-sized gaps in unevenly aged forests following canopy disturbance (Hibbs 1982*a*; Abrams et al. 1995); (*iv*) scattered white pine individuals capturing small gaps in mixed-species stands (Hibbs 1982*a*, 1982*b*; Ruffner and Abrams 1998); and (*v*) an unevenly aged physiographic climax on certain high elevation sites, sandy soils, or extreme northern forests (Cline and Spurr 1942; Holla and Knowles 1988).

The absence of older white pine dating before 1800 at the study site is intriguing, because the maximum longevity of this species is typically 300–350 years (Hough and Forbes 1943; Stearns 1950; Abrams and Orwig 1996). However, care must be taken when interpreting static age structure data because of differential mortality with various age and canopy classes and stand history events (Johnson et al. 1994). The lack of older white pine may be due to the relatively short longevity in this species on the extreme slopes of Ice Glen. White pine is known to be particularly sensitive to windthrow because of its tall stature, often growing as an emergent in eastern forests, and the fact that it tends to be shallowly rooted (Cline and Spurr 1942; Stearns 1950; Foster 1988*b*; Patterson and Foster 1990). Moreover, white pine is a high-quality lumber species, and it may have been selectively logged at Ice Glen around 1800. However, we found no evidence of cut stumps, suggesting that the old-growth portion may have escaped logging owing to the extreme rocky slope. There is also an absence of pre-1800 individuals for the northern hardwood species at the site, many of which tend to live 200–300 years.

Annual radial growth of white pine and hemlock at Ice Glen has been influenced by stand history, disturbance factors, as well as climatic variables during the last 110 years. White pine exhibited a wide range of growth patterns, including a tendency for high growth rates early on, decreasing growth over time, very low growth rates (as low as 0.07 mm per year) for protracted periods, and dramatic growth increases (up to 9.5 mm) following canopy disturbances. Similar, but more moderate, growth patterns are evident in hemlock. Decreases in the ARSTAN chronologies in the early 1900s is likely due to the drought conditions at that time. However, both species tended to have above-average growth in the 1920s, 1930s, and 1940s, despite several prolonged droughts during those decades. Moreover, the response to severe drought in the early 1960s was muted or nonexistent in the hemlock and white pine chronologies. However, a large number of radial growth releases recorded in the mid-1960s appear to be due to the cessation of severe drought followed by very high PDSI in the 1970s. Significant growth releases in *Pinus rigida* Mill. in southeastern New York resulted from large increases in precipitation and tempertaure following severe drought in the 1960s (Abrams and Orwig 1995). High growth in white pine and hemlock at Ice Glen in the 1970s and 1990s was associated with wet climate (high PDSI) during those times. It is somewhat unusual to obtain significant climatic correlations in closed-canopy forests in the eastern United States because of the profound influences of competition and ecological disturbances on tree-ring growth (Fritts 1976). This suggests that trees growing on extreme sites, such as Ice Glen, are climatically sensitive and represent an important resource for dendroclimatology studies, even in closed-canopy forests (Fritts 1976; Phipps 1982; Cook 1987; Abrams and Orwig 1995; Ruffner and Abrams 1998).

The apparent cessation of white pine recuitment after 1880 at Ice Glen may be due to the relative intolerance of this species to the understory conditions of an old-growth forest, including low light, organic seedbed, and high root competition (Cline and Spurr 1942; Abrams et al. 1995). The Master tree-ring chronology indicates the absence of major stand-wide disturbances between 1860 and 1975, which may have retarded recruitment of white pine in lieu of the later successional hemlock. Many studies suggest that white pine establishment is dependent on large-scale disturbances, and may require fire-created mineral soil (Maissurow 1941; Heinselman 1973; Foster 1988*a*). The

Fig. 7. Response function analysis for the monthly Palmer drought severity index for southwestern Massachusetts with ARSTAN ring-width index chronologies for white pine (A) and hemlock (B) at the Ice Glen Natural Area, southwestern Massachusetts.



loss of chestnut from chestnut blight at Ice Glen probably contributed to the large number of individual tree-ring releases, but not a substantial increase in tree recruitment, as only one such episode was recorded in the early 1900s. A recent fire in the stand appears to have had little impact on tree establishment, as very few tree seedlings and saplings are present at Ice Glen. In addition, a lack of tree recruitment during the 20th century in this and several old-growth forests in the mid-Atlantic region may be due to intensive deer browsing (Abrams et al. 1995; Abrams and Orwig 1996; Orwig and Abrams 1999).

The future composition of Ice Glen will be highly dependent on allogenic factors. Hemlock has a long history of dominance on the site and it certainly has the potential to dominate long into the future as a late successional or climax species. However, much of the existing hemlock in southern New England is threatened by destruction from the hemlock woolly adelgid (*Adelges tsuga* Annands) (Orwig and Foster 1998). Given its current rate of spread, the woolly adelgid is likely to destroy much of the hemlock at Ice Glen over the next 10–15 years. We believe that hardwood species will continue to play an important role as minor dominants at the site via gap capture or increases over successional time. Red oak, yellow birch, and red maple are known for their gap-phase ability in mature and old-growth forests (Morey 1936; Forcier 1975; Hibbs 1982*b*; Abrams and Downs 1990; Abrams 1998). We anticipate that large-scale disturbances in the future, such as hemlock woolly adelgid, hurricanes, and ice storms, may provide white pine and hardwood species new opportunities for recruitment (cf. Foster 1988; Foster and Boose 1992; Abrams et al. 1995). However, the continuation of intensive deer browsing will make future canopy recruitment very difficult for all of the tree species. The results of this dendrochronological study suggest that old-growth forests on extreme sites in the eastern United States may be particularly sensitive to direct and indirect allogenic factors and climatic variations, and represent important resources for understanding ecological history and the global change phenomenon.

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