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Temporal variation in species recruitment and dendroecology of an old-growth white oak forest in the Virginia Piedmont, USA

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Abstract

The composition and temporal variation in species recruitment were examined in relation to annual dendrochronological data to determine the historical development and successional history of an old-growth mixed-oak (*Quercus*) forest in northern Virginia, USA. A ridge site in the upland Piedmont, along the Potomac River, was used to survey the old-growth forest, which is dominated by *Quercus alba* L., *Q. rubra* L., *Liriodendron tulipifera* L., *Fagus grandifolia* Ehrh., and *Carya glabra* (Mill.) Sweet. The present age structure indicates that the oldest *Q. alba* established between 1748 and 1790. All tree species other than *Q. alba* in the forest were <110 years of age, excluding a 166-year-old *Nyssa sylvatica* Marsh.. *Quercus alba* had fairly continuous recruitment between 1740 and 1925. Peak recruitment of *Q. rubra* and *C. glabra* occurred between 1900 and 1930. Since 1930, tree recruitment in the forest has been dominated by *Fagus*, *Liriodendron*, and *Acer rubrum* L.. Releases in radial growth, indicative of moderate- and small-scale disturbances occurred in most of the oldest trees during the last 200 years. The master tree-ring chronology exhibited a sharp decline from 1837 to 1844, associated with an extremely cold period in the region, followed by a general increase from 1850 to 1930; growth remained high from 1930 to 1998. The shift in dominance from white oak to red oak to mixed-mesophytic tree species after 1900 is consistent with successional variation in other oak forests in the mid-Atlantic region.

Keywords: Disturbance; Tree-rings; Stand dynamics; Succession; Fire

1. Introduction

The study of tree-ring chronologies from old-growth forests has greatly increased our understanding of stand dynamics and succession (Fritts and Swetnam, 1989). Researchers have reconstructed the ecological history of forests in terms of population dynamics, species recruitment patterns, periodicity and intensity of disturbance (such as wind, fire and insect outbreaks), the impact of climate and extreme weather phenomena, and successional dynamics (Heinselman, 1973; Foster, 1988; Frelich and Graumlich, 1994; Abrams et al., 1995). Studying tree-ring chronologies coupled with age structure, land-use history, climatic data, and the ecological attributes of individual species has proven to be a particularly robust approach for understanding of long-term forest dynamics (Foster, 1988; Orwig and Abrams, 1994a; Abrams et al., 1997a, b; Ruffner and Abrams, 1998).

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Prior to European settlement, vast areas of the mid-Atlantic region of the eastern U.S. were dominated by *Quercus* (oak) species (Michaux, 1853, Spurr, 1951; Russell, 1980; Abrams, 1992; Whitney, 1994; Ruffner and Abrams, 1998). Within the genus, *Q. alba* L. (white oak) was notable for its importance in the original forests (Abrams and Downs, 1990; Abrams, 1992; Orwig and Abrams, 1994a). However, white oak typically grows on fertile valley and bottomland soils, which were extensively cleared for agriculture following European settlement. Therefore, present-day examples of old-growth white oak are extremely rare, and information on the dynamics and successional development of white oak in the original forests is lacking (Abrams and Downs, 1990; Cho and Boerner, 1995). It is generally thought that white oak, as well as other upland oak species, were exposed to recurring disturbances from Native American activity and lightning strikes, and that fire and land-clearing were important in maintaining oak and retarding the development of later successional tree species (Lorimer, 1985; Abrams, 1992). The decreases in disturbance regimes, including fire suppression, in the eastern U.S. during the 20th century appears to be important causal factors in the oak decline syndrome seen throughout the region (Abrams, 1992; Abrams, 1998a; Lorimer et al., 1994).

In this study, we report on a 250-year history of species recruitment and dendroecology for an old-growth white oak forest at the Great Falls National Park in northern Virginia. The specific objectives of this study were to (1) quantify the present composition and structure of the forest, (2) report on the long-term patterns of species recruitment and radial growth variation, (3) investigate the impacts of natural and anthropogenic disturbances on the long-term forest dynamic, and (4) gain an understanding of the ecological history and successional status of the stand. The results of this study will improve our understanding of the ecology, dynamics, and succession of old-growth white oak in the eastern U.S.

2. Site description

The 10 ha site used for study is an old-growth mixed-oak forest located on a ridge parallel to the Potomac River at the northern portion of the Great Falls National Park in northern Virginia (77°15″, 38°50′). The park lies within the Upland Piedmont physiographic section, and the average yearly temperature and precipitation for the region is 13°C and 113 cm, respectively (Braun, 1950; Porter et al., 1963). The soils of the study site are the Manor–Glenig–Elioak series, which is characterized as a shallow, highly micaceous, and well-drained upland soil (Porter et al., 1963). It is very strongly acidic and low in organic material, over-all fertility, and water-holding capacity. Old-growth characteristics exist throughout the forest in terms of large diameter trees, a variety of diameter classes and canopy layers, gap formation, and coarse woody debris on the forest floor. We observed evidence of windthrow and past fires at the site from charring on several trees and soil charcoal; cut stumps from past logging were not observed at the site.

3. Methods

On July 31 and August 1, 1998, 20 plots located at 20 m intervals along transects through the forest interior were used for vegetation and dendroecological sampling. The overstory vegetation was surveyed using the point-quarter method in which the nearest tree ($\geq$8.0 cm DBH) in each of four quadrants was recorded by species, diameter (at 1.3 m), and crown class (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). For each tree species, a relative importance value was calculated as an average of the relative frequency, relative density, and relative dominance (based on basal area) (Cottam and Curtis, 1956). At each point, two-to-four trees were cored at 1.37 m for age determination and radial growth analysis. Across all 20 plots, we obtained cores from all the major species and for a range of diameter classes. 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 $\geq$1.5 m in height but <8.0 cm in DBH and seedlings were <1.5 m in height.

4. Radial growth analysis

All increment cores ($n = 43$) from the study area were dried, mounted, sanded, and counted for age (Phipps, 1985). The older cores ($n = 17$) were skeleton plotted for cross-dating to identify signature years and help locate missing or false rings (Stokes and Smiley, 1968). The 17 cores were then scanned with a tree-ring measuring device and the annual growth increments were measured to the nearest 0.01 mm (Regents Instruments Inc. Quebec, Canada). The ring widths from each core were standardized with the expected values derived from simple linear regression or the mean growth rate (Fritts, 1976; Fritts and Swetnam, 1989). The standardized ring width chronologies (RWI) from the oldest white oak trees ($n = 11$) were then averaged to form a master chronology for the stand (Fritts, 1976). This standardization enables tree-ring series from different samples to be compared by eliminating long-term variables which have been caused by bio-ecological factors, such as tree age and microsite differences (Schweingruber, 1989). We examined all 17 cores for periods of suppression and release according to Lorimer and Frelich (1989), who defined a major release as being a >100% average growth increase lasting at least 15 years and a moderate release as a >50% average growth increase lasting at least 10 years. These criteria, coupled with tree canopy recruitment dates, were used to distinguish disturbance events within the stand.

5. Results

The contemporary forest overstory is dominated by *Q. alba* L. (white oak), *Q. rubra* L.(northern red oak), *Liriodendron tulipifera* L. (tulip poplar), *Fagus grandifolia* Ehrh. (beech), and *Carya glabra* (Mill.) Sweet (pignut hickory) (Table 1). White oak, red oak, and tulip poplar have the highest dominance (basal area) values among the overstory tree species. The sapling layer is dominated by beech and *Cornus florida* L. (dogwood), although a total of 10 species occurred as saplings in the forest (Table 2). The seedling layer is dominated by *Asimina triloba* L. (Dunal) (pawpaw) and *Lindera benzoin* (L.) Blume (spicebush) (Table 2), although neither species will grow into the forest canopy due to their inherently short stature.

The diameter distribution of the 80-surveyed trees exhibited a roughly negative exponential or inverse-J pattern, typical of uneven-aged forests, except for the scarcity of trees in the 20–30 cm class (Fig. 1). White oak, northern red oak, and tulip poplar dominated the larger diameter classes (>60 cm DBH). These species plus beech dominated the middle diameter classes from 30 to 60 cm. The smallest diameter classes (<30 cm) are dominated by beech, tulip poplar, pignut hickory and *Acer rubrum* L. (red maple).

The canopy class distribution reveals that white oak, followed by tulip poplar and northern red oak, are most important in the dominant class (Fig. 2). Red oak and tulip poplar are most important in the codominant class. Tulip poplar, beech and pignut hickory

Table 1
Total and relative frequency, density, dominance (basal area in m^2) and relative importance values (RIV) for tree species surveyed in the old-growth forest at Great Falls Park, Virginia

Species	Frequency	Density	Dominance	Relative frequency	Relative density	Relative dominance	RIV
Quercus alba	12	15	4.824	18.8	18.8	29.6	22.4
Q. rubra	11	14	3.985	17.2	17.4	24.4	19.6
Liriodendron tulipifera	15	19	4.148	23.4	23.8	25.4	24.2
Fagus grandifolia	12	15	2.055	18.8	18.8	12.6	16.7
Carya glabra	7	9	0.585	10.9	12.5	3.6	9.0
Acer rubrum	4	5	0.621	6.2	6.2	3.8	5.3
Nyssa sylvatica	2	2	0.100	3.1	2.5	0.6	2.1
Ostrya virginiana	1	1	0.012	1.5	1.2	0.1	0.9
Total	64	80	16.33	100%	100%	100%	100%

Table 2
Seedling and sapling data (#/ha) in the old-growth forest at Great Falls Park, Virginia

Species	Saplings	Seedlings
Asimina triloba	400	9900
Lindera benzoin	650	2500
Carya glabra	150	300
Fagus grandifolia	1300	500
Cornus florida	800	—
Liriodendron tulipifera	200	—
Sassafras albidum	250	—
Acer rubrum	200	—
Carpinus caroliniana	200	—
Ilex opaca	50	—
Fraxinus americana	—	500
Quercus rubra	—	100
Total	4200	13 800

are the most common tree species in the intermediate class. Beech, pignut hickory and red maple occurred most frequently among the over-topped trees.

The oldest trees in the stand are white oak of 251, 232 and 208 years old (Fig. 3). All other tree species in the forest were <100 years of age, excluding a 166-year-old *Nyssa sylvatica* Marsh. (blackgum). White oak had fairly continuous recruitment between 1748 and 1925 (Fig. 3). In general, the white oak trees comprising the master chronology exhibited lower growth rates during the 1700s and 1800s compared to the 1900s. A sharp decrease in the chronology between 1837 and 1844 corresponds to a marked cold period in the eastern U.S. (cf. Cook and Mayes, 1987; Abrams et al., 1997a). Average tree growth then increased, albeit irregularly, from 1850 to 1930. Tree radial growth remained relatively high from 1930 to 1998. Peak recruitment of northern red oak and pignut hickory occurred between 1900 and 1930. Since 1920, tree recruitment has been dominated by beech, tulip poplar, and red maple.

Releases in radial growth occurred in most of the white oak cores (Fig. 4). The release dates were different for each of the cores, which indicates that each tree was influenced mainly by small-scale disturbances that have localized impacts within the forest. White oak growth rate varied from a low of 0.08 mm/year (Fig. 4(A)) to a high of 5.03 mm/year (Fig. 4(E)), but it tended to average ca. 2.0 mm/year. Tree 13 (Fig. 4(A)) had very low growth for the first 125 years of its life, which suggests that it may have

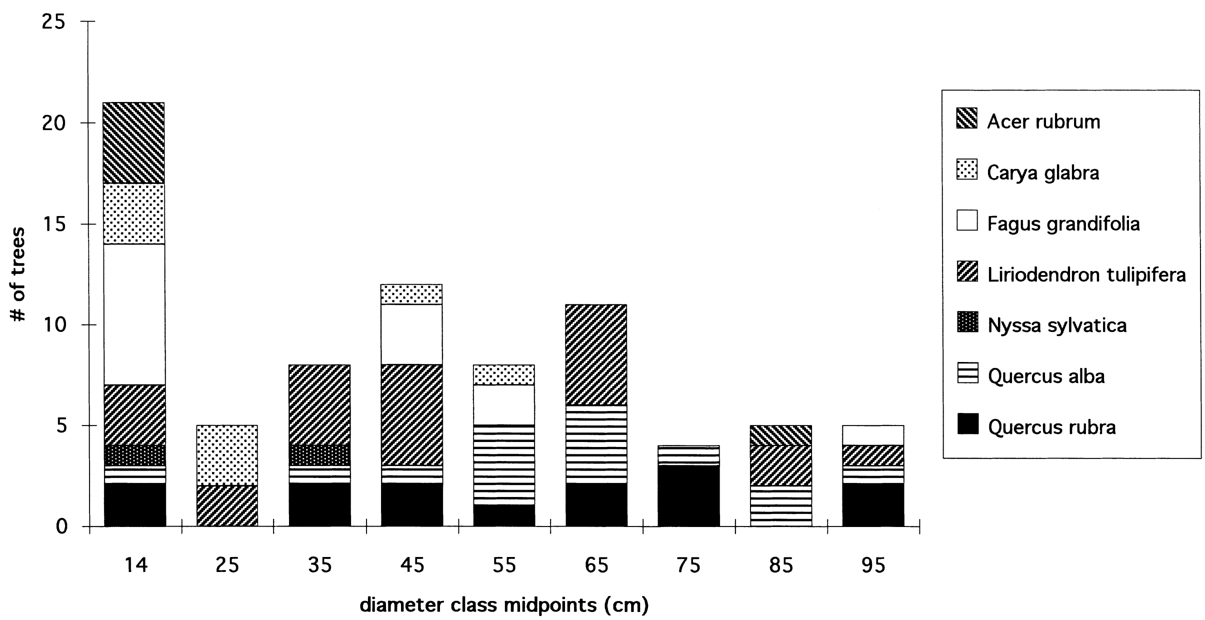

Fig. 1. Diameter (at 1.37 m) distribution of tree species in an old-growth white oak forest at the Great Falls Park in northern Virginia.

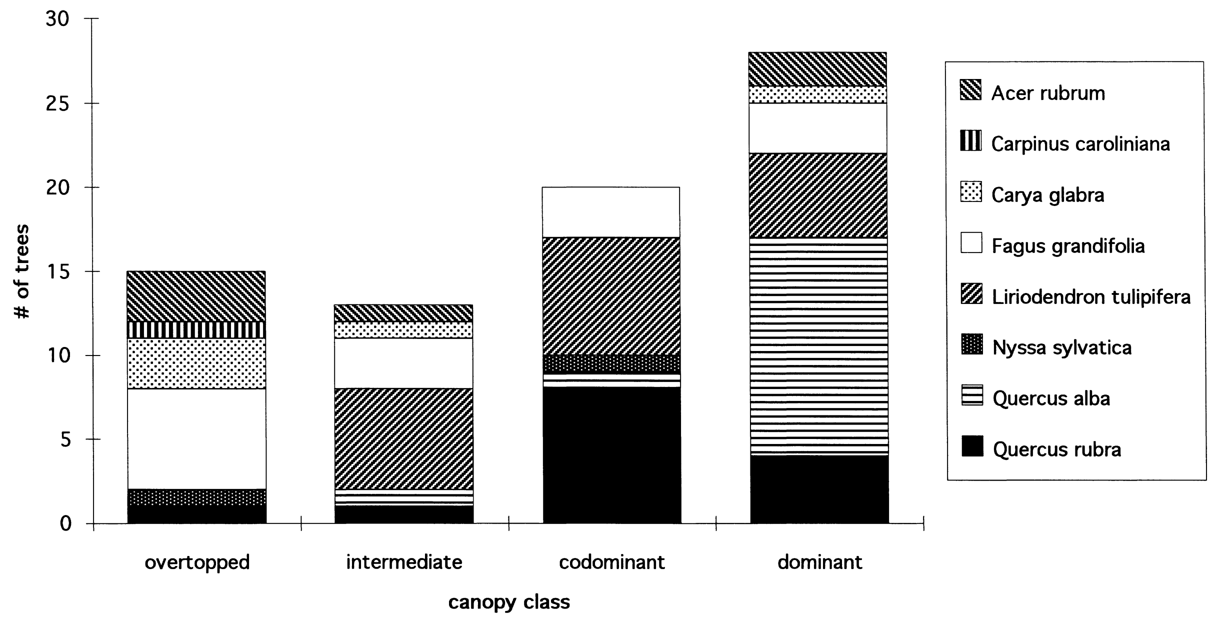

Fig. 2. Canopy class distribution of tree species in an old-growth white oak forest at the Great Falls Park, VA.

been suppressed in the understory for that protracted period. This was followed by a release in 1872 that triggered the growth of this tree into the upper forest canopy. Similarly, tree 11 (Fig. 4(B)) and tree 18 (Fig. 4(D)) apparently spent ca. 85 years in the understory prior to a canopy accession release in 1847 and 1905, respectively. Tree 26 (Fig. 4(E)) had a relatively short period of suppressed growth prior to a canopy accession release in 1922. White oak tree 31 (Fig. 4(C)) and tree 33 (Fig. 4(F)) had relatively high growth rates throughout their lives and had very few or no radial growth releases. These trees probably started life in a fairly large gap and grew into the forest canopy without any significant understory suppression.

6. Discussion

The anthropogenic history of the Great Falls Park, VA began before European settlement of the region when the site was used as a meeting place for Native Americans (Abrams, 1998b). From 1719 to 1785, the property remained in the family of Lord Fairfax and it was believed to contain significant mineral deposits. Between 1785 and 1830, the Patowmack Canal Company, organized by George Washington, constructed and operated bypass canals on the Potomac River, including one at Great Falls, VA. During the later 1800s and early 1900s, the site was used by various companies interested in manufacturing, dam building, and hydroelectric power. In 1906, an amusement park and light rail line was built at the site, which were in use until 1952. The conservation efforts for the site began in 1956, and in 1966 the National Park Service acquired the Great Falls Park property.

These land-use history events probably influenced the old-growth study site at Great Falls Park. For example, Native American Indians were known to use fire regularly for land-clearing, forest management, cooking, agriculture, and hunting (Day, 1953; Abrams, 1992; Orwig and Abrams, 1994a; Whitney, 1994). The ecology of oak forests in the mid-Atlantic region is thought to be closely tied to the occurrence of periodic understory fire and land-clearing (Abrams, 1992). The benefits of fire in oak forests include preparing a mineral soil seedbed, reducing insect and disease stresses, increasing light and nutrient availability at the forest floor, and reducing the competition to oak regeneration from later successional species (Abrams, 1992; Lorimer, 1985; Lorimer et al., 1994). Oak species dominated tree recruitment in the

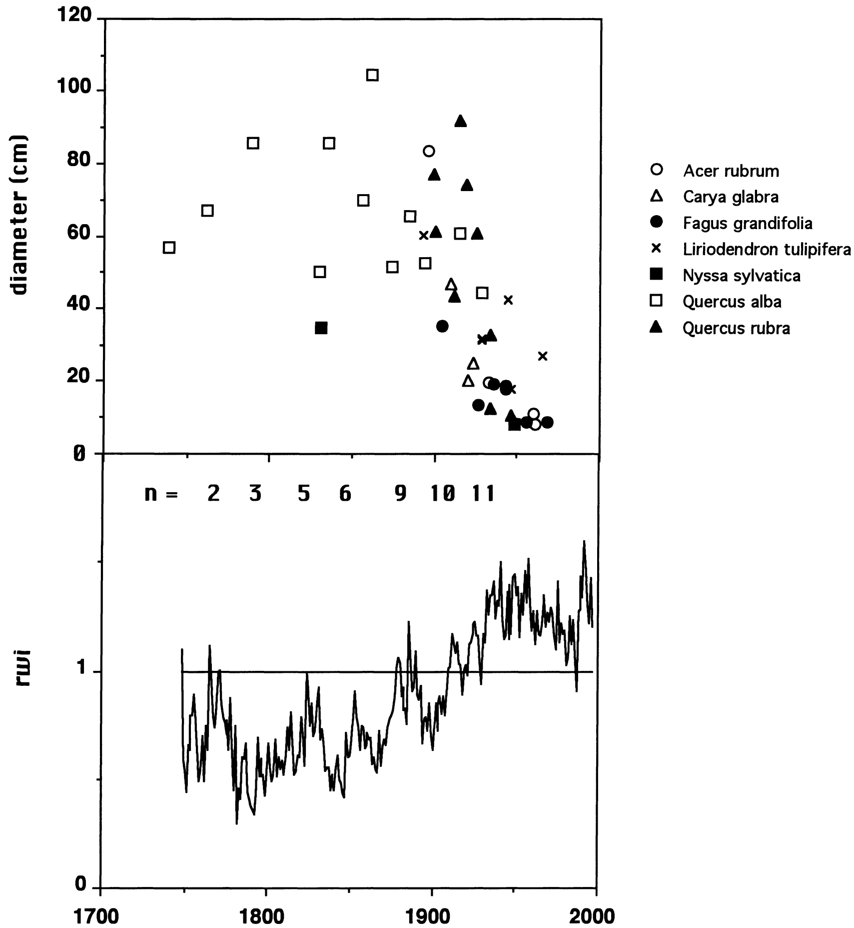

Fig. 3. (a) Age-diameter (at 1.37 m) relationships for all cored trees and (b) the mean standardized ring width index (RWI) for the 11 oldest *Quercus alba* in the old-growth forest study area at Great Falls Park, VA.

forest from 1740 to 1920, a time when fire is thought to have been an important ecological factor in the mid-Atlantic region (Orwig and Abrams, 1994a). 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 white oak was able to regenerate in uneven-aged forest conditions and grow slowly for long periods (up to 125 years; cf. Abrams and Downs, 1990). Eventually, these white oak reached the middle to upper canopy where they exhibited much higher growth rates. This may explain, at least in part, why the master chronology of 11 oldest white oaks had higher growth rates in the 1900s versus the 1700s and 1800s. Interestingly, a similar pattern of low tree-ring growth in the 1800s followed by much higher growth in the 1900s was also reported for an old-growth chestnut oak forest in the Blue Ridge Mountains of west-central Virginia (Abrams et al., 1997a). We attributed the higher growth rate in the 1900s to the impacts of chestnut blight, amelioration of the site from fire exclusion, and elevated CO_2 and N deposition. It may be possible that some of these factors, along with the canopy accession of white oak, are also responsible for the increased growth of white oak in the Great Falls forest after 1900.

In the mid-Atlantic region, northern red oak generally increased in abundance following post-European settlement disturbances, including early

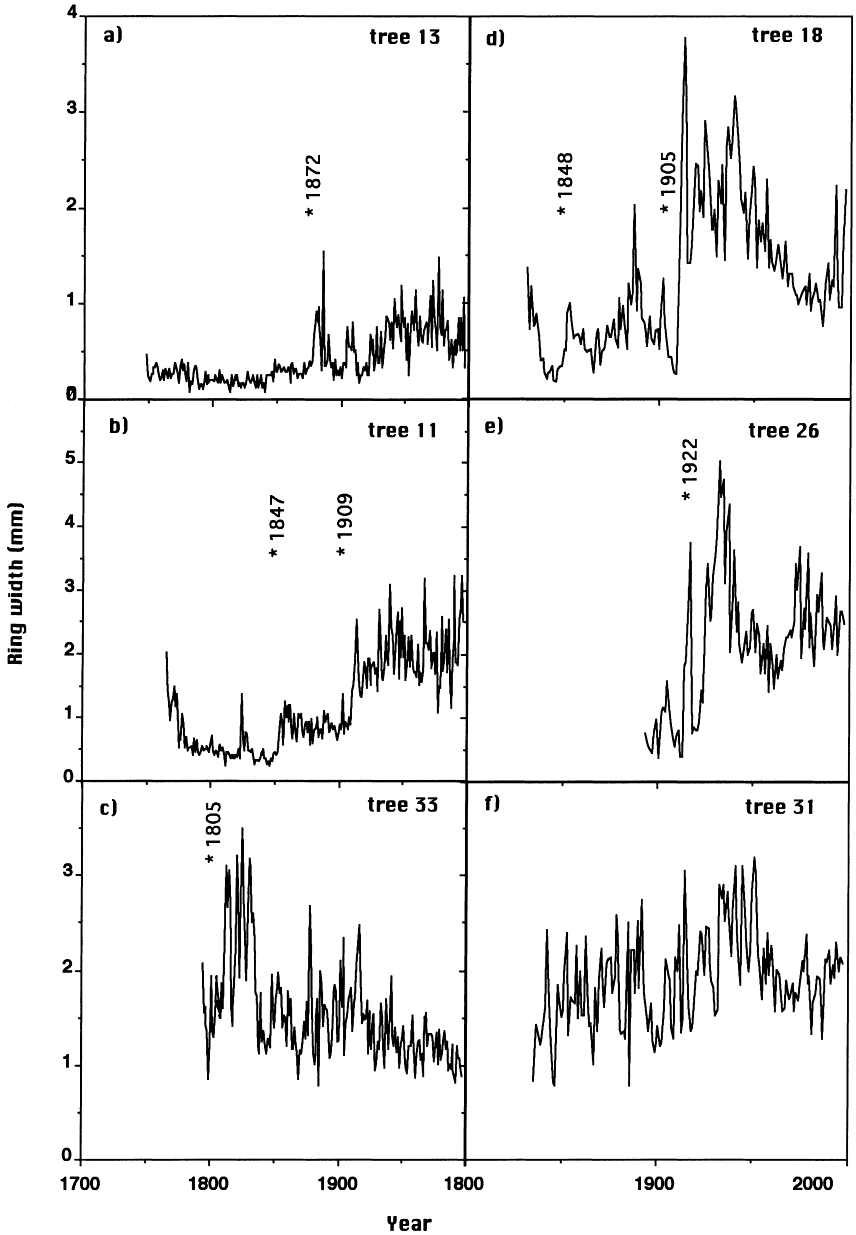

Fig. 4. Individual tree-ring chronologies and moderate release dates (star) for six selected white oak cores in the old-growth forest at Great Falls Park. Release criteria are from Lorimer and Frelich (1989).

logging, land-clearing, the charcoal iron industry, and the chestnut blight (Keever, 1953; Crow, 1988; Nowacki et al., 1990; Abrams, 1992). In the old-growth forest at Great Falls, northern red oak dominated the recruitment in the forest from 1900 to 1930, during which time there were large increases in the master chronology. The tree chronologies in Fig. 4(B,D and E) had significant growth releases during that period. The exact causes of these release events are unknown, but the occurrence of windstorms and/or fire are possibilities (evidence of old windthrow, charred trees, and soil charcoal were present). In other studies, age distribution of red oak in an old-growth forest in the Blue Ridge Mountains of west-central Virginia was uneven and the species had generally continuous recruitment from 1720 to 1940, with peak recruitment in the 1920s and 1930s following the chestnut blight and extreme drought in the region (Abrams et al., 1997a). Red oak increased dramatically in the late 1800s in an old-growth white oak and white pine (*Pinus strobus*) forest in southern West Virginia following peaks in recruitment of white pine (Abrams et al., 1995). Red oak trees were uneven-aged and exhibited long-term domination with sugar maple (*Acer saccharum* Marsh) and basswood (*Tilia americana* L.) on a high elevation, talus slope in West Virginia, apparently due to the high frequency of small-scale disturbance events in the forest (Abrams et al., 1997b). In a Wisconsin sugar maple–basswood forest, the red oak component was 60 years younger than the overstory sugar maple and was even-aged following recruitment in small gaps created by partial logging (Lorimer, 1983).

We did not find chestnut sprouts or cut stumps in our study forest understory, so it does not appear that northern red oak increased in response to the chestnut blight or selective logging in the early 1900s. Consistent with our observation, chestnut was not reported in the presettlement forests of the Fredericksburg area of northern Virginia; the dominant trees were white oak, northern red oak, and hickory (Orwig and Abrams, 1994a). An alternate explanation is that the suppression of fire and other forms of disturbance in the forest after 1900 led to a shift in recruitment from white oak to red oak domination, followed by mixed-mesophytic tree species. Among the upland oak species northern red oak is relatively sensitive to fire and it may be somewhat more shade-tolerant than other upland oak species (Crow, 1988; Abrams et al., 1997a, b). In contrast, white oak is considered very tolerant of understory fire because it has relatively thick bark and the ability to compartmentalize wounds after fire scarring. It is interesting to note that the age of red oak did not exceed 100 years in the forest. The typical longevity for the species is ca. 175 years, and individuals in the Blue Ridge of Virginia have been aged to 285 years (Abrams et al., 1997a). Therefore, some unknown factors were inhibiting red oak recruitment prior to 1900, as well as facilitating its increase after 1900 at the study site. It may be possible that the stand-wide canopy disturbances or fire around 1900, and/or fire suppression after 1900 contributed to the increased red oak dominance in the forest.

After 1930, tree recruitment in the old-growth stand was dominated by beech, tulip poplar and red maple. An increase in these mixed-mesophytic tree species was also reported for an old-growth white oak forest in southwestern Pennsylvania (Abrams and Downs, 1990). The increase in mixed-mesophytic tree species in oak forests in the eastern U.S. is thought to be related to the suppression of fire, land-clearing and selective deer browsing after 1900 (Abrams, 1992; Abrams, 1998a). Beech and red maple are considered to be shade-tolerant species, whereas oak and hickory species have low-to-intermediate shade tolerance. In forests where fires are suppressed, later successional tree species tend to increase quite rapidly, exert increasing competitive pressure on limited resources in the forest understory, and suppress the regeneration of oak and hickory species (Abrams, 1992; Lorimer et al., 1994). Most mixed-oak forests in the eastern U.S. have exhibited poor oak regeneration and recruitment during the last 50–100 years; this pattern is also evident at the study site.

It is important to note that many beech trees in the forest are large in size, including trees in the dominant canopy class and diameter classes ranging from 40 to 100 cm. Unfortunately, all of the larger beech we cored were rotten in the center; therefore their ages could not be determined. The oldest beech we aged was 92 years (with a DBH of 35.2 cm). It seems likely that some of the larger beech in the forest may have been significantly older than that, because the longevity of the species can exceed 300 years. Although, periodic fire during the 1700s and 1800s may have potentially limited the dominance of this fire sensitive species. In an old-growth, white oak forest in southwestern Pennsylvania, beech reached 70 cm DBH and were up to 170 years old; the white oak trees reached 320 years old (Abrams and Downs, 1990). Fire suppression in that forest may have started in the early 1800s due to a long history of private ownership; this possibility also exists for the Great Falls study area.

The recruitment of tulip poplar during the 1900s in this forest is interesting, yet not unexpected for this species. Tulip poplar is poorly represented as seedlings or saplings but it occurs across most diameter and canopy classes in the forest. This species is intolerant of shade, but it is an important component of many old-growth forests because it is an aggressive gap invader that often dominates its own gaps, and because it obtains large size and age (Buckner and McCracken, 1978, Abrams and Downs, 1990; Orwig and Abrams, 1994b).

7. Conclusions

The old-growth forest at Great Falls Park has been dominated by white oak since the early 1700s, and probably much longer. Paleoecological studies suggest that oak, chestnut, hickory and pine forests dominated much of the Piedmont and Coastal Plain for most of the Holocene epoch (last 10 000 years) (reviewed in Abrams, in press). It is now increasingly well accepted by ecologists that these forests types experienced periodic disturbance, such as understory fire and land-clearing by Native Americans or lightning strikes during the Holocene that facilitated long-term oak, chestnut, hickory and pine domination. Following European settlement, these species continued to dominate during the 1700s and 1800s because of the pervasive disturbances, such as land-clearing, charcoal iron industry, logging, and fire. However, fire suppression and the chestnut blight during the 20th century has greatly impacted the ecology of both old-growth and second-growth, mixed-oak forest in the mid-Atlantic region. In particular, these forests are now experiencing significant invasion by later succession tree species coupled with the loss of oak and hickory regeneration and canopy recruitment. It is now widely believed that oak forests throughout much of the eastern U.S. will show a reduction in oak dominance and an increase in later successional species, such as red maple, sugar maple, beech, blackgum, birch, and tulip poplar (Abrams, 1992).

The results of this study fit this pattern of oak forest succession, with white oak dominating recruitment from the mid-1700s until the early 1900s, followed by increases in red oak then beech, red maple, and tulip poplar. The increase in red oak in the early 1900s can not be fully explained based on the results of this study. It does not appear that this old-growth forest was greatly disturbed by anthropogenic factors, particularly logging, nor did it seem to have experienced a loss of chestnut from the blight, factors that normally facilitate an increase in northern red oak. However, this stand serves as a very good example of the potential for beech, tulip poplar and red maple to replace old-growth white oak in the mid-Atlantic region in the absence of fire. Maintaining the original composition of the forest will require active management. We suggest the introduction of a prescribed understory fire at a 5- to 10-year interval to slow the invasion of later successional tree species and promote the regeneration and recruitment of oak and hickory species.

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