

Dendroecology and climatic impacts for a relict, old-growth, bog forest in the Ridge and Valley Province of central Pennsylvania, U.S.A.

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Abstract: We report on the 440-year dendrochronological history of a relict, bog forest in the Ridge and Valley Province of central Pennsylvania that contains extreme southern, disjunct populations of *Picea mariana* (Mill.) BSP and *Abies balsamea* (L.) Mill. The forest is dominated by *Tsuga canadensis* (L.) Carr. (49% relative importance value), *Picea mariana* (16%), and *Acer rubrum* L. (15%). The few remaining *Abies balsamea* trees are in an advanced state of decline. Many *Nyssa sylvatica* Marsh. and *T. canadensis* trees recruited from 1560 and 1700, respectively, until 1890. However, the majority of the other tree species recruited during a 40-year period following selective logging of the forest in the 1890s and fires in about 1900 and 1914. We found a scarcity of tree saplings and no evidence of recruitment into the tree-size class for any species after 1950. The master tree-ring chronology for both *N. sylvatica* and *T. canadensis* exhibits a marked increase after the 1890s logging and a decrease after a 1900 fire. In addition, a large number of releases in individual tree chronologies occurred over the last 400 years, indicating the frequent occurrence of small-scale disturbances. Tree-ring growth during the 20th century was reduced by droughts and cool temperatures in the 1920s and in the early to middle 1960s. *Abies balsamea* cores exhibit a marked growth decline in 1986. *Tsuga canadensis* growth was very low between 1970 and 1998, despite a generally warm and wet climate during that time. *Picea mariana* had a dramatic increase in growth during very warm and wet climate between 1995 and 1998. Most *Abies balsamea* trees have reached their pathological age of 50–85 years and have active *Armillaria* root rot, insect infestations, and very poorly developed crowns. These symptoms or severe growth declines are not present in *Picea mariana*. It appears that the 10 000 year history of *Abies balsamea* presence at Bear Meadows will end soon, with no opportunity to reestablish itself because of the lack of a local seed source. The results of this study suggest that relict tree populations in the eastern United States may be particularly sensitive to direct and indirect anthropogenic impacts and climatic variations, and represent important benchmarks for comparisons with future studies.

Key words: tree rings, disturbance, climate, global change, central Pennsylvania.

Résumé : Les auteurs font état des 440 ans d'histoire dendrochronologique d'une forêt tourbeuse vestigiale de la province Ridge and Valley au centre de la Pennsylvanie, laquelle contient les populations disjointes les plus méridionales du *Picea mariana* (Mill.) BSP et de l'*Abies balsamea* (L.) Mill. La forêt est dominée par le *Tsuga canadensis* (L.) Carr. (importance relative de 49 %), le *Picea mariana* (16 %), et l'*Acer rubrum* L. (15 %). Les quelques tiges de l'*Abies balsamea* qui restent sont dans un état avancé de dépérissement. Plusieurs des tiges du *Nyssa sylvatica* Marsh. et du *T. canadensis* ont été recrutées entre 1560 et 1700, respectivement, jusqu'en 1890. Cependant, la majorité des autres espèces arborescentes se sont installées au cours d'une période de 40 ans qui a suivi une coupe sélective de la forêt dans les années 1890 et des feux en 1900 et 1914. On observe une rareté de jeunes plants d'arbre et aucune évidence de recrutement de tiges aux dimensions d'arbres chez aucune des espèces, après 1950. La chronologie maîtresse des anneaux de croissance chez le *N. sylvatica* et le *T. canadensis* montre une importante augmentation après la coupe des années 1890, et une diminution après le feu de 1900. De plus, on observe un grand nombre de recrudescences dans les chronologies d'arbres individuels au cours des 400 ans, ce qui indique l'intervention fréquente de perturbations localisées. La croissance annulaire des arbres au cours du 20ième siècle a été réduite par des sécheresses et des températures fraîches au cours des années 1920 et entre le début et la moitié des années 1960. Les carottes de l'*Abies balsamea* montrent un déclin rapide en 1986. La croissance du *T. canadensis* fut très faible entre 1970 et 1998, en dépit d'un climat chaud et humide au cours de cette période. Le *Picea mariana* montre une croissance très marquée au cours de la période très chaude et humide de 1995 à 1998. La plupart des tiges de l'*Abies balsamea* ont atteint le stade pathologique entre 50 et 85 ans et sont envahis par l'*Armillaria*, causant une pourriture racinaire, et infestés d'insectes; ils montrent des cimes très pauvrement développées. Ces symptômes ou importants déclin de croissance ne se

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retrouvent pas chez le *Picea mariana*. Il semble qu'après 10 000 ans d'histoire à Bear Meadows, l'*Abies balsamea* soit en voie d'extinction, sans possibilité de se rétablir faute de semence locales. Les résultats de cette étude suggèrent que les populations d'arbres vestigiales dans l'est des Etats-Unis pourraient être particulièrement sensibles aux impacts anthropogènes directs et indirects ainsi qu'aux variations climatiques, et représentent des repaires importants pour comparaisons avec des études futures.

Mots clés : anneaux de croissance des arbres, perturbation, climat, changement global, centre de la Pennsylvanie.

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Introduction

Tree-ring analysis and tree-age structure are key aspects in the study of stand dynamics and ecological history (Fritts and Swetnam 1989; Abrams et al. 1995). From this approach, researchers have been able to reconstruct the historical development of forests in terms of species recruitment patterns, periodicity and intensity of disturbances, the impacts of yearly climatic variation and extreme weather phenomena, and populations and successional dynamics (Foster 1988; Abrams and Orwig 1995; Abrams et al. 1995). Coupling tree-ring chronologies, age structure, and land-use history has proven to be a particularly robust approach for understanding long-term variation in forest dynamics and history (Foster 1988; Abrams and Orwig 1995; Abrams et al. 1995). Tree-ring analysis also is central to the study of forest decline and global change phenomena (Adams et al. 1985; Cook and Zedaker 1992).

During the last glaciation, in the late-Quaternary period, cooler climatic conditions in the eastern United States facilitated the southward migration of northern tree species to the mid-Atlantic and southern Appalachian regions (Braun 1950; Delcourt and Delcourt 1988). With glacial retreat and climatic warming at the beginning of the Holocene (10 000 years B.P.), many northern tree species migrated northward and were displaced in the southern latitudes (White and Cogbill 1992). However, northern tree species persisted on specialized sites, forming disjunct populations, in the mid-Atlantic and southern Appalachians that provided a cool, moist habitat, such as high-elevation mountains, elevated bogs, and frost pockets. In the case of *Picea mariana* (Mill.) BSP, the southernmost population of the species exists in a relict bog in central Pennsylvania, called Bear Meadows Natural Area (Westerfeld 1959; Little 1971). A disjunct population of *Abies balsamea* (L.) Mill. also exists at Bear Meadows, although the southernmost populations for the species includes several locations in West Virginia and Virginia (Little 1971; Stephenson and Adams 1986). Declines in *Abies balsamea* growth have been reported in West Virginia (Adams et al. 1985), and we have observed frequent mortality of this species at Bear Meadows over the last decade. Moreover, mortality and growth decline in several *Picea* and *Abies* species throughout the Appalachian Mountains has been the subject of considerable study and debate (Rheinhardt 1984; Adams et al. 1985; Cook and Zedaker 1992; White and Cogbill 1992). The reasons for the *Picea* or *Abies* decline are not well understood, particularly for bog communities such as Bear Meadows. Therefore, the study of relict tree species populations is particularly important for monitoring the

impacts of global change phenomena and other direct and indirect anthropogenic impacts.

Old-growth forests presently occupy an extremely small area of the eastern United States. Most of the remaining old-growth stands are located in very remote or inaccessible upland locations that were difficult to log, e.g., steep talus slopes (Mikan et al. 1994; Ruffner and Abrams 1998). Private ownership and land disputes among logging companies harvesting the original forest have also allowed old-growth stands to persist (Abrams and Downs 1990; Nowacki and Abrams 1994). Nonetheless, very few old-growth examples presently exist on bottomland sites because of their easy accessibility and suitability for farming, especially in the mid-Atlantic region. There exist a substantial number of dendroecology papers involving old-growth forests on upland sites (Cook and Zedaker 1992; Mikan et al. 1994; Abrams and Orwig 1995, 1996; Abrams et al. 1995; Ruffner and Abrams 1998) but very few involving old-growth forests on bottomland sites in the United States (Nowacki and Abrams 1994; Cho and Boerner 1995; Orwig and Abrams 1999). Therefore, the ecological history, periodicity and intensity of disturbances, and successional development in old-growth, bottomland sites are very poorly understood, and this information is practically nonexistent for bog forests (Motzkin et al. 1993; Heitzman et al. 1997). Most tree-ring studies of relict northern conifer populations focus on high-elevation *Picea rubens* Sarg. in the central and southern Appalachians (Adams et al. 1985; McLaughlin et al. 1987; Cook and Zedaker 1992). To our knowledge, no investigations have been conducted in old-growth, bog forests in the mid-Atlantic region to study the dynamics and dendroclimatology of relict *Picea mariana* and *Abies balsamea* populations.

In this study, we investigate the dendrochronology of a relict, old-growth, mixed northern conifer – hardwood bog forest at the Bear Meadows Natural Area in central Pennsylvania. *Nyssa sylvatica* Marsh. trees in the forest are up to 440 years old, which probably represent the oldest trees present in relict bogs in the mid-Atlantic region. However, the forest was selectively logged in the 1890s, burned in the early 1900s, and is subject to increasing deer browsing pressure, characteristic of most Pennsylvania forests during the 20th century (Bramble and Goddard 1953; Westerfeld 1959). Based on the long tree-ring chronology available for this forest, it represented a rare opportunity to study ecological history prior to European settlement and the direct and indirect impacts of natural and anthropogenic disturbances and climate over the last 110 years. The specific objectives of the study are to (i) document the composition and diameter distribution of the forest, (ii) investigate the current age struc-

Table 1. Results of the 1998 vegetation survey at Bear Meadows Bog, Pennsylvania.

Species	Frequency	Density (stems/ha)	Dominance (m ² /ha)	Relative frequency	Relative density	Relative dominance	Importance value
<i>Acer rubrum</i>	14	95	5.85	19.7	13.1	13.3	15.4
<i>Betula alleghaniensis</i>	11	55	1.40	15.5	7.6	3.2	8.8
<i>Fraxinus pennsylvanica</i>	1	2	0.13	1.4	0.0	0.3	0.6
<i>Nyssa sylvatica</i>	6	17	1.45	8.5	2.3	3.3	4.7
<i>Picea mariana</i>	15	37	9.76	21.1	5.1	22.1	16.1
<i>Pinus strobus</i>	4	17	3.46	5.6	2.3	7.9	5.3
<i>Tsuga canadensis</i>	20	502	22.05	28.2	69.2	50.0	49.1
Totals	71	725	44.10	100	100	100	100

Note: Frequency is the number of plots where the species occurred. Density is the number of individuals of a species. Dominance is the basal area of a species. Importance value was calculated by averaging the relative frequency, relative density, and relative dominance scores for each species. Relative values are percentages.

Table 2. Seedling and sapling data collected at Bear Meadows Bog, Pennsylvania.

Species	Seedlings less than 10 cm (no./ha)	Seedlings taller than 10 cm (no./ha)	Saplings (no./ha)
<i>Acer rubrum</i>	99 121	282	0
<i>Betula alleghaniensis</i>	1 130	188	12
<i>Nyssa sylvatica</i>	1 413	0	0
<i>Picea mariana</i>	5 747	3203	0
<i>Pinus strobus</i>	942	0	0
<i>Tsuga canadensis</i>	274 563	4616	170
Totals	382 916	8289	182

Note: Seedlings less than 10 cm include first-year seedlings.

ture and tree-ring variation, (iii) document the forest responses to natural and anthropogenic disturbances and climate variation, and (iv) describe the ecological history, including *Abies balsamea* decline, in this relict, bog forest at Bear Meadows.

Study area

This study was conducted within a 20-ha area of bog forest known as Bear Meadows Natural Area (40°48'52"N, 77°55'50"W). The study site is located within an elevated basin (610 m a.s.l.) in the Seven Mountains of Centre County in the Ridge and Valley Province of central Pennsylvania. Bear Meadows is considered an unusual boreal bog relict that lies well south of the Wisconsin glacial border (Braun 1950; Kovar 1965). The water is typically cold, shallow, acid, and dark with humus. A floating organic, sphagnum-dominated mat approximately 220 cm thick forms the forest floor (Westerfeld 1959; Kovar 1965). The climate of the region is a combination of dry continental and humid maritime (Braker 1981). Daily maximum and minimum temperatures averaged 15.0 and 4.6°C, respectively, and average yearly precipitation is 98 cm. The frost-free season is about 170 days. The forest was selectively logged between 1888 and 1894 and burned around 1900 and 1914 (Westerfeld 1959; Potter 1970). Flooding of the site due to beaver damming occurred several times in the early 1900s (Potter 1970). It has been reported that both *Picea mariana* and *Picea rubens* are present at Bear Meadows (Gordon 1976), with the former growing mainly on the wetter areas and the latter growing mainly on the drier areas nearer the edge of the bog forest (Dr. Kim Steiner, Penn State University, personal communication). To avoid edge effect with the upland

forests, our research transects were concentrated in the wetter areas of the bog forest. We determined that *Picea mariana*, not *Picea rubens*, dominated our study plots based on an examination of the needles and cones for many of the *Picea* trees.

Materials and methods

In October 1998, 20 fixed-area plots, located at 20-m intervals along parallel transects separated by 20 m through the forest interior, were used for vegetation and dendroecological sampling. Species, diameter, and crown class were recorded for all trees ≥8.0 cm diameter at breast height (DBH) occurring within 0.02-ha circular plots at each point. Tree crowns were classified into four categories (dominant, codominant, intermediate, and overtopped) based on canopy position (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 trees were cored for age determination and radial growth analysis. Trees were cored at 0.5 m height, with the exception of the large *Tsuga canadensis* (L.) Carr trees, with significant stem taper near the ground, which were cored at 1.37 m. Across the 20 study plots, we obtained cores from all the major species and a full range of diameter classes. However, none of the surviving *Abies balsamea* occurred in our study plots because of their very low number and clumped distribution. Therefore, additional trees were cored outside the study plots ($n = 116$), but within the bog forest, to increase our sampling of older trees for species' tree-ring chronologies and to include *Abies balsamea*. The number of cores obtained for each species was *T. canadensis*, 53; *Acer rubrum* L., 37; *N. sylvatica*, 35; *Abies balsamea*, 24; *Picea mariana*, 27; *Pinus strobus* L., 12; and *Betula alleghaniensis* Britton, 8 for a grand total of 196 cores. The 24 *Abies balsamea* we cored outside of our plots included the vast majority of live

Fig. 1. Diameter (at 1.37 m) distribution of tree species in an old-growth bog forest at Bear Meadows Natural Area in central Pennsylvania.

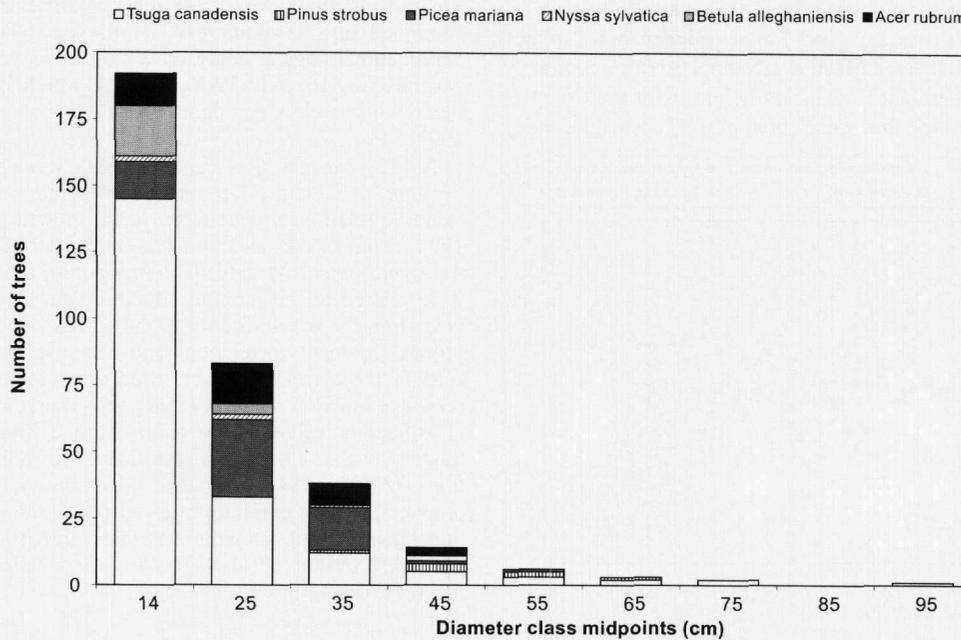
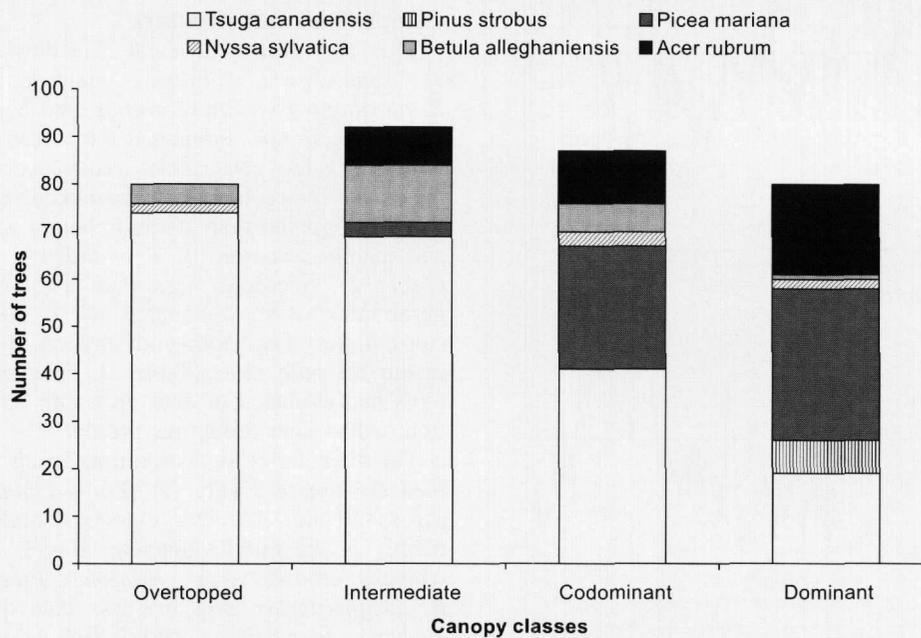


Fig. 2. Canopy class distribution of tree species in an old-growth bog forest at Bear Meadows Natural Area in central Pennsylvania.



trees for this species remaining at Bear Meadows. Saplings were counted by species in the entire 0.02-ha overstory plots. Saplings were classified as tree species ≥ 1.5 m in height but < 8.0 cm DBH. Seedlings (tree species < 1.5 m in height) were counted by species and sizeclass (less than vs. greater than 10 cm in height) in 5-m² plots nested within each of the overstory plots. Many of the seedlings less than 10 cm were first-year germinants. The frequency of deer droppings and deer browsing on woody vegetation was recorded in forty, 1-m² plots along the study transects.

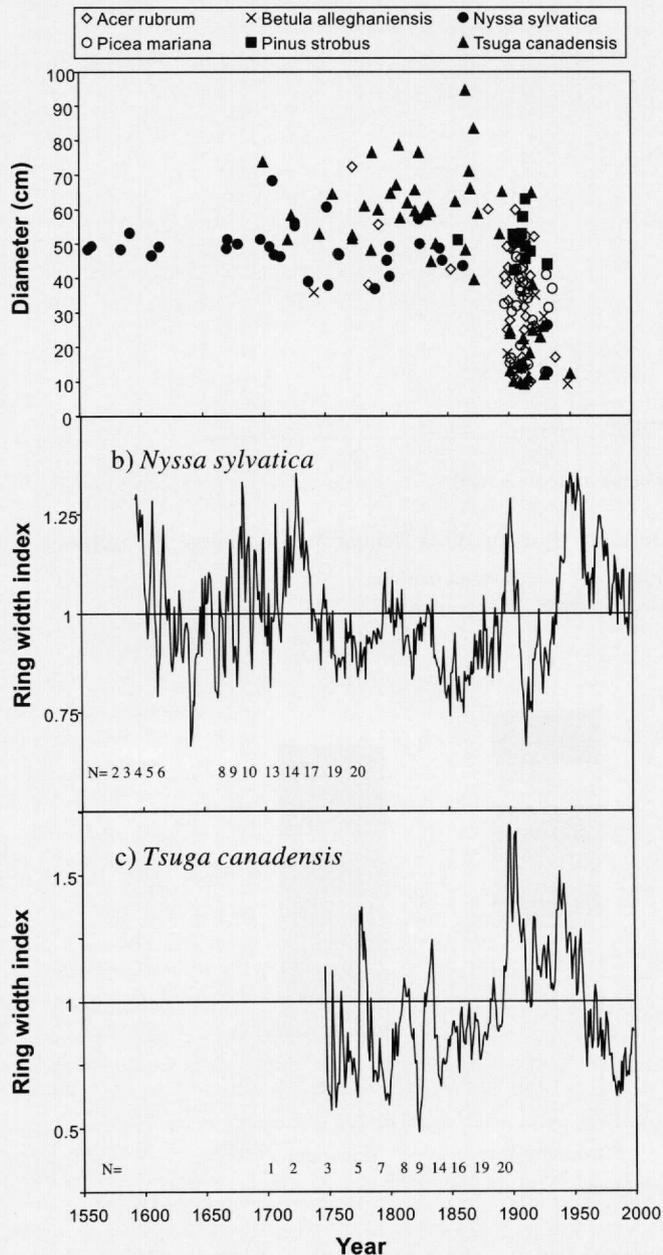
Radial growth analysis

All increment cores ($n = 196$) from the study area were dried, mounted, and sanded (Phipps 1985). All cores were skeleton plotted to identify signature years for cross dating to help identify

missing, partial, or false rings (Stokes and Smiley 1996). The age for all cores was identified using cross dating. 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 *Abies balsamea*, 20 *N. sylvatica*, 20 *Picea mariana*, 20 *T. canadensis*, 1 *Acer rubrum*, 10 *Pinus strobus*, and 2 *B. alleghaniensis* were measured for annual radial growth. Annual growth rings were measured to the nearest 0.01 mm on each tree core using either the MACDENDRO program (Regents Instruments Inc., Quebec, Canada) or the UniSlide "TA" Tree-Ring Measurement System (Velmex Inc., Bloomfield, N.Y.).

Moderate and major release dates (Lorimer and Frelich 1989) were calculated for a total of 70 *N. sylvatica*, *Picea mariana*, *T. canadensis*, *Acer rubrum*, and *Pinus strobus* cores from

Fig. 3. Age–diameter relationships for all cored trees, excluding balsam fir (a), and the mean standardized ring-width index for the oldest 20 *Nyssa sylvatica* (b) and *Tsuga canadensis* (c) in an old-growth bog forest at Bear Meadows Natural Area in central Pennsylvania. Trees were cored at 0.5 m height, with the exception of the larger hemlock that were cored at 1.37 m height.



overstory trees. We defined a moderate release as a growth increase of at least 25% sustained for 10 years and a major release as a growth increase of at least 50% sustained for 10 years (Nowacki and Abrams 1997). We defined recruitment as the date when trees reached 0.5 m height (or 1.37 m in case of the largest *T. canadensis* trees).

For the dendroecological analysis, raw ring widths were measured in the 20 cores of *Abies balsamea*, *N. sylvatica*, *Picea mariana*, and *T. canadensis*. The raw ring widths of each species were detrended with a negative exponential curve or negative linear function using the program ARSTAN available in the ITRDBL ver-

sion 2.1 (Cook et al. 1997). Detrending removes the effects of tree age and microsite and allows trees of different growth rates to be combined into a standardized chronology (Fritts 1976). For the dendroclimatic analysis, we used the ARSTAN chronology generated by the ARSTAN program, which is intended to reveal the strongest climatic signal in the tree-ring data (Cook et al. 1997).

A 113-year record of central Pennsylvania's precipitation, temperature, and Palmer Drought Severity Index (PDSI) was used to examine relationships between radial growth and climate (NOAA 1999, central Pennsylvania Division 5). ARSTAN chronologies of *Abies balsamea*, *N. sylvatica*, *Picea mariana*, and *T. canadensis* were related to the monthly climatic data using a dendroclimatic year from the previous July to the current August using Pearson's product-moment correlations and response function analysis. Results of the correlations were used as a guide for interpreting the response function analysis (Fritts and Xiangding 1986). The PDSI classification values range from extreme drought at -4.0 to extremely wet at 4.0; values less than -1.0 indicate drought conditions (Alley 1984). Response function analysis and Pearson's product-moment correlation tested for significant ($p < 0.05$) relationships between climatic variables and prior growth with the ARSTAN master chronologies of *Abies balsamea*, *N. sylvatica*, *Picea mariana*, and *T. canadensis*.

Results

Composition and structure

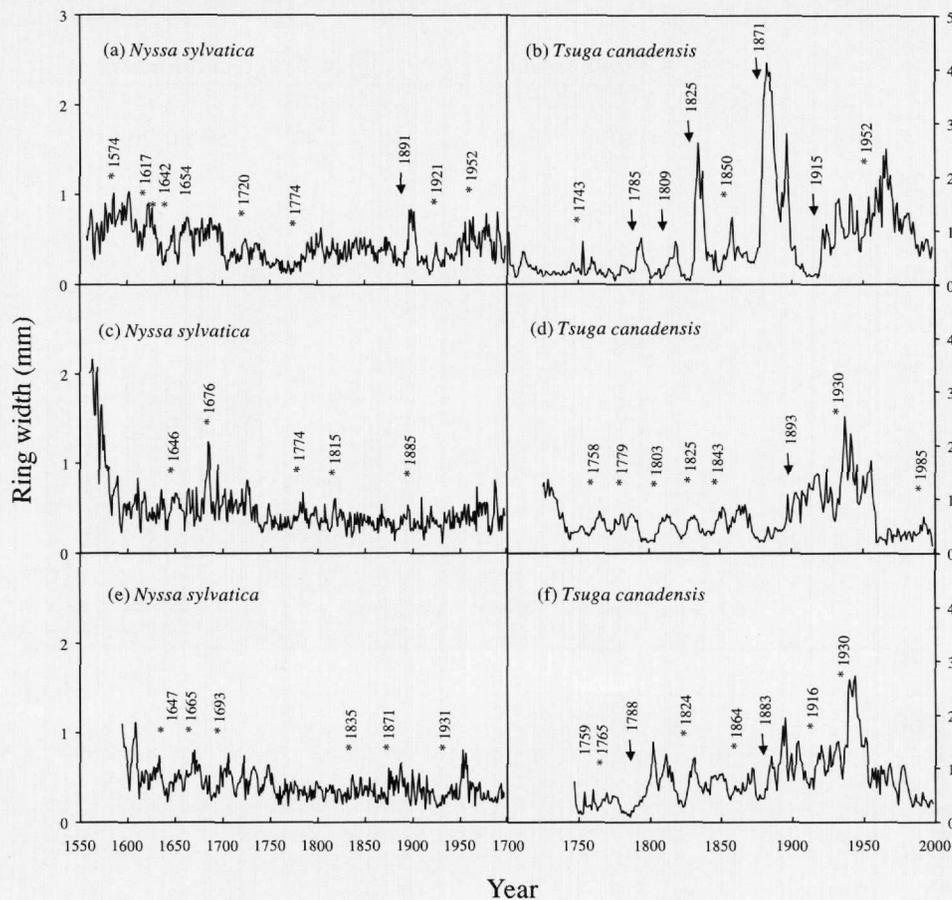
The bog forest at Bear Meadows is dominated by *T. canadensis*, *Picea mariana*, *Acer rubrum*, *B. alleghaniensis*, *Pinus strobus*, and *N. sylvatica* (Table 1). *Tsuga canadensis* dominated the forest across all three importance value categories: frequency, density, and dominance. No living *Abies balsamea* occurred in the study plots. Seedlings greater than 10 cm in height were relatively scarce and mainly consisted of *T. canadensis* and *Picea mariana* (Table 2). Seedlings less than 10 cm, mainly first-year germinants, were dominated by *T. canadensis* and *Acer rubrum*. Very few saplings of any tree species were recorded in our research plots (Table 2). Fifty percent of our study plots had evidence of deer browsing on the woody vegetation or had deer droppings present.

The diameter-class distribution for all trees closely resembled an inverse J (Fig. 1). *Tsuga canadensis* is important across all the diameter classes. *Pinus strobus* trees are mainly in the middle diameter classes from 30 to 70 cm, whereas most *Acer rubrum*, *Picea mariana*, and *B. alleghaniensis* trees are less than 40 cm DBH. *Picea mariana*, *Acer rubrum*, and *T. canadensis* are the most frequent species in the dominant and codominant canopy positions (Fig. 2). *Tsuga canadensis* dominates the intermediate and overtopped canopy positions.

Dendroecology

Four *N. sylvatica* trees are greater than 400 years (441 year maximum), and another five *N. sylvatica* are over 300 years old (Fig. 3). Long tree-ring chronologies also exist for *T. canadensis* (300 years old), *B. alleghaniensis* (257 years old), and *Acer rubrum* (225 years old). A large number of *N. sylvatica* trees were recruited from 1557 to 1870, excluding the period from 1620 to 1660. *Tsuga canadensis* and *N. sylvatica* had frequent recruitment from 1700 to 1890.

Fig. 4. Individual tree-ring chronologies and release dates for six selected *Nyssa sylvatica* and *Tsuga canadensis* cores in the old-growth bog forest at Bear Meadows Natural Area in central Pennsylvania. Asterisks show moderate release dates, and arrows show major release dates (criteria from Nowacki and Abrams 1997).



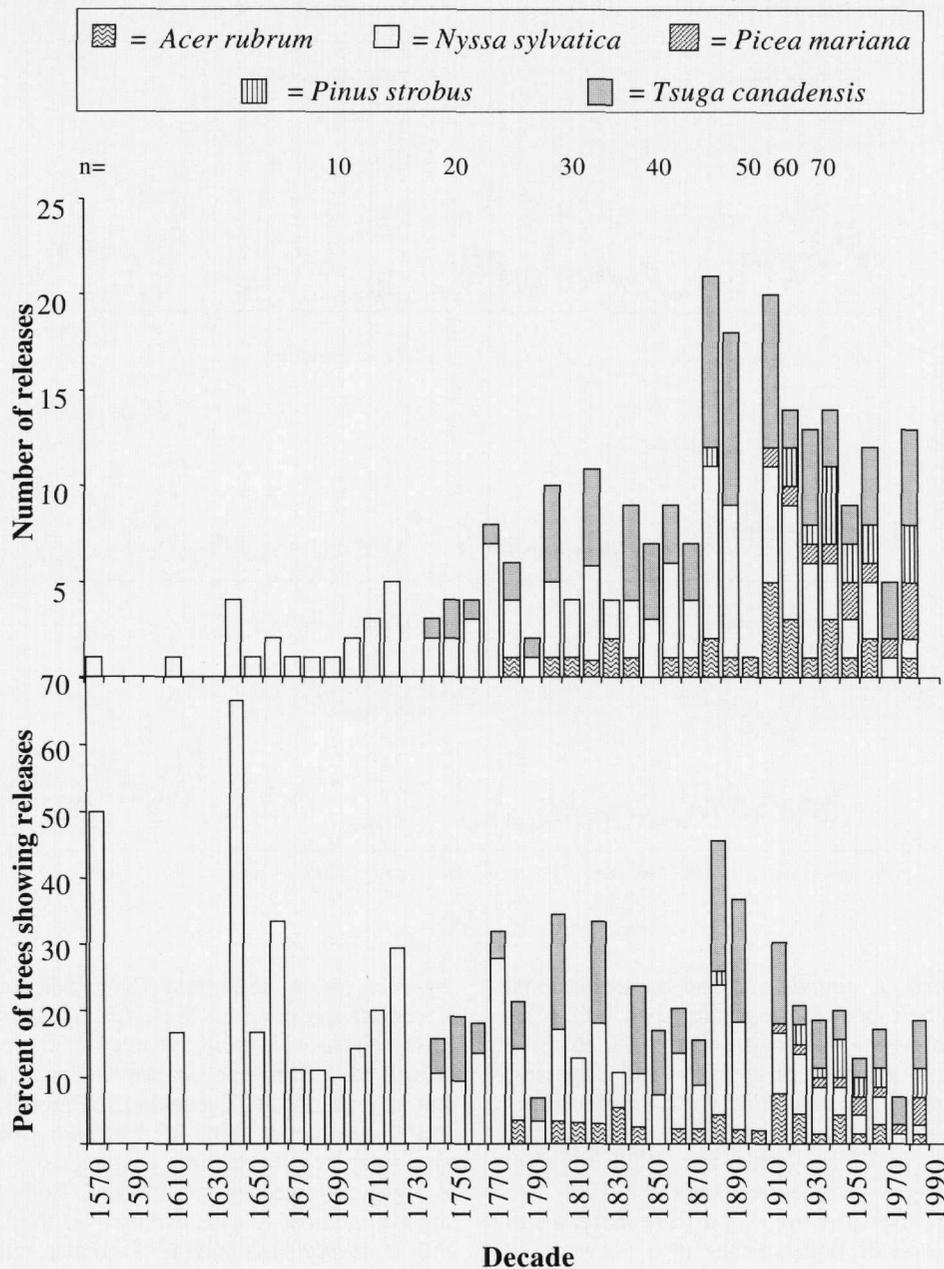
Other than *N. sylvatica*, *T. canadensis*, and the occasional *Acer rubrum*, few other species are greater than 100 years old in the forest. Following the logging in 1888, massive amounts of recruitment occurred for all of the major species, with the exception of *N. sylvatica* (Fig. 3). Large increases in the master tree-ring chronologies for both *N. sylvatica* and *T. canadensis* were associated with the 1888 logging. Marked decreases in growth occurred after the 1900 fire and, to a lesser extent, the 1914 fire. Significant increases in tree-ring growth of one or both species also occurred in 1700, 1770, 1800, 1857, 1888, 1915, 1935, and 1965, indicative of major or moderate standwide disturbance events. However, a general decline from highly elevated growth levels occurred from the 1940s or 1950s to the present for *N. sylvatica* and *T. canadensis*. *Tsuga canadensis* growth reached a minimum in the mid-1980s, followed by an increasing trend to 1998.

Representative cores of *N. sylvatica* and *T. canadensis* are presented to illustrate the variation in growth patterns and frequency of release dates (Fig. 4). *Nyssa sylvatica* generally exhibited fairly constant, low radial growth, averaging about $0.7 \text{ mm}\cdot\text{year}^{-1}$. In contrast, *T. canadensis* typically had a much higher average growth rate, $1.3 \text{ mm}\cdot\text{year}^{-1}$, and growth variation between $0.3 \text{ mm}\cdot\text{year}^{-1}$ and $4.0 \text{ mm}\cdot\text{year}^{-1}$. The *T. canadensis* core in Fig. 4b had peak growth rates follow-

ing releases in 1825 and 1871, whereas peak growth in *T. canadensis* cores in Figs. 4d and 4f followed a 1930 release. *Nyssa sylvatica* averaged 130 years per core with growth $<0.5 \text{ mm}\cdot\text{year}^{-1}$, compared with only 35 years with that growth rate in *T. canadensis*. *Nyssa sylvatica* (Fig. 4c) and *T. canadensis* (Fig. 4d) had high early growth followed by a steep growth decline, characteristic of trees originating in a gap followed by gap closure. Both species exhibited a large number of release events over the last 250–400 years, with *T. canadensis* having a greater number of major releases and the more conservative *N. sylvatica* having a greater number of moderate releases. Very few releases were recorded in the same year, indicating that the forest experienced a large number of small-scale disturbances each of which impacted a relatively small number of trees.

Releases in radial growth were recorded in nearly all decades over the last 360 years in the major tree species within the bog forest (Fig. 5). The actual number of releases is fairly low prior to 1700 because of the scarcity of trees greater than 300 years old. However, on a relative basis, the percentage of trees showing releases each decade has remained fairly constant over the last four centuries. The highest number of actual releases was recorded in the 1880s, 1890s, and 1910s associated with post-European settlement logging and fire in the stand. A very low number of releases

Fig. 5. Decadal distribution of the total and relative number of tree-ring releases by species in cores of the major species in the old-growth forest at Bear Meadows (criteria from Nowacki and Abrams 1997).



occurred between 1900 and 1909, reflecting the high growth activity during the preceding two decades and low growth after the 1900 fire.

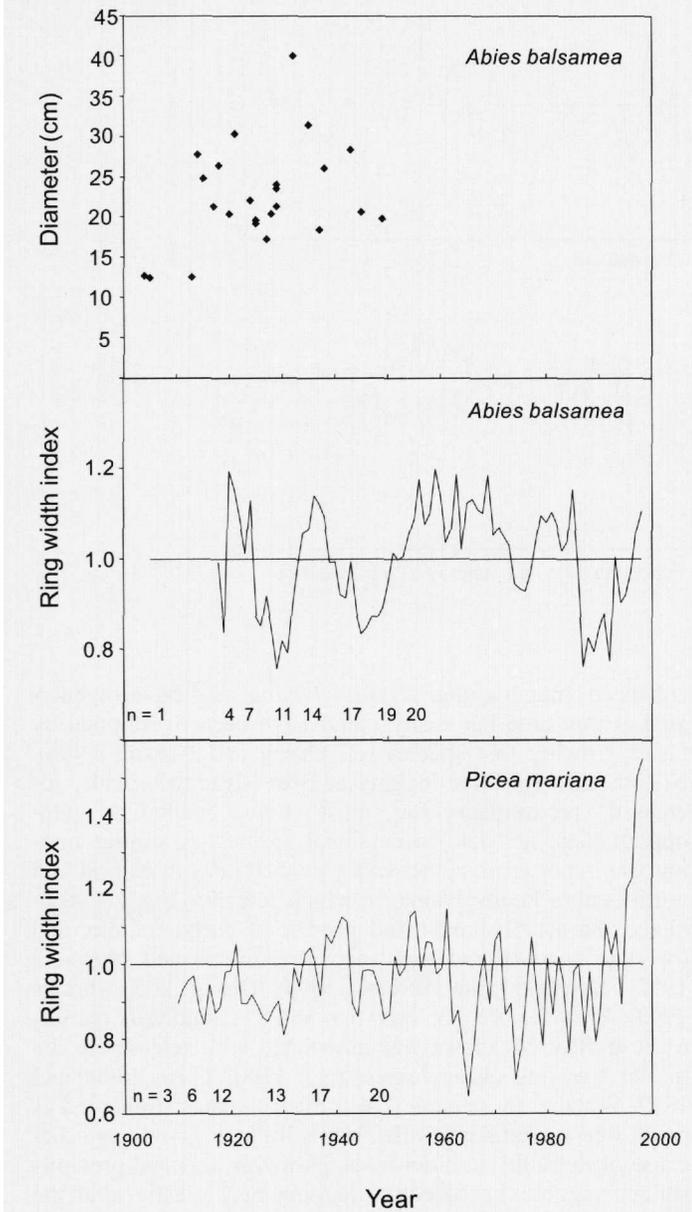
Twenty-four *Abies balsamea* trees occurring outside of our study plots had recruitment dates between 1903 and 1951 (Fig. 6). The master tree-ring chronologies for *Abies balsamea* and *Picea mariana* exhibit a fairly similar pattern of periodic rise and fall during the 20th century. This has resulted in distinct growth troughs for 1924–1932, 1943–1950, 1973–1977, and 1986–1995. However, the rapidity of decrease in *Abies balsamea* growth after 1986 is particularly dramatic and is not present in the *Picea mariana* chronology. A sharp increase in growth in both species occurred af-

ter 1993, elevating *Picea mariana* growth to its highest level and returning *Abies balsamea* growth to above average.

Dendroclimatology

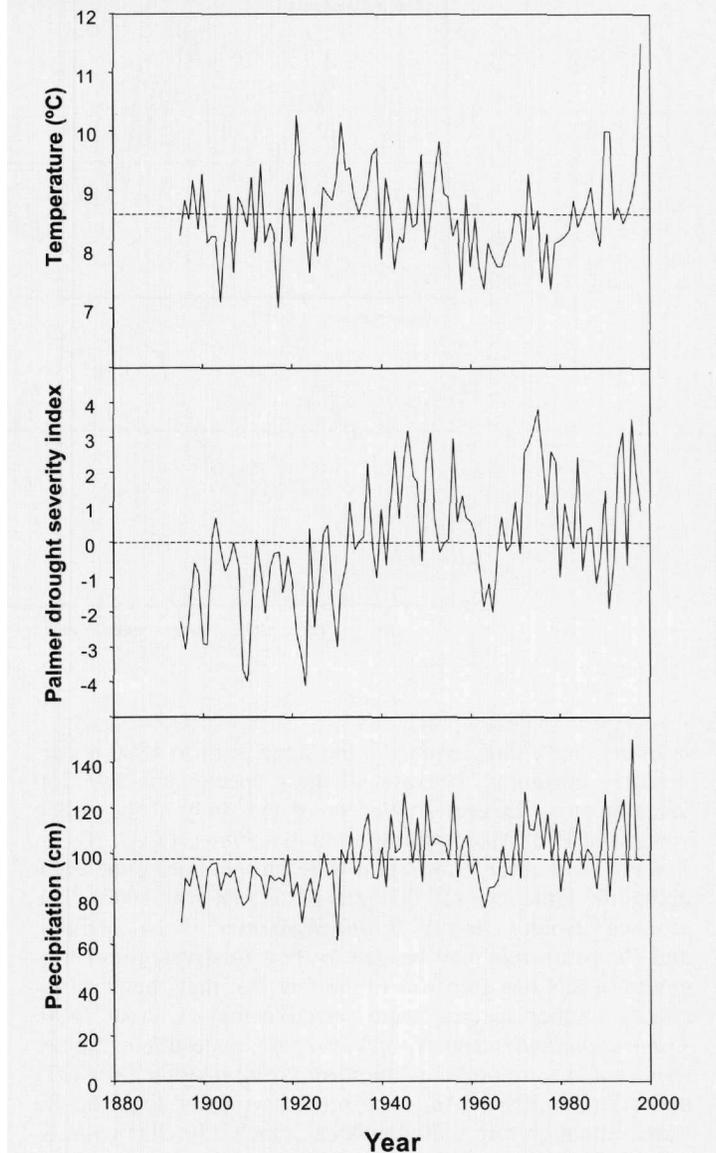
Annual temperature in central Pennsylvania was often below the 100-year mean during 1900–1918 and 1958–1990, above the 100-year mean from 1920 to 1957, and highest in 1998 (Fig. 7). Precipitation and the Palmer drought severity index (PDSI) were consistently below the 100-year average (i.e., drought conditions) from 1895 to 1932 and from 1960 to 1965 and generally well above average in the interim and latest periods (Fig. 7). Droughts in the 1890s, 1900s, and 1920s were particularly severe, while the 1960s droughts are

Fig. 6. Age–diameter relationships for 20 *Abies balsamea*, and the mean standardized ring-width index for the oldest 20 *Abies balsamea* and *Picea mariana* in an old-growth bog forest at Bear Meadows Natural Area in central Pennsylvania. Trees were cored at 0.5 m height.



notable for their long duration. The 1940s and 1950s were generally wet and warm with high PDSI. The wettest and warmest years on record are 1996 and 1998, respectively. Using correlation and response function analysis, the ARSTAN tree-ring chronology in *N. sylvatica* (Fig. 8) is positively related ($p < 0.05$) with July precipitation, February and June PDSI, and July PDSI from the prior year and negatively related to temperature from the prior September. The *Picea mariana* ARSTAN chronology is positively related to February, April, July, August, September, October, and annual temperature; November precipitation; and October PDSI from the prior year and negatively related with July PDSI of the current year. The ARSTAN chronology of

Fig. 7. Mean annual temperature, Palmer drought severity index, and precipitation for central Pennsylvania. The broken line shows the 100-year mean.



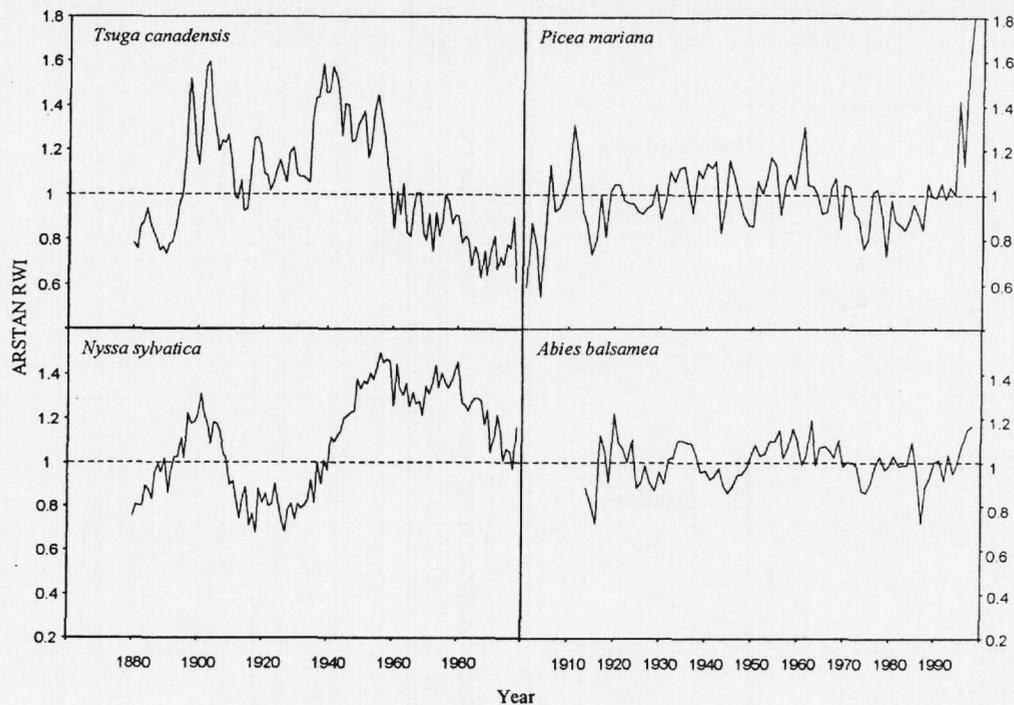
Abies balsamea (Fig. 8) is negatively related to July PDSI from the prior year. *Tsuga canadensis* ARSTAN is positively related with March temperature and February PDSI. In all four species, current-year ring width is significantly related ($p < 0.05$) to the prior year's growth, and the relationship holds for up to 3 years in the case of *N. sylvatica*.

Discussion

Ecological history

Prior to 1890, the old-growth bog forest at Bear Meadows consisted of a large number of *N. sylvatica* and *T. canadensis*, with *Acer rubrum* as a distant third, based on current ages. 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 *B. alleghaniensis*, *Picea*

Fig. 8. ARSTAN ring width index (RWI) chronologies for *Nyssa sylvatica*, *Tsuga canadensis*, *Abies balsamea*, and *Picea mariana* at Bear Meadows in central Pennsylvania. For *Nyssa* and *Tsuga*, only the portion of the chronologies after 1880 are shown.



mariana, and *Pinus strobus* in the stand prior to 1890 is particularly intriguing, because all these species can live 250 years or more. Indeed, a paleoecological study of the pollen content of Bear Meadows reported that *Pinus*, *Picea*, *Nyssa*, *Abies*, *Tsuga*, *Acer*, and *Betula* were present during the early or middle Holocene (10 000 years B.P.) (Kovar 1965). The absence of older trees of *B. alleghaniensis*, *Picea mariana*, and *Pinus strobus* may be due to their relatively short longevity in this bog forest or to the fact that they, being high-quality lumber species, were selective logged about 1890. *Tsuga canadensis* and *N. sylvatica* are undesirable lumber species and were probably avoided during logging (Nowacki and Abrams 1994). *Abies balsamea* typically lives 60–80 years, although rare individuals can reach 150–200 years of age (Burns and Honkala 1990). Of all of the major species in the forest, *Picea mariana* is most characteristic of wet, organic soils (Burns and Honkala 1990). The other dominant tree species typically grow over a wide array of soils, topography, and moisture conditions, including uplands and bogs. All of the species are characteristic of late-successional forests, although they differ in their shade-tolerance ranking and population dynamics. For example, *B. alleghaniensis* and *Pinus strobus* have moderate understory tolerance but are a component of many late-successional forests by being gap-opportunistic species (Forcier 1975; Hibbs 1982; Abrams et al. 1995). *Abies balsamea* can also be an important gap-phase species in southern boreal forests (Kneeshaw and Bergeron 1998).

A major recruitment period in the forest occurred after the 1890 logging, especially for *Acer rubrum*, *B. alleghaniensis*, *Pinus strobus*, *Picea mariana*, and *T. canadensis*. Of all the major species, only *N. sylvatica* recruitment was not greatly

enhanced after logging. *Nyssa sylvatica* may have regenerated at this time but easily could have been overtopped by faster growing tree species (cf. Orwig and Abrams 1994). Nonetheless, selective logging at Bear Meadows greatly increased recruitment for most trees, including gap-opportunistic and late-successional species. A similar finding was reported for other old-growth forests in central and northwestern Pennsylvania, in which selective logging stimulated the establishment and growth of early, middle, and (or) late successional tree species (Abrams and Nowacki 1992; Nowacki and Abrams 1994; Orwig and Abrams 1999). Prior to 1890, *N. sylvatica* and *T. canadensis* recruitment at Bear Meadows was associated with releases in the master tree-ring chronologies, e.g., 1700, 1770, 1800, and 1857. Whether these natural disturbance events stimulated as much tree recruitment as the 1890s logging is unknown because of mortality in older trees. However, this and previous studies suggest that selective logging may greatly alter the composition and number of tree recruits in old-growth forests relative to natural disturbances (Abrams and Nowacki 1992; Nowacki and Abrams 1994; Orwig and Abrams 1999).

The 1890s logging caused a large increase in the ring-width index of remaining *N. sylvatica* and *T. canadensis*, which lasted about 25 years. The duration of this increase is not substantially different than other pre-1890s disturbances in the forest. In contrast, early selective logging in other old-growth bottomland forests in Pennsylvania resulted in an unprecedented growth release, both in magnitude and duration (100–140 years), relative to releases from the natural disturbances (Nowacki and Abrams 1994; Orwig and Abrams 1999). Fires at Bear Meadows in 1900 and 1914 appear to be responsible, at least in part, for dramatic growth declines

from the post-logging climax in *N. sylvatica* and *T. canadensis*, as well as stimulating a large amount of tree recruitment during that time.

Dendroclimatology

Annual radial growth in *T. canadensis*, *N. sylvatica*, *Picea mariana*, and *Abies balsamea* at Bear Meadows was influenced by climatic variables over the last 110 years. Radial growth of *N. sylvatica*, an inherently slow-growing tree species (Orwig and Abrams 1994), was significantly influenced by growth from the prior 3 years, compared with only 1-year "memory" in the three other species. Decreases in the ARSTAN chronologies of *T. canadensis* and *N. sylvatica* in the early 1900s may be due to the cool and dry macroclimate of that time. ARSTAN chronologies of both of these species increased during the 1930s and 1940s when the climate was warmer and wetter. The above-average growth in *N. sylvatica* persisted until the 1990s. Tree-ring growth in *T. canadensis* declined in the late 1950s and early 1960s associated with dry, cold temperatures. *Picea mariana* and *Abies balsamea* had dramatic growth increases during the warm and wet years of the late 1990s. In contrast, ARSTAN values for *T. canadensis* remained below average from 1970 to 1998. 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 in eastern bogs or floodplains are climatically sensitive and represent an important resource for dendroclimatology studies, even in closed-canopy forests (Stahle et al. 1988; Tardif and Bergeron 1997; Abrams et al. 1998). Moreover, the individualistic nature and wide range of tree ring – climate responses in this study suggest that dendroclimatology is better studied using several species, rather than a single species, per site.

The bog forest at Bear Meadows is unique because it contains extreme southern, disjunct populations of *Picea mariana* and *Abies balsamea* (Little 1971). Isolated occurrences of *Picea mariana*, *Picea rubens*, and *Abies balsamea* in the central mid-Atlantic region is a result of their southward migration during cooler climate conditions in the late Quaternary or early Holocene (Braun 1950; Watts 1980). *Picea* and *Abies* species in the eastern United States have been the subject of considerable study and debate, including population and growth declines during the latter part of the 20th century (Rheinhardt 1984; Adams et al. 1985; White and Cogbill 1992). The *Picea* and *Abies* decline has been attributed to insect, disease, acid rain, drought, and other global change phenomena. A 1967 survey of the bog forest at Bear Meadows (Potter 1970), reported that *Abies balsamea* had a relative importance value of 4.7%, which substantiates the decline we observed in this species over the last decade. We observed a majority of dead *Abies balsamea* throughout the forest, and the few living trees have very poor crown development, chlorotic foliage, high infestation of spruce spider mite (*Oligonychus ununguis* (Jacobi)), and active mycelial fans of *Armillaria mellea* (Vahl:Fr) Kummer root rot. These factors may be responsible for the precipitous growth decline in *Abies balsamea* in 1986. We predict that the species will be totally or very nearly extirpated from

Bear Meadows during the next few decades. Once this occurs, we see almost no opportunity for *Abies balsamea* to reestablish itself in this disjunct, relict bog based on the lack of local seed source. In contrast, *Picea mariana* appears healthy, and it remains the second-rank dominant in the forest.

Mortality in the adult *Abies balsamea* seems to be related to most reaching their pathological age of 40–70 years. However, the exact reason for the absence of younger *Abies balsamea* recruits and saplings is not known, but may involve deer browsing, seed predation, and poor seed crops in the declining trees. Many Pennsylvania forests have been subjected to increasing deer browsing pressure during the 20th century, resulting in a scarcity of tree regeneration and recruitment (Bramble and Goddard 1953; Abrams and Orwig 1996). At Bear Meadows we observed deer browsing or deer droppings in half of the study plots. *Abies balsamea* has low to moderate browse preference for deer but will be eaten as winter forage along with *T. canadensis*, *Acer rubrum*, *N. sylvatica*, *Picea mariana*, and *B. alleghaniensis* (Bramble and Goddard 1953; Cypher and Cypher 1988; Burns and Honkala 1990). It is possible that the absence of saplings and tall seedlings of most species and the scarcity of tree recruitment after 1940, including *Abies balsamea*, is due, at least in part, to deer browsing.

Because *Abies balsamea* is the shortest lived of the major tree species at the site, it is presently the most threatened by the lack of regeneration and recruitment. Thus, the 10 000-year history of *A. balsamea* presence at Bear Meadows may soon be ending. However, more work is necessary to determine the exact causes of *Abies balsamea* decline in relict forests such as Bear Meadows. Future studies could evaluate the effects of deer exclosures on fir regeneration or explore the effects of global warming under controlled greenhouse conditions. Other longer lived trees species may also be lost from the site if future recruitment does not occur. However, an increase in *T. canadensis* dominance in the forest over the short term is likely based on the ingrowth of its many overtopped and intermediate canopy trees. The results of this study suggest that disjunct, relict tree populations in the mid-Atlantic region may be particularly sensitive to anthropogenic impacts and represent important case studies and benchmarks for comparisons with future studies.

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References

- Abrams, M.D., and Downs, J.A. 1990. Successional replacement of old-growth white oak by mixed-mesophytic hardwoods in south-west Pennsylvania. *Can. J. For. Res.* **20**: 1864–1870.
- Abrams, M.D., and Nowacki, G.J. 1992. Historical variation in fire, oak recruitment, and post-logging accelerated succession in central Pennsylvania. *Bull. Torrey Bot. Club.* **119**: 19–28.

- Abrams, M.D., and Orwig, D.A. 1995. Structure, radial growth dynamics and recent climatic variations for a 320-year-old *Pinus rigida* rock outcrop community. *Oecologia*, **101**: 353–360.
- Abrams, M.D., and Orwig, D.A. 1996. A 300-year history of disturbance and canopy recruitment for co-occurring white pine and hemlock on the Allegheny Plateau, USA. *J. Ecol.* **84**: 353–363.
- Abrams, M.D., Orwig, D.A., and DeMeo, T.E. 1995. Dendroecological analysis of successional dynamics for a presettlement-origin white pine – mixed oak forest in the southern Appalachians, USA. *J. Ecol.* **83**: 123–133.
- Abrams, M.D., Ruffner, C.M., and Morgan, T.A. 1998. Tree-ring responses to drought across species and contrasting sites in the Ridge and Valley of central Pennsylvania. *For. Sci.* **44**: 550–558.
- Adams, H.S., Stephenson, S.L., Blasing, T.J., and Duvick, D.N. 1985. Growth-trend declines of spruce and fir in mid-Appalachian subalpine forests. *Environ. Exp. Bot.* **25**: 315–325.
- Alley, W.M. 1984. The Palmer drought severity index: limitations and assumptions. *J. Clim. Appl. Meteorol.* **23**: 1100–1109.
- Braker, W.L. 1981. Soil survey of Centre County, Pennsylvania. USDA Soil Conservation Service, Washington, D.C.
- Bramble, W.C., and Goddard, M.K. 1953. Seasonal browsing of woody plants by white-tailed deer in the Ridge and Valley section of central Pennsylvania. *J. For.* **51**: 815–819.
- Braun, E.L. 1950. Deciduous forests of eastern North America. Free Press, New York.
- Burns, R.M., and Honkala, B.H. (Technical coordinators). 1990. Silvics of North America. Vol. 1. Conifers. Vol. 2. Hardwoods. U.S. Dep. Agric. Agric. Handb. No. 654.
- Cho, D.S., and Boerner, R.E.J. 1995. Dendrochronological analysis of the canopy history of two Ohio old-growth forests. *Vegetatio*, **120**: 173–183.
- Cook, E.R., and Zedaker, S.M. 1992. The dendroecology of red spruce decline. In *Ecology and decline of red spruce in eastern North America*. Edited by C. Eager and M.B. Adams. Springer-Verlag, New York. pp. 192–231.
- Cook, E.R., Holmes, R.L., Bosch, O., Varem-Sanders, T., Grissino-Mayer, H.D., and Krusic, P.J. 1997. International tree-ring data bank program library, version 2.1. <http://www.ngdc.noaa.gov/paleo/treering.html>
- Cottam, G., and Curtis, J.T. 1956. The use of distance measures in phytosociological sampling. *Ecology*, **37**: 451–460.
- Cypher, B.L., and Cypher, E.A. 1988. Ecology and management of white-tailed deer in northeastern coastal habitats. U.S. Fish Wildl. Serv. Biol. Rep. No. 88(38).
- Delcourt, H.R., and Delcourt, P.A. 1988. Quaternary landscape ecology: relevant scales in space and time. *Landsc. Ecol.* **2**: 23–44.
- Forcier, L.K. 1975. Reproductive strategies and co-occurrence of climax tree species. *Science* (Washington, D.C.), **189**: 808–810.
- Foster, D.R. 1988. Disturbance history, community organization and vegetation dynamics of the old-growth Pisgah Forest, southwestern New Hampshire, USA. *J. Ecol.* **76**: 105–134.
- Fritts, H.C. 1976. *Tree rings and climate*. Academic Press, London.
- Fritts, H.C., and Swetnam, T.W. 1989. Dendroecology: a tool for evaluating variations in past and present forest environments. *Adv. Ecol. Res.* No. 19. pp. 111–188.
- Fritts, H.C., and Xiangding, W. 1986. A comparison between response-function analysis and other regression techniques. *Tree-Ring Bull.* **46**: 31–46.
- Gordon, A.G. 1976. The taxonomy and genetics of *Picea rubens* and its relationship to *Picea mariana*. *Can. J. For. Res.* **54**: 781–813.
- Heitzman, E., Pregitzer, K.S., and Miller, R.O. 1997. Origin and early development of white-cedar stands in northern Michigan. *Can. J. For. Res.* **27**: 1953–1961.
- Hibbs, D.E. 1982. White pine in the transition hardwood forest. *Can. J. Bot.* **60**: 2046–2053.
- Johnson, E.A., Miyashita, K., and Kleb, H. 1994. The hazards of interpretation of static age structures as shown by stand reconstructions in a *Pinus contorta* – *Picea engelmannii* forest. *J. Ecol.* **82**: 923–931.
- Kneeshaw, D.D., and Bergeron, Y. 1998. Canopy gap characteristics and tree replacement in the southeastern boreal forest. *Ecology*, **79**: 783–794.
- Kovar, A.J. 1965. Pollen analysis of the Bear Meadows bog of central Pennsylvania. Pa. Acad. Sci. Publ. No. 38. pp. 16–24.
- Little, E.L. 1971. Atlas of United States trees. Vol. 1. Conifers and important hardwoods. U.S. Dep. Agric. Misc. Publ. No. 1146.
- Lorimer, C.G., and Frelich, L.E. 1989. A method for estimating canopy disturbance frequency and intensity in dense temperate forests. *Can. J. For. Res.* **19**: 651–663.
- McLaughlin, S.B., Downing, D.J., Balsing, T.J., Cook, E.R., and Adams, H.S. 1987. An analysis of climate and competition as contributors to decline of red spruce in high elevation Appalachian forests of the eastern United States. *Oecologia*, **72**: 487–501.
- Mikan, C.J., Orwig, D.A., and Abrams, M.D. 1994. Age structure and successional dynamics of a presettlement-origin chestnut oak forest in the Pennsylvania Piedmont. *Bull. Torrey Bot. Club*, **121**: 13–23.
- Motzkin, G., Patterson, W.A., III, and Drake, N.E.R. 1993. Fire history and vegetation dynamics of a *Chamaecyparis thuyoides* wetland on Cape Cod, Massachusetts. *J. Ecol.* **81**: 391–402.
- National Oceanic and Atmospheric Administration (NOAA). 1999. Climate visualization website: URL. (<http://www.ncdc.noaa.gov/onlineprod/>).
- Nowacki, G.J., and Abrams, M.D. 1994. Forest composition, structure, and disturbance of the Alan Seeger Natural Area, Huntingdon County, Pennsylvania. *Bull. Torrey Bot. Club*, **121**: 277–291.
- Nowacki, G.J., and Abrams, M.D. 1997. Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. *Ecol. Monogr.* **67**: 225–249.
- Orwig, D.A., and Abrams, M.D. 1994. Contrasting radial growth and canopy recruitment patterns in *Liriodendron tulipifera* and *Nyssa sylvatica*: gap-obligate and gap-facultative tree species. *Can. J. For. Res.* **24**: 2141–2149.
- Orwig, D.A., and Abrams, M.D. 1999. Impacts of early selective logging on the dendroecology of an old-growth, bottomland hemlock – white pine – northern hardwood forest on the Allegheny Plateau. *J. Torrey Bot. Soc.* **126**: 234–244.
- Phipps, R.L. 1985. Collecting, preparing, cross-dating, and measuring tree increment cores. U.S. Geol. Surv. Water Resour. Invest. Rep. No. 85-4148.
- Potter, F.W., Jr. 1970. A study of some plant communities of the Bear Meadows Basin, Centre County, Pennsylvania. M.Sc. thesis, Pennsylvania State University, University Park, Pa.
- Rheinhardt, R.D. 1984. Comparative study of composition and distribution patterns of subalpine forests in the Balsam Mountains of southwest Virginia and the Great Smoky Mountains. *Bull. Torrey Bot. Club*, **111**: 489–493.
- Ruffner, C.M., and Abrams, M.D. 1998. Relating land-use history and climate to the dendroecology of a 326-year-old *Quercus prinus* talus slope forest. *Can. J. For. Res.* **28**: 347–358.
- Smith, D.M. 1986. *The practice of silviculture*. John Wiley & Sons, Inc., New York.
- Stahle, D.W., Cleaveland, M.K., and Hehr, J.G. 1988. North Carolina climate changes reconstructed from tree-rings: A.D. 372 to 1985. *Science* (Washington, D.C.), **240**: 1517–1519.

- Stephenson, S.L., and Adams, H.S. 1986. An ecological study of balsam fir communities in West Virginia. *Bull. Torrey Bot. Club*, **113**: 372–381.
- Stokes, M.A., and Smiley, T.L. 1996. An introduction to tree-ring dating. Reprinted edition. University of Arizona Press, Tucson, Ariz.
- Tardif, J., and Bergeron, Y. 1997. Comparative dendroclimatological analysis of two black ash and two white cedar populations from contrasting sites in the Lake Duparquet region, northwest Quebec. *Can. J. For. Res.* **27**: 108–116.
- Villalba, R., and Veblen, T.T. 1997. Improving estimates of total tree ages based on increment cores samples. *EcoScience*, **4**: 535–542.
- Watts, W.A. 1980. Late Quaternary vegetation of the central Appalachians and the New Jersey Coastal Plain. *Ecol. Monogr.* **49**: 427–469.
- Westerfeld, W.F. 1959. Flora of Centre and Huntingdon Counties with related historical, geological, and physiographic features. Pa. State Univ. Agric. Exp. Stn. Bull. No. 647.
- White, P.S., and Cogbill, C.V. 1992. Spruce–fir forests of eastern North America. *In Ecology and decline of red spruce in eastern North America. Edited by C. Eager and M.B. Adams.* Springer-Verlag, New York. pp. 3–39.