Dendroecology and successional status of two contrasting old-growth oak forests in the Blue Ridge Mountains, U.S.A.

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Abstract: Dendroecological techniques were used to investigate the dynamics and successional development spanning three centuries of two virgin, old-growth forests dominated by *Quercus rubra* L. (mesic site) and *Quercus prinus* L. (xeric site) on the Blue Ridge Mountains of west-central Virginia. In the *Q. rubra* stand, a large increase in recruitment of this species between 1820 and 1850 was associated with a sharp increase followed by a larger decrease in the master tree ring chronology. The decrease in growth between 1837 and 1844 coincided with a predicted southward displacement of the summertime position of the polar front from eastern Canada (E.R. Cook and P. Mayes. 1987. Decadal-scale patterns of climatic change over eastern North America inferred from tree rings. *In* Abrupt climatic change. *Edited by* W.H. Berger and L.D. Labeyrie. D. Reidel Publishing Company, Dordrecht, Holland. pp. 61–66). There was a virtual cessation of tree recruitment between 1850 and 1910, suggesting that the *Q. rubra* stand went through a “midlife” stem exclusion stage. However, another period of peak recruitment between 1920 and 1940 coincided with chestnut blight (*Endothia parasitica*) and extreme drought in the region. Oak recruitment in the *Q. prinus* stand was fairly continuous and exhibited peaks from 1710 to 1730 and in the 1940s that were associated with releases in radial growth. An increase in *Q. rubra* in this stand occurred between 1860 and 1950. There was also a trend of increasing growth in the oldest *Q. prinus* trees from 1860 to the present, particularly between 1930 and 1960. The xeric *Q. prinus* stand had only a small component of potential oak replacement species and appears to represent an edaphic climax for this genus. The large increase of mixed-mesophytic species during the 1900s in the *Q. rubra* stand indicates its transitional nature in the absence of periodic fire.

Résumé : Des techniques dendro-écologiques ont été utilisées pour examiner la dynamique et la succession couvrant trois siècles de développement de deux vieilles forêts vierges dominées par *Quercus rubra* L., sur site mésique, et par *Quercus prinus* L., sur site xérique, dans les montagnes Blue Ridge du Centre-Ouest de la Virginie. Dans le peuplement de *Q. rubra*, une forte augmentation dans le recrutement de cette espèce, entre 1820 et 1850, a été associée avec un net élargissement des cernes suivi d’une réduction plus marquée de leur largeur dans la série de référence. La diminution de la croissance entre 1837 et 1844 a coïncidé avec le déplacement prévu, vers le sud, de la position estivale du front polaire en provenance de l’Est du Canada (E.R. Cook et P. Mayes. 1987. Decadal-scale patterns of climatic change over eastern North America inferred from tree rings. *Dans* Abrupt climatic change. *Editeurs* : W.H. Berger et L.D. Labeyrie. D. Reidel Publishing Company, Dordrecht, Holland. pp. 61–66). Entre 1850 et 1910, il y eut un réel arrêt de recrutement des arbres, indiquant que le peuplement de *Q. rubra* a connu un stade d’exclusion des tiges à mi-chemin dans son développement. Cependant, entre 1920 et 1940, un autre maximum de recrutement a coïncidé avec l’apparition de la brûlure du châtaigner (*Endothia parasitica*) et avec une extrême sécheresse dans la région. Le recrutement du chêne dans le peuplement de *Q. prinus* a été assez continu, et a présenté des maxima de 1710 à 1730 ainsi que dans les années 1940, lesquels ont été associés à des augmentations de croissance radiale. Le nombre de tiges de *Q. rubra* a augmenté dans ce peuplement entre 1860 et 1950. La croissance a aussi eu tendance à augmenter chez les plus vieux *Q. prinus* de 1860 à nos jours, particulièrement entre 1930 et 1960. Le peuplement xérophile de *Q. prinus* n’a eu qu’une petite composante d’espèces potentiellement aptes à remplacer le chêne; il semble représenter, pour ce genre, un climax édaphique. La forte augmentation d’espèces mixtes-mésophiles dans le peuplement de *Q. rubra*, pendant les années 1900, confirme le caractère de transition de ce peuplement en l’absence de feux périodiques. [Traduit par la Rédaction]

Introduction

Prior to European settlement, vast areas of eastern North America were dominated by oak (*Quercus*) forests (Michaux 1853; Bromley 1935; Abrams and Downs 1990; Whitney 1994). The importance of oak on upland sites in the original forests is thought to be related, at least in part, to the occurrence of periodic fire caused by lightning and Native American activity (Buell et al. 1954; Lorimer 1985; Abrams 1992). Over the last two decades, researchers have documented numerous examples of the transitional nature of oak forests to later successional species on sites in which periodic fire has been excluded during the twentieth century (Adams and Anderson 1980; Lorimer 1984; Pallardy et al. 1988; Nowacki et al. 1990; Abrams et al. 1995). The successional replacement of oak forests is particularly apparent on mesic sites in the northeast, midwest, and Lake States regions of the United States (cf. Abrams 1992, 1996).

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Examples of stable oak populations in forests of the eastern United States are scarce and often poorly documented, but may exist on extremely xeric and nutrient-poor sites (Adams and Anderson 1980; Dooley and Collins 1984; Little 1974; McCune and Cottam 1985). It has been suggested that dry oak forests located to the south and west of the of the northern hardwood and maple–beech–basswood forests may be experiencing relatively little successional pressure (Abrams 1996). Indeed, this was the conclusion of studies of xeric oak forests in central and southwestern Virginia, in which the forests had a scarcity of later successional, potential oak replacement species and a significant amount of oak recruitment into the tree size classes throughout the twentieth century (Ross et al. 1982; Orwig and Abrams 1994). The future dominance of these forests will apparently be shared among oak and several mixed-mesophytic species. Nonetheless, relatively little is known about the historical development and dendroecology of oak forests in the southern and central United States in relation to disturbance and climatic impacts and successional status.

Extensive land clearing and repeated cutting of eastern forests following European settlement has left few intact virgin forests, especially those dominated by oak. Therefore, we know very little about oak recruitment and dendroecology of intact forests that existed before the late eighteenth century (Abrams and Downs 1990; Mikan et al. 1994; Cho and Boerner 1995; Abrams et al. 1995). The dendroecological technique that couples tree ring chronologies with species age structure has proven to be an important approach to the study of disturbance history and population dynamics in forests (Fritts and Swetnam 1989; Lorimer and Frelich 1989; Abrams and Nowacki 1992; Frelich and Graumlich 1994; Abrams and Orwig 1995, 1996). The results of our community and dendroecology studies of second- and third-growth forests in the Piedmont and Coastal Plain of Virginia stimulated our interest in old-growth oak ecology in the southern mid-Atlantic region. Subsequently, we learned of two virgin oak forests dominated by *Quercus rubra* L. (northern red oak) and *Q. prinus* L. (chestnut oak) on contrasting sites (mesic versus xeric, respectively) located in close proximity to each other in the Blue Ridge Mountains of west-central Virginia (E.R. Cook, personal communication). This represented a rare opportunity for the detailed study of long-term species recruitment patterns and radial growth dynamics before and after the period of European settlement. The specific objectives of this study were to characterize the composition, size and age structure, successional development, and tree ring chronologies spanning a 300-year period in the contrasting old-growth *Quercus* forests. These data were coupled with published reports on extreme climatic anomalies to better understand the dendrochronology of the two stands.

Study area

Two old-growth *Quercus* stands, each approximately 6 ha in area, were selected for study within the Jefferson National Forest in Bedford County, Va. (37°30′N 79°28′W). The study sites are located along Thunder Ridge within the Blue Ridge Physiographic Province in west-central Virginia with elevations ranging from 792 to 975 m in the *Q. prinus* dominated stand and from 1036 to 1097 m in the *Q. rubra* dominated stand. Only 3 km separate the two stands, although they differed greatly in topographic features. The *Q. rubra* stand was located on a flat to gently rolling, exposed ridgetop with an average slope of 9% (range 0–19%) and a northern aspect, while the *Q. prinus* stand was located on a steep talus sideslope with an average slope of 52% (range 50–55%) and a southerly aspect. Soils at both sites were of the Edneyville series, which are deep, extremely stony, fine sandy loams derived from residuum of granite and gneiss (Bailey and Arnold 1986). The *Q. prinus* stand was characterized by exposed granite stones, cobbles, and rock outcrops distributed over approximately 50% of the ground surface, while the *Q. rubra* stand contained sparse, scattered rock fragments. There was evidence of past and recent fires in the *Q. prinus* stand in the form of fire scars, burned stumps, and soil charcoal but no evidence of recent fire in the *Q. rubra* stand. However, many trees in the *Q. rubra* stand had snapped tops and broken branches from apparent wind and ice damage on this exposed site. Mean annual precipitation for the area is 107 cm and the mean annual temperature is 14°C, with a January mean of 3°C and a July mean of 24°C (McDaniel et al. 1989).

Methods

On 27–28 October 1994, 20 fixed-area plots located at 20-m intervals along transects through the forest interior were used for vegetation sampling at the two study sites. The species, diameter, and crown class were recorded for all trees (diameter at breast height (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 categories (dominant, codominant, intermediate, and overtopped) was based on the amount and direction of intercepted light (Smith 1986). At each plot, two to four trees were cored at 1.37 m for age determinations and radial growth analysis. Across all 20 plots in each stand, we obtained cores from all the represented species and range of diameter classes. Coring location on each tree was determined individually by tree shape and size to facilitate the interception of the pith. All suitable cores from each stand ($n = 60$ and 72 *Q. prinus* and *Q. rubra*, respectively) were brought to the laboratory for examination. Saplings and seedlings were counted in nested circular plots of 9 and 5 m^2, respectively, located within each of the overstory plots. Saplings were classified as tree species ≥1.5 m in height but <8.0 cm DBH and seedlings were <1.5 m in height.

Radial growth analysis

Age determinations (at 1.37 m) for all cores were made using a dissecting microscope after the cores were dried, sanded, and mounted. Cores from the five oldest *Q. rubra* and *Q. prinus* trees were used to construct a master growth chronology of each site spanning approximately 300 years. Trees comprising each master growth chronology were within a 50-year age range to minimize the potential impact of age-dependent growth variations (Szeicz and MacDonald 1994). Annual growth increments were measured to the nearest 0.01 mm with a tree ring measuring device (Regents Instruments Inc., Quebec, Canada) and recorded using the MACDENDRO microcomputer program. A ring width index (RWI) was created for each tree chronology by dividing yearly mean measured growth values by the expected values obtained from either linear or negative exponential regression, depending on which regression procedure gave the “best fit” (Fritts and Swetnam 1989). This standardization technique effectively removes age-related growth trends. After cross-dating using signature years (in the raw data) and the quality control program COFECHA (Holmes 1983), the annual RWI values from each core were averaged to obtain a mean growth chronology for the dominant *Quercus* species on each site. Annual growth increments were measured for an additional 22 or 23 of the most suitable tree cores in each stand for growth comparisons across other species and age classes. Cores 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 ≥100% average growth increase

Table 1. Density, frequency, dominance, and importance values for tree species in an old-growth *Q. rubra* forest on the Blue Ridge of west-central Virginia.

Species	Density (ha^{-1})	Frequency (no. of plots)	Dominance ($\text{m}^2\cdot\text{ha}^{-1}$)	Relative density	Relative frequency	Relative dominance	Relative importance
Quercus rubra	187.5	20	34.25	43.3	25.6	78.1	49.0
Fraxinus americana L.	35.0	8	0.83	8.1	10.3	1.9	6.8
Prunus serotina Ehrh.	25.0	6	2.83	5.8	7.7	6.4	6.6
Betula lenta L.	57.5	10	2.12	13.3	12.8	4.8	10.3
Betula alleghaniensis Britton	5.0	1	0.18	1.2	1.3	0.4	1.0
Acer pensylvanicum L.	30.0	8	0.44	7.0	10.3	1.0	6.1
Acer saccharum Marsh.	12.5	4	0.25	2.9	5.1	0.6	3.0
Acer rubrum L.	5.0	2	0.15	1.2	2.6	0.3	1.4
Tilia americana L.	27.5	5	0.47	6.4	6.4	1.1	4.6
Carya spp.[a]	15.0	5	0.22	3.5	6.4	0.6	3.5
Ostrya virginiana (P. Mill.) K. Koch	7.5	1	0.09	1.7	1.3	0.2	1.1
Magnolia acuminata (L.) L.	5.0	2	0.41	1.2	2.6	0.9	1.6
Tsuga canadensis (L.) Carr.	5.0	2	0.31	1.2	2.6	0.7	1.5
Others[b]	15.0	4	1.33	3.5	5.2	3.0	3.9
Total	432.5	78	43.88				

[a] Includes *C. cordiformis* (Wangenh.) K. Koch, *C. glabra* (Mill.) Sweet, and *C. tomentosa* (Poir.) Nutt.

[b] Includes *Quercus alba* L., *Hamamelis virginiana* L., *Castanea dentata* (Marsh.) Borkh., and *Robinia psuedoacacia* L.

Table 2. Density, frequency, dominance, and importance values for tree species in an old-growth *Q. prinus* forest on the Blue Ridge of west-central Virginia.

Species	Density (ha^{-1})	Frequency (no. of plots)	Dominance ($\text{m}^2\cdot\text{ha}^{-1}$)	Relative density	Relative frequency	Relative dominance	Relative importance
Quercus prinus	175.0	18	27.88	60.9	38.3	77.9	59.0
Quercus rubra	60.0	12	6.00	20.9	25.5	16.8	21.1
Acer rubrum	25.0	7	0.81	8.7	14.9	2.3	8.6
Acer pensylvanicum	2.5	1	0.04	0.9	2.1	0.1	1.0
Carya glabra	10.0	3	0.67	3.5	6.4	1.9	3.9
Nyssa sylvatica Marsh.	5.0	2	0.12	1.7	4.3	0.3	2.1
Sassafras albidum (Nutt.) Nees	2.5	1	0.01	0.9	2.1		1.0
Prunus serotina	2.5	1	0.07	0.9	2.1	0.2	1.1
Betula lenta	2.5	1	0.03	0.9	2.1	0.1	1.0
Fraxinus americana	2.5	1	0.18	0.9	2.1	0.5	1.2
Total	287.5	47	35.81				

Table 3. Seedling and sapling densities (ha^{-1}) for tree species in old-growth *Q. prinus* and *Q. rubra* forests.

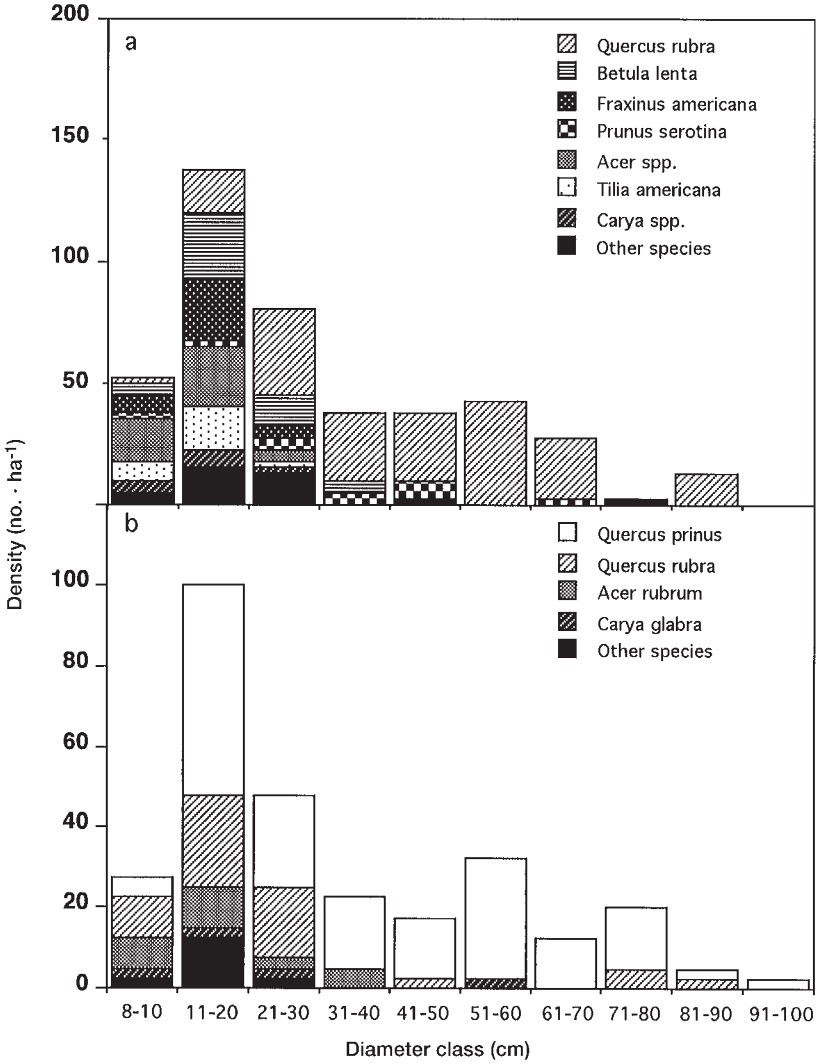
	Q. rubra		*Q. prinus*	
Species	Seedlings	Saplings	Seedlings	Saplings
Quercus prinus			700	111
Quercus rubra	2300	722	700	333
Prunus serotina	700	222	100	167
Sassafras albidum			2100	222
Carya glabra		56	400	
Castanea dentata		222	200	111
Fraxinus americana	800	278		
Tilia americana		111		
Betula lenta	500			
Total	4300	1611	4200	944

lasting at least 15 years and a moderate temporary release as a ≥50% average growth release lasting from 10 to 15 years. These criteria, coupled with tree canopy recruitment dates, were used to distinguish disturbance events from responses attributed to climatic factors (Lorimer and Frelich 1989; Abrams and Orwig 1996).

Results

A total of 19 tree species were recorded in the *Q. rubra* dominated forest, compared with only 10 tree species in the *Q. prinus* stand (Tables 1 and 2). The high importance value of *Q. rubra* and *Q. prinus* in the respective stands mainly reflects their very high relative basal area and density. Total density, frequency, and basal area were substantially greater in the *Q. rubra* than in the *Q. prinus* stand. The second rank species in the *Q. prinus* stand was *Q. rubra* with 21% importance, compared with *Betula lenta* in the *Q. rubra* stand with only 10% importance. The total density of seedlings and saplings was fairly low in both stands, but lowest in the *Q. prinus*

Fig. 1. Diameter (at 1.37 m) distribution of tree species in the old-growth (*a*) *Q. rubra* and (*b*) *Q. prinus* stands in the Blue Ridge Mountains, west-central Virginia. For other species, see Tables 1 and 2.



stand (Table 3). *Quercus rubra* was the dominant seedling and sapling species in the *Q. rubra* stand and the dominant sapling species in the *Q. prinus* stand.

The diameter distribution in both stands approximated a negative exponential pattern, typical of an uneven-aged forest, except for the scarcity of stems in the 8–10 cm class (Fig. 1; Smith 1986). *Quercus* was represented across all diameter classes in both stands. In the *Q. rubra* stand, this species dominated only the middle and larger classes, with mixed-mesophytic species representing most of the smaller trees (Fig. 1*a*). *Quercus prinus* followed by *Q. rubra* dominated all diameter classes in the *Q. prinus* stand, with relatively few mixed-mesophytic species present (Fig. 1*b*).

In the *Q. rubra* stand, the oldest tree was 275 years (at 1.37 m) and this species had fairly continuous recruitment from 1710 to 1850 and peak numbers between 1820 and 1850 (Fig. 2*a*). Only one instance of *Q. rubra* recruitment occurred between 1850 and 1910 in this uneven-aged stand, after which a large number of *Q. rubra* and a variety of mixed-mesophytic species became established in the 1920s and 1930s. Between 1940 and 1980, many mixed-mesophytic species, but only one *Q. rubra*, recruited into the tree-size classes. In this stand, major and moderate releases occurred in most decades after 1750 (Fig. 2*b*). The larger number of release events recorded in the 1900s was attributed to the larger number of younger versus older trees in the stand. The high frequency of *Q. rubra* recruitment in the 1840s and 1920s and 1930s was associated with a large number of growth release events at those times. There was also agreement between the lack of recruitment and lack of growth releases between 1850 and 1900 in this stand, although the high frequency of releases between 1900 and 1910 and between 1960 and 1980 apparently did not stimulate widespread recruitment. Radial growth analysis of five of the oldest *Q. rubra* trees revealed a period of decreasing and then increasing growth from 1740 to 1780 (Fig. 2*c*). Growth increased in the 1820s, but then dropped precipitously between 1837 and 1844. By 1870, growth increased to the expected rate (RWI = 1). This pattern repeated itself in the early twentieth century, with a rapid growth increase starting in 1909 and a sharp decline in the 1920s. Peak recruitment of *Q. rubra* from 1820 to 1840 and in the 1930s followed the dramatic growth from variations from 1820 to 1844 and from 1909 to 1927.

Fig. 2. (*a*) Age class (at 1.37 m) distribution for all aged trees (*n* = 72), (*b*) number of moderate and major growth releases by decade for tree chronologies (*n* (over each bar) = number of tree cores measured in each decade for releases), and (*c*) mean RWI for the five oldest *Q. rubra* trees in the old-growth *Q. rubra* stand in the Blue Ridge Mountains.

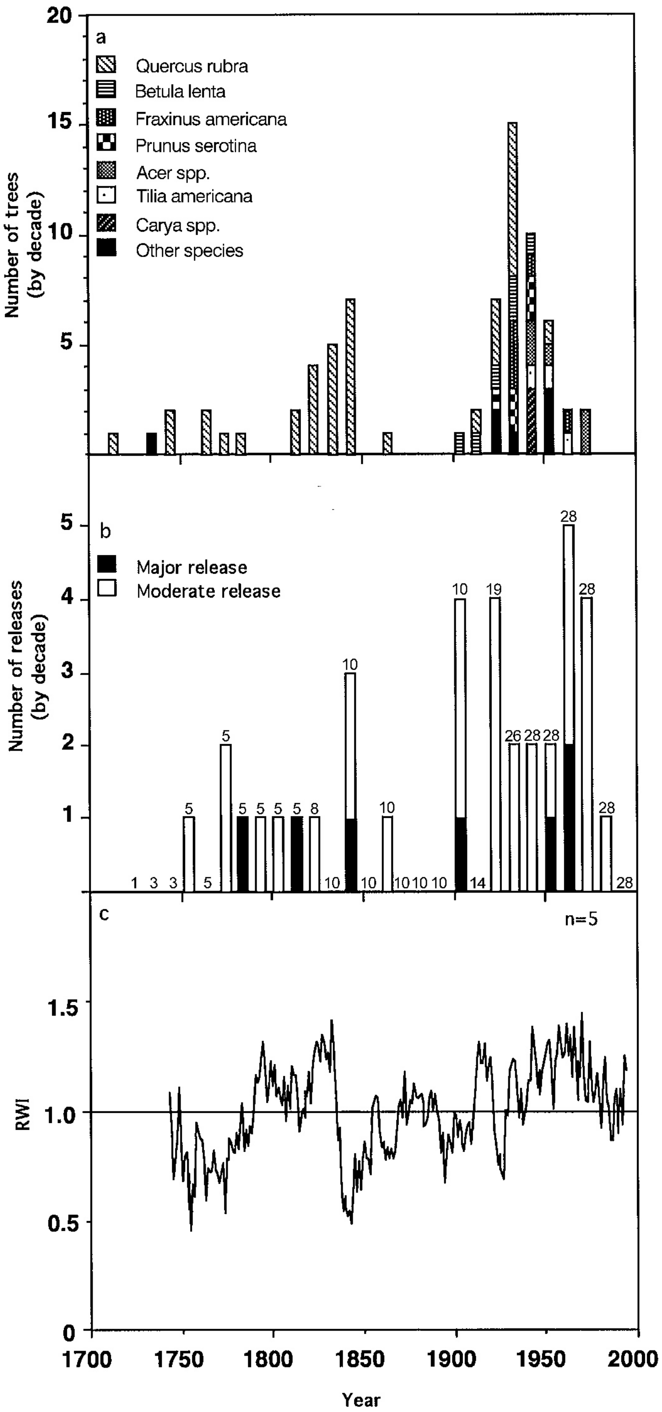
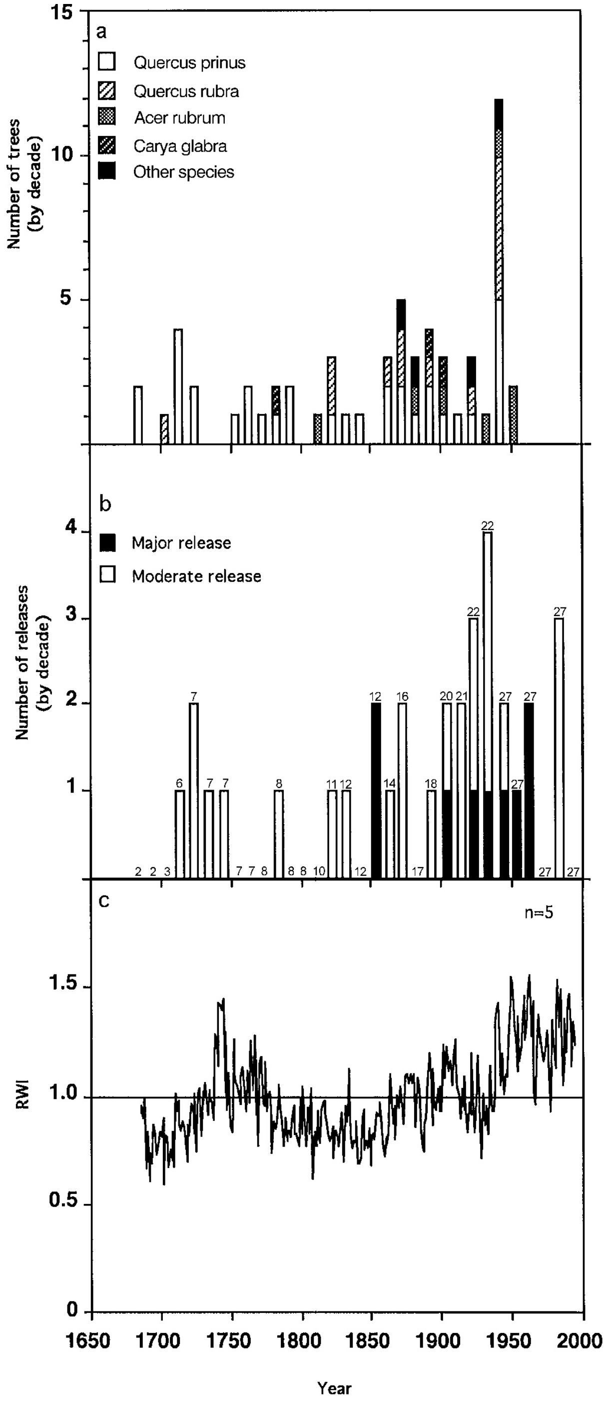


Fig. 3. (*a*) Age class (at 1.37 m) distribution for all aged trees (*n* = 60), (*b*) number of moderate and major growth releases by decade for tree chronologies (*n* (over each bar) = number of tree cores measured in each decade for releases), and (*c*) mean RWI for the five oldest *Q. prinus* trees in the old-growth *Q. prinus* stand in the Blue Ridge Mountains.



In the *Q. prinus* dominated stand, a 311- and 305-year-old *Q. prinus* and a 287-year-old *Q. rubra* were the oldest trees (Fig. 3*a*). *Quercus prinus* recruited in most decades between 1670 and 1960, with peak numbers in the 1940s in this uneven-aged stand. Most *Q. rubra* in the stand recruited between 1860 and 1950, predominantly in the 1940s. Some *Acer rubrum* recruitment occurred in most decades between 1880 and 1960, while the oldest tree of this species dated to 1813. We recorded growth releases in only one half of the decades between 1700 and 1850 in the *Q. prinus* stand (Fig. 3*b*). All the major releases recorded in this stand occurred between 1852 and 1964. The decade of peak tree recruitment in the 1940s followed a substantial number of growth releases in the 1920s and 1930s. Radial growth in the five oldest *Q. prinus* trees was relatively low between 1690 and 1709, but greatly increased between 1710 and 1735 and peaked between 1740 and 1744 (Fig. 3*c*). Growth decreased rapidly and then more slowly until 1850, but it generally increased from 1860 to 1994, except for the decrease in growth between 1909 and 1930. The growth anomalies between 1820 and 1844 and between 1909 and 1927 in the *Q. rubra* stand were much less obvious in the *Q. prinus* stand. Tree recruitment was fairly constant in this stand and appeared to be associated with increases in the RWI master chronology between 1710 and 1730 and in the 1940s.

Discussion

Pre-European settlement forests in the Ridge and Valley Physiographic Province of the mid-Atlantic region were dominated by *Quercus*, *Castanea*, *Carya*, and *Pinus* (Spurr 1951; Abrams et al. 1995; Abrams and Ruffner 1995; Abrams and McCay 1996). The ecology of upland forests in the region is often linked with the occurrence of periodic fire. Studies concerning the ecological history of the Ridge and Valley Province and central and southern Appalachians indicate that Native American settlement of the region dates to at least 10 000 years BP and that the use of fire by these people was pervasive throughout the forests (Maxwell 1910; Wilhelm 1972; Van Lear and Waldrop 1989; Hammett 1992; Stephenson et al. 1992). We observed evidence of a fire at the *Q. prinus* study site in the form of basal fire scars and soil charcoal, as well as charred boles and branches from a recent low-intensity fire. In addition, high-elevation forests in the eastern United States, such as those used in this study, are periodically influenced by a variety of wind- and ice-related disturbances that cause mechanical damage to trees and canopy openings (Carvell et al. 1957; Lemon 1961; Boerner et al. 1988).

The oldest and largest trees at both of our study sites were *Quercus* species, and the domination of these uneven-aged forests by *Quercus* apparently dates back at least 300 years. Pollen studies suggest that *Quercus* domination of central Appalachian forests dates back to 10 000 years BP (Watts 1980; Webb 1988). A unique dendroecological feature of the *Q. rubra* stand is the high frequency of recruitment of this species between 1820 and 1850. The period between 1820 and 1830 was characterized by a sharp increase in tree RWI at the site. A dendroclimatological investigation of a network of forests throughout the eastern United States noted that 1827–1835 was a period of persistent above-average tree growth that is indicative of wetter than average conditions (Cook and Mayes 1987). These authors also reported a precipitous decline in growth rates between 1837 and 1847, very much like the pattern in the *Q. rubra* chronology in this study. This growth decline throughout the eastern United States was attributed to a southward displacement of the summertime position of the polar front in eastern Canada, allowing for enhanced advection of cool, dry air and a southward displacement of storm tracks (Cook and Mayes 1987). This series of events is consistent with growth variations in the *Q. rubra*, but not in the *Q. prinus*, stand during the second quarter of the nineteenth century.

From previous dendroecological studies, we concluded that simultaneous increases in growth rates, growth releases, and tree recruitment are a result of disturbance whereas increases in radial growth not associated with sustained releases and a high incidence of tree recruitment are more likely to be a result of favorable climate (Lorimer and Frelich 1989; Abrams and Nowacki 1992; Abrams and Orwig 1995). However, the sharp increase in *Q. rubra* ring width in the 1820s and 1830s may involve both climate and disturbance because it was associated with a particularly high frequency of tree recruitment. Similarly, the dramatic growth decrease between 1837 and 1844 may involve both climate and disturbance if the occurrence of cold air and severe storms caused extensive injury to the tree canopies (Foster 1988; Abrams and Orwig 1996). The location of the *Q. rubra* stand on an exposed ridgetop would make it particularly susceptible to storm damage. The virtual cessation of tree recruitment in the *Q. rubra* stand between 1850 and 1910 is suggestive of a “midlife” stem exclusion stage following the peak recruitment in the 1840s (cf. Oliver 1980; Oliver and Larson 1990). Our interpretation is that a pulse of new stems established following the climatic anomaly and disturbances during the 1830s likely filled the available growing space and effectively monopolized resources at the site for a 60-year period. The appearance of tree recruitment after 1910 seems to signal the start of understory reinitiation following the stem exclusion stage. However, the interpretation of stand dynamics from static age structure may be problematic due to differential mortality with various age and canopy classes and stand history events (Johnson et al. 1994).

The large number of releases between 1900 and 1910 and in the 1920s and the high frequency of species recruitment from 1920 to 1930 suggest a series of substantial ecological impacts in the *Q. rubra* stand. Prevalent ecological factors in the 1920s and 1930s in western Virginia were the chestnut blight (*Endothia parasitica*), the severe drought of 1930, and the exclusion of fire (Stephenson et al. 1992). Canopy openings created by the loss of *Castanea* and drought-induced overstory mortality may have been responsible for growth releases and recruitment episodes in the stand between 1920 and 1940 (Agrawal 1995). Throughout the mid-Atlantic region, *Q. rubra* was a primary beneficiary following the loss of *Castanea* (Keever 1953; McCormick and Platt 1980; Stephenson 1986; Abrams and Ruffner 1995). Between 1910 and 1940 the recruitment of mixed-mespophytic tree species equalled that of *Q. rubra*. After 1940, almost all *Q. rubra* recruitment beyond the sapling stage ceased, despite many growth release events in the stands from 1960 to 1980. This recruitment pattern is consistent with the fundamental ecological change that has occurred in many mesic and dry-mesic *Quercus* forests in the eastern United States, namely, the replacement of *Quercus* by later successional species following fire exclusion after 1900 (cf. Abrams 1992). Nonetheless, the decades of low oak recruitment may be a temporary phenomenon and episodic stand events may allow for increased oak in the future (Hett and Loucks 1976; Glitzenstein et al. 1986).

The *Q. prinus* stand differed from the *Q. rubra* stand in many dendroecological aspects. The recruitment of species was fairly continuous, and rarely episodic, except during 1710–1730 and the 1940s. The protracted increase in radial growth from 1710 to 1735 culminated in a sharp peak between 1740 and 1745, which suggests the occurrence of a stand-level disturbance about 1710 and a period of favorable climate from 1740 to 1745 (cf. Abrams and Orwig 1995). The presumed climate-induced growth anomalies of 1820–1847 in the *Q. rubra* stand were limited to a few trees in the *Q. prinus* stand (data not shown). The greater sensitivity of the *Q. rubra* stand to the predicted climatic variation at that time is difficult to explain, but may be due to differences in site (more mesic, exposed ridgetop versus xeric, sideslope) and the differential tolerance of these species to environmental stress. Studies comparing the demography and physiology of the two species indicate greater drought resistance in *Q. prinus* than in *Q. rubra* (Hursh and Haasis 1931; Bourdeau 1954; Abrams et al. 1990; Clinton et al. 1993).

The differential tolerance to drought of *Q. rubra* and *Q. prinus* does not preclude their widespread coexistence on high-elevation sites throughout the Ridge and Valley and Appalachian regions (Braun 1950; Stephenson and Adams 1991; Nowacki and Abrams 1992; Hurst 1994). At the *Q. prinus* study site, recruitment of *Q. rubra* increased after 1860, with peak frequency in the 1940s following a large number of growth releases in the 1920s and 1930s. RWI values in the master chronology increased after 1930 and peaked between 1940 and 1994. The influence of the chestnut blight and the potential amelioration of the *Q. prinus* study site from fire exclusion and atmospheric factors such as elevated CO_2 and nitrogen deposition may have contributed to the tree recruitment and growth increases after 1900 (Ohmann and Grigal 1979; Adams and Anderson 1980; Aber et al. 1989; Agrawal 1995; Nicolussi et al. 1995). A study of wildfire effects on forest floor characteristics in *Pinus–Quercus* forests in the Blue Ridge Mountains concluded that fire exclusion results in increased thickness, nutrient status, and water-holding capacity in the organic layer (Groeschl et al. 1993). On xeric sites, the exclusion of fire may allow for the invasion of species (e.g., *Q. rubra*) that lacked the physiological capability to invade the sites when periodically burned. However, we can offer no compelling argument as to why *Q. rubra* recruitment in this stand increased between 1860 and 1890, prior to the fire exclusion era for the region (Wilhelm 1972; Stephenson et al. 1992). The absence of *Q. prinus* on the *Q. rubra* site may be related to the superior growth rate and competitiveness of *Q. rubra* on sites with favorable soil moisture, nutrients, and texture in the Blue Ridge Province (Racine 1971).

Another study of Appalachian *Quercus* forests in southwest Virginia suggested that *Quercus* will maintain future dominance on xeric sites whereas succession to *Nyssa sylvatica*, *Sassafras albidum*, and *A. rubrum* will occur on mesic sites (Ross et al. 1982). This general conclusion is consistent with the successional patterns at our study sites. There was not a large influx of later successional tree species during the 1900s in the *Q. prinus* stand, during which time wildfires were actively suppressed in the region. Thus, any potential improvement in site quality following fire exclusion that facilitated an increase in *Q. rubra* in the stand was seemingly inadequate to support a large increase in other mixed-mesophytic species. This fact, coupled with the continuation of *Quercus* recruitment this century, suggests that this stand may represent an edaphic climax, although there was evidence of a recent low-intensity fire at the site. This is a unique example among *Quercus* forests in the eastern United States, and it is consistent with the hypothesis that *Quercus* forests in eastern North America located to the south and west of the peak distribution of the primary *Quercus* replacement species (e.g., *Acer saccharum*, *A. rubrum*, *Fagus grandifolia* Ehrh., and *Prunus serotina*) should experience less successional pressure than more northern forests, even in the absence of fire (Abrams 1992, 1996).

In conclusion, this study represented a rare opportunity to study the dynamics of contrasting old-growth *Quercus* forests in the eastern United States. Despite their close proximity, these stands differed greatly in topographic and edaphic properties, which we believed formed the basis of their contrasting dendroecology and successional development. Extreme weather phenomena played a large role in sustained growth suppression and releases and recruitment pattern, including growth releases in the closed *Q. rubra* forest. Old-growth trees, such as those used in this study, are an invaluable resource for future dendroclimatological and dendroecological research. However, because of their advanced age the opportunity to study pre-European settlement origin *Quercus* trees in the eastern United States will be short-lived. We hope this study will stimulate further interest in the impacts of disturbance, climate, and land-use history in the study of old-growth forest dynamics and dendroecology.

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