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Dendroecology and species co-existence in an old-growth *Quercus–Acer–Tilia* talus slope forest in the central Appalachians, USA

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Abstract

Dendroecological techniques were used to examine the disturbance history and patterns of species recruitment in an old-growth *Quercus rubra* L. (northern red oak)–*Acer saccharum* Marsh. (sugar maple)–*Tilia americana* L. (basswood) forest on a steep, talus slope in eastern West Virginia. The forest was uneven-aged as were the populations of red oak. Sugar maple dominated the sapling layer, which comprised little or no basswood and red oak. A compilation of major and moderate releases (indicative of disturbance) in 25 cores revealed single or multiple release events in every decade from 1870–1990. The high elevation of the forest coupled with a fertile sub-soil beneath the talus ameliorated the outwardly harsh conditions of the site, allowing for the domination of typically mesophytic, nutrient demanding tree species. We observed several fire scarred trees as well as extensive small-scale blow-down throughout the forest. Frequent disturbance events were probably crucial to the co-existence and continuous canopy recruitment of the relatively light demanding red oak with highly shade tolerant sugar maple and basswood. The strong successional replacement tendencies of red oak by northern hardwoods noted elsewhere in the eastern US may be less apparent on high elevation, rocky sites in the central Appalachians. Thus, this is a unique case study of long-term red oak domination with later successional species in an old-growth forest. © 1998 Elsevier Science B.V.

Keywords: Disturbance; Succession; Canopy gaps; Tree rings; Shade tolerance

1. Introduction

During the last decade it has become well established that the vast majority of *Quercus* (oak) forests in the northern half of the eastern deciduous biome of the United States are transitional to later successional species in the absence of periodic disturbance (Adams and Anderson, 1980; Lorimer, 1984; Pallardy et al., 1988; Nowacki et al., 1990; Abrams and Downs, 1990; Abrams et al., 1995). The successional nature of many oak forests may be due, at least in part, to historical changes in the pattern of fire frequency, in particular fire exclusion during the 20th century throughout the eastern US (Lorimer, 1985; Abrams, 1992). Some of the most striking examples of oak replacement by more shade tolerant species have been reported on mesic sites, often involving *Quercus rubra* L. (northern red oak) (Host

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et al., 1987; Fralish, 1988; Nowacki et al., 1990; Abrams, 1992; Lorimer et al., 1994). Nonetheless, northern red oak seems to have the ability to act as a gap-phase species and may maintain itself in mature forests, although empirical evidence of this phenomenon is lacking (Bray, 1956; Barden, 1981; Abrams and Downs, 1990).

We recently became aware of a virgin forest on a talus slope in eastern West Virginia where apparently northern red oak has co-existed with *Acer saccharum* Marsh. (sugar maple), *Tilia americana* L. (basswood) and other northern hardwood species for the last 175 years or more. While the existence of a sugar maple–basswood–red oak forest type in the Lake States was reported in the early ecological literature (Daubenmire, 1936; Eggler, 1938; Braun, 1950), we know very little about their disturbance history or gap dynamics. Using dendroecological techniques it is possible to reconstruct the history of disturbance (gap formation) and species recruitment in forests (Fritts and Swetnam, 1989; Lorimer and Frelich, 1989; Abrams et al., 1995). Thus, in addition to a detailed community analysis of the species composition and structure of the forest we characterized a 175 year record of disturbance and patterns of canopy recruitment from the tree ring record. Finally, we were interested in elucidating the mechanisms of co-existence of red oak among the more shade tolerant sugar maple–basswood dominants and the successional status of the forest.

2. Site description

The study site comprises a 6.7 ha old-growth area nested within an 85 ha tract of Monongahela National Forest land on Spruce Mountain, southwest of the village of Onego, Pendleton County, WV. This tract was privately owned from 1795 until purchased by the Federal Government in 1934. Records at the time of purchase describe the study site as 'virgin timber'. The site elevation is 994 m, and it lies at 38°50′N, 79°27′W. Ecologically, the stand falls within the Spruce Mountain System landtype association, just west of the Allegheny Front, the boundary between the Ridge and Valley and Allegheny Mountain physiographic provinces (sections) (McNab and Avers, 1994). Annual precipitation averages 132 cm. The median temperature for July is 18.6°C and approximately −1.1°C for December. The growing season is approximately 151 days (Owenby and Ezell, 1992). The site slope ranges from 45–55% and faces southeast. The forest floor is extremely rocky, characterized by sandstone boulders from 0.5 to 3.0 m in diameter that entirely cover the soil surface. Underlying this boulder field is soil of the Cateache series, a productive silt loam derived from Mauch Chunk siltstone and shale (Soil Conservation Service, 1992). The soil is well-drained and probably remains moist year-round because of underground seeps. Vegetation is mixed mesophytic (Kuchler, 1964), specifically a red oak–sugar maple association. Basswood and white ash (*Fraxinus americana* L.) are also notable overstory components. The herbaceous layer is characterized by jewelweed (*Impatiens* spp.), wood nettle (*Laportea canadensis* (L.) Wedd.), and Jack-in-the pulpit (*Arisaema triphyllum* (L.) Schott), all indicators of moist, nutrient-rich sites (Strausbaugh and Core, 1977). The site is old-growth in structure, with large trees of a variety of diameters, abundant woody debris, snags, and canopy gaps.

3. Method

On 18 May, 1995, 16 fixed-area plots located at 20-m intervals along transects through the tract were used for vegetation sampling. The species, diameter and crown class were recorded for all trees (DBH ≥ 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 and Curtis, 1956). Classification of tree crowns into four classes (dominant, codominant, intermediate and overtopped) was based on the amount and direction of intercepted light (Smith, 1986). At each plot, two trees across all species and age classes were cored at 1.37 m for age determinations and radial growth analysis. Across all plots, we attempted to collect tree cores from all the major species and diameter classes. All suitable cores ($n = 30$) 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

Table 1
Density, frequency, dominance and importance values for tree species in an old-growth sugar maple–basswood–red oak forest on North Spruce Mountain in eastern West Virginia

Species	Density (ha^{-1})	Frequency (# plots)	Dominance $(\text{m}^2\ \text{ha}^{-1})$	Relative density	Relative frequency	Relative dominance	Relative importance
A. saccharum	163	16	8.62	36.7	25.0	21.1	27.6
T. americana	144	14	7.94	32.4	21.9	19.4	24.6
Q. rubra	53	9	17.77	12.0	14.1	43.5	23.2
F. americana	22	7	3.12	4.9	10.9	7.6	7.8
C. glabra	13	4	0.34	2.9	6.2	0.8	3.3
M. acuminata	9	3	1.66	2.1	4.7	4.1	3.6
A. rubrum	9	2	0.12	2.1	3.1	0.3	1.8
P. serotina	6	2	0.39	1.4	3.1	1.0	1.8
O. virginiana	12	3	0.07	2.7	4.7	0.2	2.5
Other[a]	13	4	0.84	2.9	6.2	2.1	3.7
Total	444	64	40.87				

[a] Includes *Ulmus americana*, *Robinia psuedoacacia*, and *Betula lenta*.

within each of the overstory plots. Saplings were classified as tree species ≥ 1.5 m in height but less than 8.0 cm DBH and seedlings were < 1.5 m in height.

4. Radial growth analysis

Age determinations for all cores were made using a dissecting microscope. Cores from the oldest red oak ($n = 5$) and sugar maple ($n = 4$) trees were used to construct a growth chronology of the site spanning 175 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 Quebec, Canada) and recorded using the MACDENDRO microcomputer program. A ring width index was created for each tree chronology by dividing yearly measured growth values by the expected values obtained from linear regression (Fritts and Swetnam, 1989). After cross-dating using signature years (Fritts, 1976), ring width indices were averaged to obtain a mean growth chronology from the four or five cores per species. Annual growth increments were also measured for an additional 16 of the most suitable tree cores for growth comparisons across other species and age classes. All cores ($n = 25$) were examined for periods of suppression and release based on conservative and moderate criteria established by Lorimer and Frelich (1989), who defined a major sustained release as a $\geq 100\%$ 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 establishment dates, were used to distinguish disturbance events from responses attributed to climatic and thinning factors (Lorimer and Frelich, 1989).

5. Results

Sugar maple, basswood and red oak dominated the forest, although a total of 12 hardwood species were recorded in the overstory plots (Table 1). The high importance of sugar maple and basswood was due to their high density and frequency and moderate

Table 2
Seedling and sapling densities (ha^{-1}) for tree species in an old-growth sugar maple-basswood-red oak forest

Species	Seedlings	Sapling
F. americana	6250	–
A. saccharum	2000	1041
A. rubrum	500	–
A. pensylvanicum	125	–
T. americana	250	69
B. lenta	250	–
Q. rubra	250	–
C. glabra	–	69
R. pseudoacacia	125	–

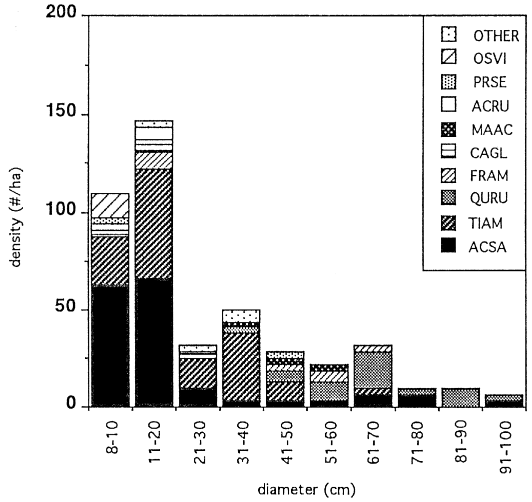

Fig. 1. Diameter (at 1.37 m) distribution of tree species in an old-growth red oak-sugar maple-basswood forest in eastern West Virginia. Other species are listed in Table 1.

levels of basal area (dominance), whereas the importance of red oak was due primarily to its high basal area. The stand basal area of 40.87 m^2 ha^{-1} is somewhat greater than that reported for other oak forests in the mid-Atlantic region (e.g., Nowacki and Abrams, 1992; Orwig and Abrams, 1994; Mikan et al., 1994), but within the expected range for sugar maple–basswood forests (Whitney, 1994; p. 62). *F. americana* (white ash) followed by sugar maple dominated the seedling layer (Table 2). Sugar maple was the only species establishing a significant number of saplings.

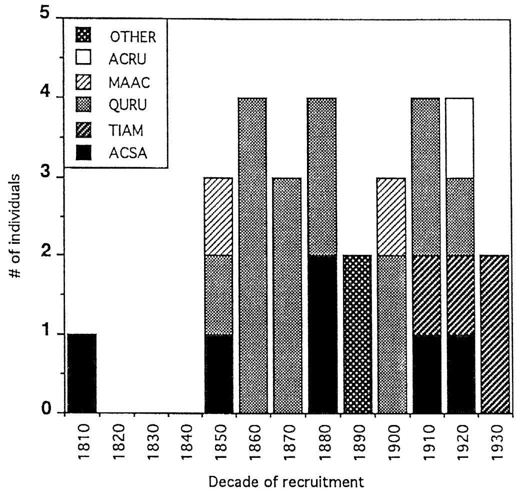

Fig. 2. Age class (at 1.37 m) distribution of tree species in the old-growth forest. Other species are listed in Table 1.

The diameter distribution of trees approached an inverse-J pattern indicative of an uneven-age forest (Fig. 1; Smith, 1986). Red oak dominated the larger

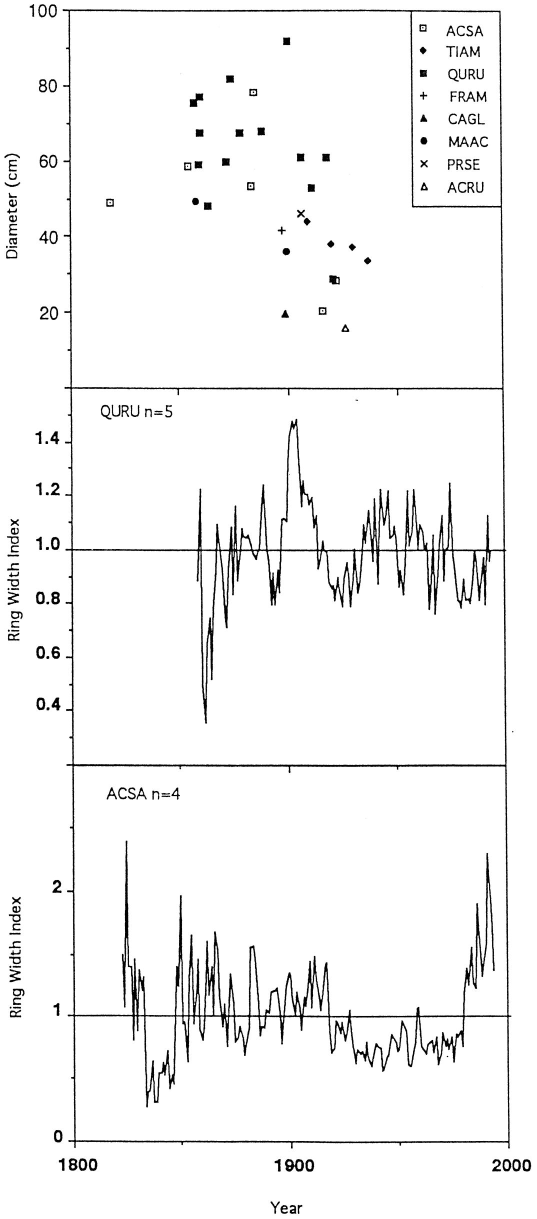

Fig. 3. Age-diameter data for all cored trees (top panel) and the mean ring width index for the oldest red oak (QURU) and sugar maple (ACSA) in the old-growth forest.

diameter classes and was poorly represented among the smaller trees. Sugar maple occurred in almost every diameter class, but was best represented in the smaller classes. Basswood also dominated among the smaller trees as well as the 20–50 cm diameter classes.

The uneven-aged condition of the forest was indicated by the age data from all suitable cores (Fig. 2). Unfortunately, heart rot was very prevalent in many of the larger trees, which limited our ability to age what may have been some of the older trees in the stand. For example, the maximum longevity of sugar maple, basswood and red oak may exceed 200–300 years (Burns and Honkala, 1990). We were able to determine that oldest tree present was a 173-year-old (at 1.37 m) sugar maple, but all other individuals

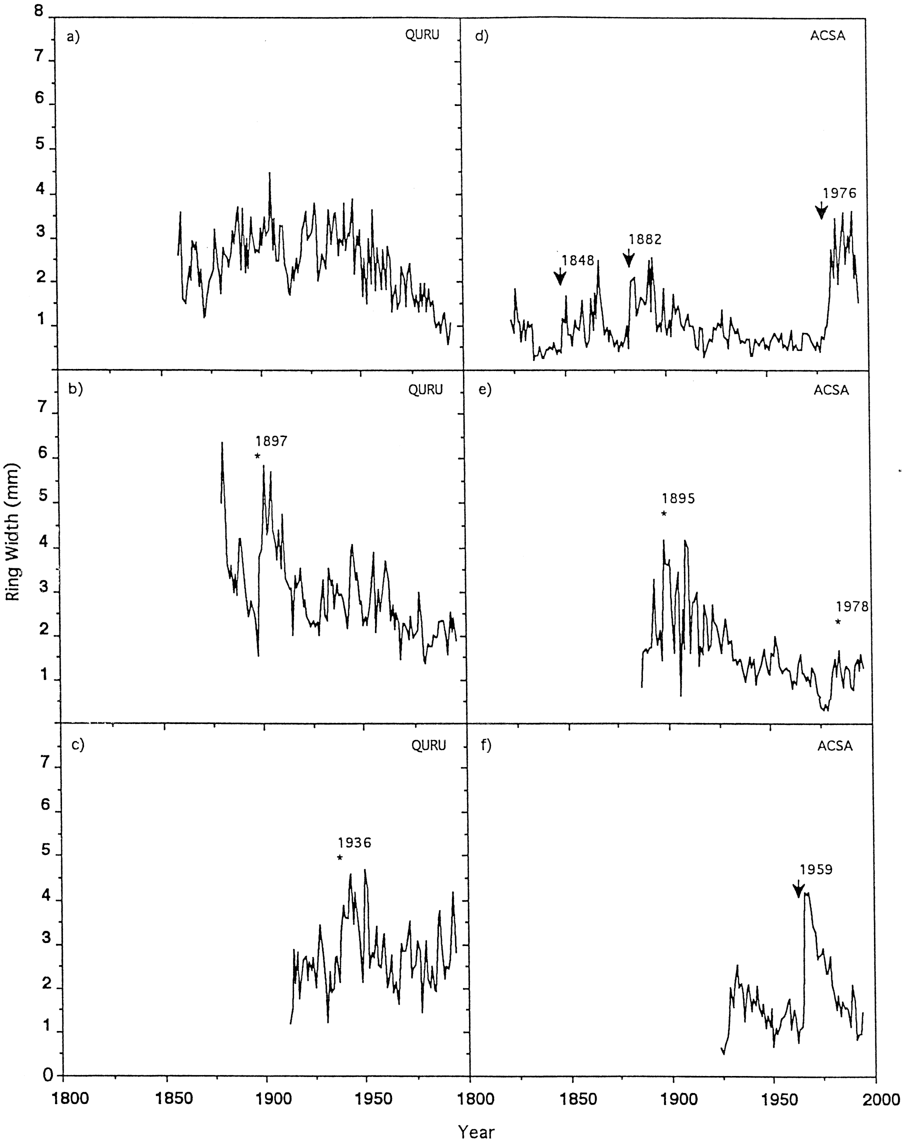

Fig. 4. Radial growth chronologies of selected red oak (QURU) and sugar maple (ACSA). * = moderate release dates; arrows = major release dates (from Lorimer and Frelich, 1989).

recruited beyond the seedling stage less than 150 years ago. A remarkable feature of this stand is the continuous recruitment exhibited by red oak into an uneven-aged canopy between 1850 and 1940. The four aged basswood trees all recruited during the 20th century. None of the trees cored in the stand were < 55 years old.

A composite ring width index for the five oldest red oak in the forest reveals a period of generally below average growth between 1860–1897 (Fig. 3). This was followed by a rapid growth increase between 1898–1904 and decrease between 1905–1920, indicative of extensive canopy opening and closure throughout the stand. Growth then increased, with

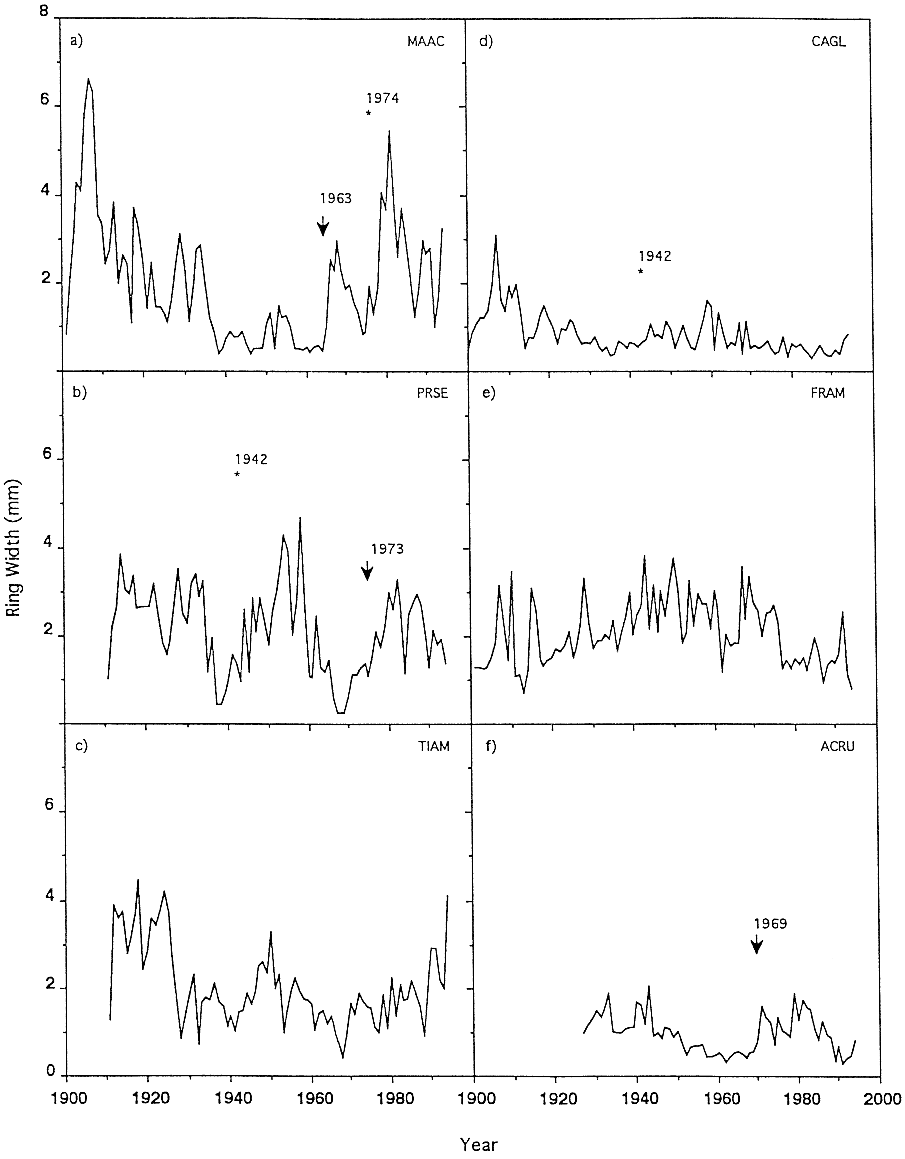

Fig. 5. Radial growth chronologies of selected *M. acuminata* (MAAC), *P. serotina* (PRSE), *T. americana* (TIAM), *C. glabra* (CAGL), *F. americana* (FRAM) and *A. rubrum* (ACRU). * = moderate release dates; arrows = major release dates.

much year-to-year variation, until 1945 and fluctuated around the mean (RWI = 1) during the last 50 years (ending in 1995). A similar analysis for sugar maple revealed some striking differences with the red oak chronology (Fig. 3). Growth in the oldest sugar maple was initially high but it rapidly declined between 1825–1832, indicative of seedling establishment in a small gap. Growth remained low until 1848 when it increased and decreased dramatically from year-to-year for the following 20 years. From 1890–1920 sugar maple growth was typically above average but from 1920–1980 it was consistently suppressed. Between 1980–1995 the ring width index increased sharply resulting in some of the highest RWI values during the last 125 years. Neither the prolonged suppression nor the very high RWI values in sugar maple in the 20th century were recorded in the red oak chronology. We speculate that the dramatic growth variations in sugar maple during the 20th century were due to an interaction of disturbance caused damage to trees, changes in resource availability and climatic variation (Foster, 1988; Abrams and Orwig, 1995). Recruitment of all tree species was evenly distributed between 1850–1940 and not clearly associated with releases in either the sugar maple or red oak chronology (Fig. 3).

Radial growth patterns and release dates of individual trees varied among and within species (Figs. 4 and 5). A 136 year-old red oak exhibited moderate growth rates generally between 2.0–3.5 mm yr^{-1} until 1965 after which growth declined to 1.0 mm yr^{-1} (Fig. 4a). Another red oak had an initial growth > 6.0 mm yr^{-1} and a moderate release in 1897 (Fig. 4b). After a large growth decline between 1902–1925, the annual increment in this tree varied between 2.0–4.0 mm yr^{-1}. A third red oak typically grew at 2.0–3.5 mm yr^{-1}, except following a moderate release in 1936 when growth exceeded 4.5 mm yr^{-1} (Fig. 4c). Prolonged periods of suppressed growth were not found in any of the red oak chronologies. A 173 year-old sugar maple exhibited several periods of growth suppression < 1.0 mm yr^{-1}, followed by major releases in 1848, 1982, and 1976 (Fig. 4d). Another sugar maple had high initial growth reaching 4.0 mm yr^{-1}, followed by declining growth during the next 80 years (Fig. 4e). The annual increment in this tree fell below 0.4 mm yr^{-1} in the 1970s until a moderate release in 1978. A third sugar maple exhibited moderate then declining growth rates, followed by its maximum rates of 5.0 mm yr^{-1} after a major release in 1959 (Fig. 4f). All six of the red oak and sugar maple chronologies presented in Fig. 4 were from dominant or codominant canopy trees.

A 94 year-old codominant *Magnolia acuminata* had high initial growth exceeding 6.0 mm yr^{-1} followed by 62 years of declining growth (Fig. 5a). Large growth increases in this tree occurred after a major and moderate release in 1963 and 1974, respectively. A codominant *Prunus serotina* had maximum growth rates > 4.0 mm yr^{-1} and minimum growth < 0.5 mm yr^{-1} prior to a moderate and major release in 1942 and 1973, respectively (Fig. 5b). A basswood and white ash typically grew between 1.0–4.0 mm yr^{-1} and neither of these dominant trees exhibited significant releases or severe growth depressions this century (Fig. 5c, e). An overtopped *Carya glabra* typically grew < 1.0 mm yr^{-1} despite a moderate release in 1942 (Fig. 5d); a similar pattern was reported for this species in another old-growth forest in West Virginia (Abrams et al., 1995). An overtopped *Acer rubrum* L. also had low growth between 0.5–2.0 mm yr^{-1} despite a major release in 1969 (Fig. 5f). A compilation of all moderate and major releases measured in 25 cores across all tree species revealed that one or more

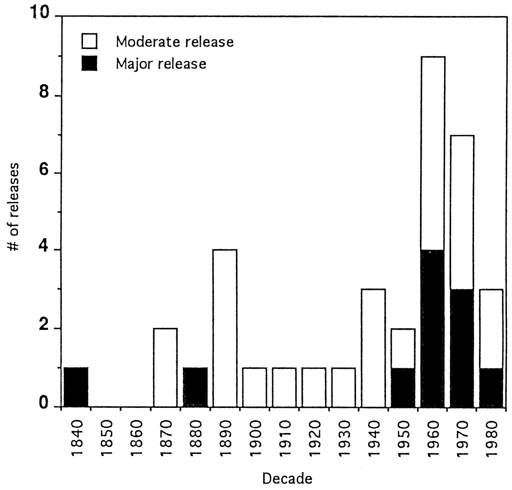

Fig. 6. Frequency of major and moderate releases by decade in 25 tree chronologies in the old-growth forest.

releases occurred in each decade between 1870–1990, with peak frequency in the 1960s and 1970s (Fig. 6).

6. Discussion

In contrast to the lack of recent canopy recruitment of northern red oak in many forests of the eastern US, red oak at this study site exhibited continuous recruitment between 1850 and 1940 and presently shares overstory dominance with sugar maple and basswood. The red oak component in the stand is therefore uneven-aged, which is unusual for this species. For example, in a sugar maple–basswood forest in Wisconsin, the red oak was even-aged due to past disturbance (e.g., fire) (Eggler, 1938). It was suggested that without fire red oak would die-out and the forest would return to a maple–basswood climax. In another Wisconsin maple–basswood forest, the red oak component was 60–100 years younger than the overstory sugar maple and was even-aged following recruitment in small gaps following partial cutting (Lorimer, 1983). In old-growth forests in the southern and mid-Atlantic regions, red oak existed via occasional gap-capture but was a very minor component of the stands (Barden, 1981; Abrams and Downs, 1990; Abrams et al., 1995).

The persistence of red oak at our study site indicates that the community is not clearly successional to a regional climax, e.g., sugar maple–basswood. Many present-day red oak forests in the eastern US are considered to be an artifact of cutting and fire in the late 1800s and early 1900s and are now returning to later successional northern hardwood forests (Host et al., 1987; Crow, 1988; Nowacki et al., 1990; Abrams, 1992). This is not the situation for this virgin forest. We believe the key to understanding the co-existence of red oak with sugar maple and basswood co-dominants are the edaphic and disturbance factors at the site. This is a high elevation, steep, talus slope forest. It is intriguing to find typically mesophytic and nutrient demanding species such as sugar maple, basswood and red oak growing on this outwardly harsh site. However, the cool, moist conditions within the forest may be explained by orographic lifting of clouds, the slow melting of ice and snow trapped between the boulders which provide moisture in the spring and early summer, the occurrence of springs and seeps, and runoff from the mountain top (Hack and Goodlett, 1960). The fertile nature of the site is apparently due to the rich silt loam soil beneath the talus. The relatively high growth rates and large size of many of the trees, particularly red oak, is consistent with the idea of generally favorable growing conditions in the forest. Indeed, a gradient analysis of forest types on the Monongahela National Forest of eastern West Virginia determined that both red oak–sugar maple and sugar maple–basswood forests were associated with steep, rocky sideslopes (Hurst, 1994).

Disturbances occurred frequently in this forest, with as many as 1–9 trees exhibiting major sustained or moderate temporary growth releases in every decade during the last 125 years. Blow-down was present throughout the forest and we observed occasional fire scars, including some on the larger sugar maple. The presence of fire scars in this talus slope forest is particularly intriguing considering the discontinuous nature of heavy fuel accumulations. Because red oak is relatively light demanding compared to the shade tolerant sugar maple and basswood, we suggest that red oak has persisted as a dominant in this forest due to the high disturbance frequency. In addition, the talus substrate may reduce the ability of sugar maple, in particular, to establish vast numbers of seedlings typical of low elevation, mesic red oak forests (Adams and Anderson, 1980; Fralish, 1988; Nowacki et al., 1990). Nonetheless, the relatively high density of sugar maple saplings at the study site is comparable to other red oak stands. Interestingly, red oak and basswood had very low numbers of seedlings and saplings, despite low deer predation typical of talus slopes (personal observation). Basswood is known to replace itself with stump sprouts following the top-killing of the tree (Daubenmire, 1936; Bray, 1956). The dendroecological data provided here suggests that red oak may recruit into gaps without substantial density of advance regeneration. Although this is speculative because we are comparing past red oak canopy recruitment with present-day regeneration numbers. However, if the current regeneration numbers are representative of the past 140 years, the ability of red oak to fill gaps in the presence of dense sugar maple saplings is intriguing, and probably related to the impact of disturbances on the forest floor and rapid growth under canopy gaps.

7. Conclusions

The composition and dynamics of this forest can be explained by a complex interaction of climatic, edaphic and disturbance factors. The cool, moist conditions of the forest, coupled with a fertile sub-soil ameliorated the outwardly harsh conditions of this steep, talus slope forest. We found continuous recruitment of red oak, forming an uneven-age canopy, probably due to the high frequency of disturbance. Thus, we believe that this is a unique example of long-term red oak domination with later successional species. However, the site is atypical relative to the entire range of this species, and the results of this study should not be viewed as representative for other regions of the eastern US. Therefore, we agree with the many studies, including our own, that have reported the successional replacement of northern red oak along the northern tier of the eastern deciduous biome. However, in the central Appalachians, where red oak occupies many high elevation, rocky sites the transitional nature of this species may be less certain. Understanding the complex disturbance history and mechanisms of co-existence in this mixed-species forest was enhanced by the dendroecological approach used in this study.

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