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Impacts of early selective logging on the dendroecology of an old-growth, bottomland hemlock-white pine-northern hardwood forest on the Allegheny Plateau¹

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ORWIG, D.A. (Harvard University, Harvard Forest, P.O. Box 68, Petersham, MA 01366) AND M.D. ABRAMS (School of Forest Resources, Pennsylvania State University, University Park, PA 16802). 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. 1999.—The temporal variation in species recruitment was examined in relation to annual dendrochronological data to determine the historical development and disturbance history of an old-growth bottomland hemlock-hardwood forest in the Cook Forest State Park in North-western Pennsylvania. This 15 ha forest, located at the headwaters of a stream, contains a mixture of *Tsuga canadensis* (hemlock), *Fagus grandifolia* (beech), *Quercus rubra* (northern red oak), *Pinus strobus* (white pine), and *Acer rubrum* (red maple). The present age structure indicates that a cohort of *Quercus alba* (white oak) established between 1680 and 1710, and that the oldest hemlocks became established in the early 1700s. A period of almost 100 years followed in which there was virtually no recruitment. Tree recruitment resumed about 1800 and consisted primarily of hemlock and beech until 1855. A period of episodic recruitment associated with a concomitant radial growth increase, indicative of a major disturbance, began in many of the oldest trees in the stand during the 1850s and persisted for 70 years. Approximately two-thirds of all trees aged in this study became established between 1855 and 1930. The presence of decayed, cut stumps of several different species scattered throughout the stand is evidence that selective logging occurred, probably during the middle to late 1800s. This activity greatly altered the structure and composition of the forest and created conditions favorable for the establishment of even-aged cohorts of relatively shade intolerant *Q. rubra* and *P. strobus*, not recorded in the stand prior to cutting, as well as cohorts of late-successional tree species. In response to canopy closure and a large increase in deer populations, few new trees were recruited since 1930. Therefore, this forest has experienced dramatic changes following Euro-American settlement of the region that continue to the present, despite the fact that it retains many old-growth characteristics. This study represented a rare opportunity to investigate the impacts of direct and indirect anthropogenic influences on an old-growth forest. The results are relevant for the restoration ecology of other eastern forests, because they point out that certain silvicultural techniques may differ broadly from natural disturbances and result in unique and uncharacteristically diverse assemblages of species.

Key words: tree-ring, stand dynamics, age structure, succession, disturbance, fire, deer browsing.

The study of tree-ring chronologies from old-growth forests has greatly increased our understanding of disturbance process, stand dynamics and forest history (Fritts and Swetnam 1989). Reconstructive studies of old-growth forests have shed new insights on 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

(Foster 1988; Frelich and Graumlich 1994; Abrams and Orwig 1995; Abrams et al. 1995). Studies that integrate tree-ring data with age structure, land-use history, and climatic data have proven to be particularly important for understanding long-term forest dynamics and assessing the impacts of European settlement on forest structure and composition (Foster 1988; Foster et al. 1996; Abrams and Orwig 1995; Abrams et al. 1997).

In the northern mid-Atlantic region of the U.S., old-growth forests are very scarce. Of the remaining old-growth stands, many are located on upland ridge or mountain sites that were not logged due to their inaccessibility on rugged terrain or remote location. In contrast, there are very few old-growth forests on bottomland sites in the eastern U.S. because they were accessible for logging and suitable for farming after the

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land was drained (Dahl and Zoltai 1997). Moreover, bottomland sites comprise a very limited land area in the mid-Atlantic region compared to the abundance of upland sites (Whitney 1994). Although there is a growing database on the dendroecology and dynamics of old-growth forests on upland sites, very little (cf. Cho and Boerner 1995) is known about recruitment dynamics and disturbance history of old-growth bottomland forests located beyond the southeastern U.S.

In this study, we report on the dendroecology of an old-growth, bottomland northern hardwood-conifer forest in northwest Pennsylvania with trees as old as 325 years. The site was selectively logged during the middle 19th century. More recently, deer populations increased markedly throughout Pennsylvania, and particularly in this region, causing extensive browsing and profoundly affecting tree regeneration and recruitment (Whitney 1984). Thus, this site presented an unusual opportunity to study forest dynamics before and after the direct and indirect influences of Euro-American settlement in an old-growth forest. 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 dynamics, and 4) gain an understanding of the ecological history and successional status of the stand and how it has been impacted by selective logging and deer browsing.

Site history and Description. The study area was first settled by John Cook in 1828, when he established the village of Cooksburg on the banks of the nearby Clarion River (Cook 1997). The Cook family developed a large lumber business that peaked in the 1880s and consisted of three sawmills, a flouring mill, a planing mill, extensive boat scaffolding on the Clarion River, and many dwelling houses (Cook 1997). Ironically, over 1000 ha of virgin timber were preserved immediately surrounding the sawmills as lumbering activities were largely confined to the northern portion of the present day park. In 1928, the Cook Forest became a state park and was the first area in the Commonwealth acquired for the purpose of preserving a national natural landmark (Cook 1997).

We examined a section of the Cook Forest State Park called the Swamp Forest Natural Area

(SFNA), located in the headwaters of Brown's Run in Clarion and Forest Counties, in northwest Pennsylvania (41°19'22N, 79°09'51W). Prior to this study, the site was considered by Park officials to be one of 3 remaining tracts in the park to have never been timbered. The region is part of the unglaciated Allegheny Plateau, which consists of level uplands, dissected mountain coves, rolling hills, and deep stream valleys (Braun 1950, Patton 1958). The SFNA is approximately 15 ha in area at an elevation of 485 m a.s.l. The forest topography is nearly level (0–2% slope). The soils are primarily Nolo and Lickdale silt loams, derived from acid sandstone or shale, and are acidic, poorly drained, but well supplied with plant nutrients (Patton 1958). The region has an annual rainfall of 117 cm and a mean annual temperature of 8°C.

Old-growth characteristics exist throughout the forest in terms of large diameter trees, a variety of diameter classes and canopy layers, gap formation, abundant coarse woody debris on the forest floor, and large standing dead trees. However, evidence of early logging at the site in the form of cut stumps scattered throughout the stand still exists. We also observed evidence of past fires at the site including deep V-notched fire scars on several trees, generally *Tsuga canadensis* (eastern hemlock) and *Pinus strobus* (eastern white pine), and soil charcoal.

Methods. On July 12, 1994, 20 fixed area plots, located at 30 m intervals along transects through the forest interior, were used for vegetation and dendroecological sampling. The species, diameter, and crown class were recorded for all trees > 8.0 cm dbh occurring within 0.02 ha circular plots at each point. Classification of tree crowns into four categories (dominant, co-dominant, 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 (basal area) (Cottam and Curtis 1956). At each point, two to four trees were randomly 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. Additional cores from large trees located outside of plots were also obtained to aid in reconstructing long-term dynamics. Saplings and seedlings were counted in nested circular plots of 9 and 5 m², respectively, located within each of the over-

Table 1. Density, basal area, frequency and importance values for overstory tree species (>8.0 cm dbh) in the Swamp Forest Swamp Area, northwestern Pennsylvania.

Species	Density (#/ha)	Relative density	Basal area (m ² /ha)	Relative basal area	Frequency (# plots)	Relative frequency	Relative importance
<i>Acer rubrum</i>	40	8.6	3.4	5.5	9	13.2	9.1
<i>Betula alleghaniensis</i>	10	2.2	0.9	1.5	3	4.4	2.7
<i>Fagus grandifolia</i>	86	18.8	11.1	17.9	15	22.1	19.6
<i>Pinus strobus</i>	20	4.3	7.9	12.7	8	11.8	9.6
<i>Prunus serotina</i>	7	1.6	1.9	3.0	3	4.4	3.0
<i>Quercus alba</i>	7	1.6	5.1	8.1	3	4.4	4.7
<i>Quercus rubra</i>	22	4.8	12.3	19.8	7	10.3	11.6
<i>Quercus velutina</i>	2	0.5	0.5	0.8	1	1.5	1.0
<i>Tsuga canadensis</i>	264	57.5	19.8	31.8	19	27.9	39.1
Totals	458		62.9				

story plots. Saplings were classified as tree species > 1.5 m in height but < 8.0 cm in dbh and seedlings were < 1.5 m in height. Nomenclature follows Gleason and Cronquist (1991).

All increment cores (n = 70) collected from the study area were dried, mounted, sanded, and counted for age (Phipps 1985). The best cores among the older trees (n = 55) were used for skeleton plots and examined for signature years for crossdating to help identify missing or false rings (Stokes and Smiley 1968). Master tree-ring chronologies from nearby forests within the Cook Forest State Park were also used as an additional cross-dating reference (Abrams and Orwig 1996; International Tree Ring Data Base (ITRDB), Boulder, CO). All cores were then scanned with a tree ring measuring device and the annual growth increments measured to the nearest 0.01 mm (Regents Instruments Inc. Quebec, Canada). The majority of the oldest cores in this stand did not exhibit any discernable growth trend with time, and therefore the ring widths of the eight oldest *Quercus alba* (white oak) trees and two of the four oldest *T. canadensis* were standardized via the horizontal straight-line method of Veblen et al. (1991). Two additional old *T. canadensis* cores were standardized by fitting them to negative exponential

curves. Ring-width indices (RWI) were constructed by dividing the observed ring widths by the predicted ring widths and then averaging to form a master chronology for each species (Fritts 1976; Fritts and Swetnam 1989). This standardization procedure has been shown to be particularly useful in identifying long periods of release associated with major canopy disturbances (Veblen et al. 1991). We examined all cores for periods of suppression and release according to Lorimer and Frelich (1989), who defined a major release as being a greater than 100% average growth increase lasting at least 15 years and a moderate release as a greater than 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.

Results. The forest is dominated by *T. canadensis*, *Fagus grandifolia* (beech), *Quercus rubra* (northern red oak), *P. strobus*, and *Acer rubrum* (red maple) (Table 1). The high relative importance value for *T. canadensis* is due to it dominating all three importance value categories, especially the relative density. *Fagus grandifolia* was also well represented across all three importance value categories. In contrast, *Q. rubra* and *P. strobus* have fairly low density values, but have some of the highest basal area values in the forest. The total basal area of 62.9 m² ha⁻¹ is very high for eastern U.S. forests, but not unprecedented for northern hardwood-conifer dominated stands (cf. Baldwin 1951; Whitney 1994; Abrams and Orwig 1996).

The seedling layer is dominated by *A. rubrum* and *F. grandifolia*, although there are few saplings of any species present (Table 2). The diameter distribution of 458 trees exhibited a roughly negative exponential or inverse-J pat-

Table 2. Seedling and sapling densities (#/ha) in the Swamp Forest Swamp Area, northwestern Pennsylvania.

Species	Seedling density	Sapling density
<i>Acer rubrum</i>	26,244	—
<i>Fagus grandifolia</i>	7,668	54
<i>Prunus serotina</i>	972	108
<i>Quercus rubra</i>	540	—
<i>Tsuga canadensis</i>	756	54
Totals	36,180	216

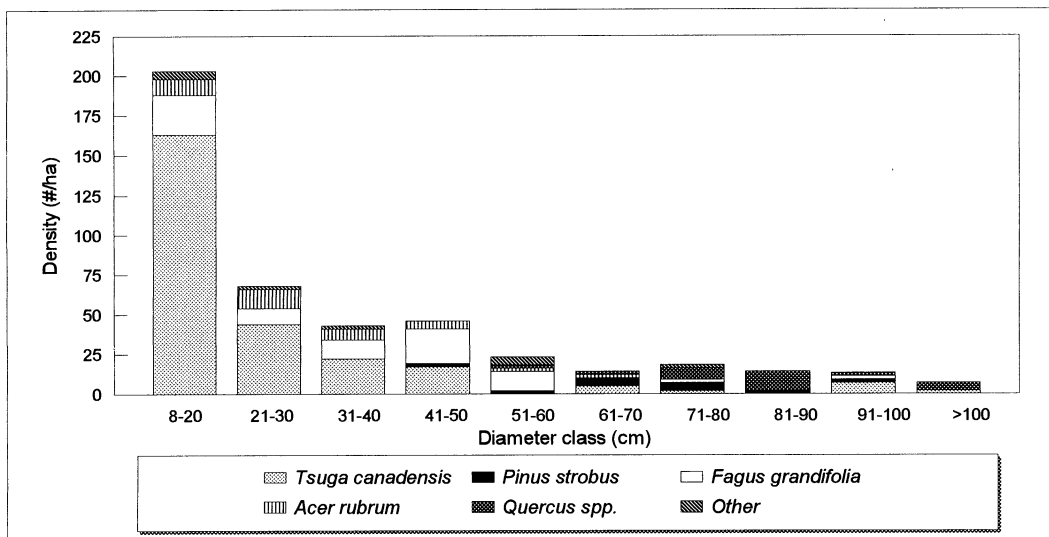


Fig. 1. Diameter (at 1.37 m) distribution of tree species in the old-growth Swamp Forest Natural Area, Cook Forest, northwest Pennsylvania.

tern, typical of uneven-aged forests (Fig. 1). *Tsuga canadensis* dominates the smaller diameter classes (< 50 cm dbh) and is also present in the larger classes. Most of the *F. grandifolia* and *A. rubrum* trees are between 11–60 cm dbh, whereas *Quercus* trees were almost all 51 to > 100 cm dbh. *Pinus strobus* trees are between 41–100 cm dbh. In terms of tree canopy position, all of the dominant species were fairly equally represented in the dominant class (Fig. 2). *Fagus grandifolia* had the highest percent frequency in the codominant class, whereas *T. canadensis* dominated the intermediate and overtopped classes. *Quercus* and *P. strobus* were best represented in the dominant class and did not occur as intermediate or overtopped trees. *Acer rubrum* had its highest frequency among intermediate trees, but was represented, along with *F. grandifolia* and *T. canadensis*, in all canopy classes.

The oldest trees in the stand are a cohort of *Q. alba* that established between 1660 and 1725 (Fig. 3A). The next oldest trees are *T. canadensis* that recruited between 1710 and 1735. None of the sampled trees that presently occur in the stand were recruited between 1735 and 1795. The oldest *F. grandifolia* we recorded became established about 1800. The vast majority of the trees that now occupy the forest were recruited between 1855 and 1930, including many *Q. rubra*, *P. strobus*, *T. canadensis*, *F. grandifolia*, and *A. rubrum*. Only three of the sampled trees became established after 1930. The master chro-

nology for eight of the oldest white oak reveals a pattern of high ring width index (RWI) growth in the late 1600s followed by fairly constant growth until 1845 (Fig. 3B). From 1845–1885, a dramatic increase in radial growth occurred, and growth remained high until 1915; there has been a steady growth decline from that time until the present. The master chronology for the four oldest *T. canadensis* exhibits a period of generally high growth from 1715 to 1770 and below average growth from 1775 to 1855 (Fig. 3C). Radial growth increased markedly from 1855 to 1920, after which growth declined sharply to 1930. Growth remained low until 1975, but has increased dramatically from that time until the 1994.

Major and moderate releases occurred in most decades between 1730 and 1990 (Fig. 4). Two distinct periods in which 20–30% of sampled trees experienced releases were recorded between 1840–1870 and in the 1970s. A relatively low frequency of releases occurred before 1840, particularly in the major release category, although fewer trees were involved in this analysis. An examination of raw ring-width data from a broad array of trees that became established following the first release period in the late 1800s indicate initial sustained periods of radial growth ranging from 4 to 7 mm per year (Fig. 5). In addition, both early and late successional species exhibited negative exponential growth curves, indicative of initially open canopy conditions.

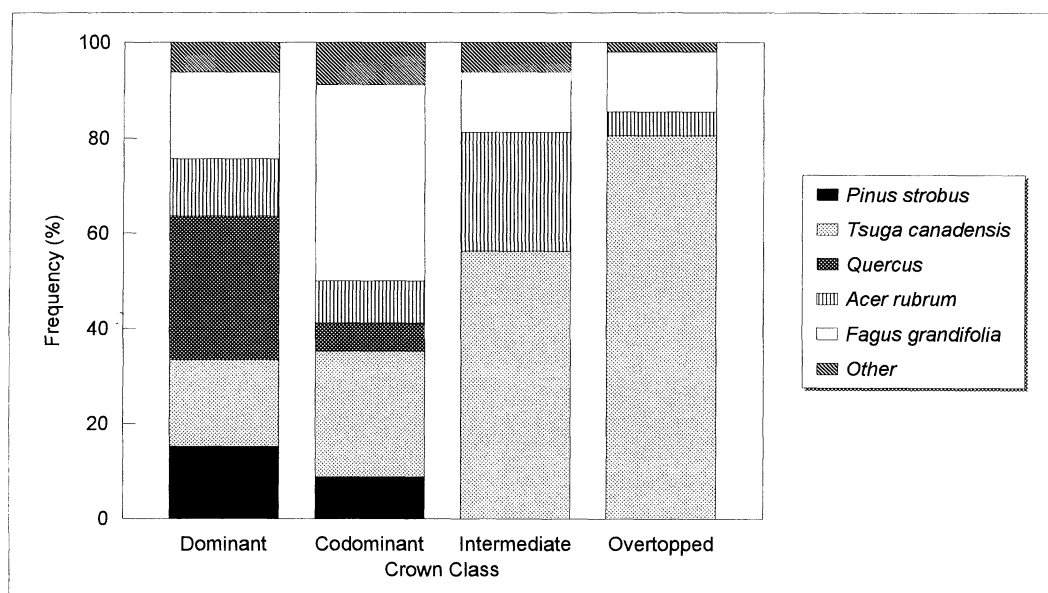


Fig. 2. Crown class distribution of tree species in the Swamp Forest Natural Area.

Discussion. A major period of increased radial growth and concomitant tree recruitment between 1850 and 1925 indicates a significant canopy disturbance occurred in this old-growth, bottomland hemlock-hardwood forest. We believe that these changes are in response to selective logging during Euro-American settlement in the second half of the 19th century. Although park officials have no record of logging in the stand, we found scattered cut stumps throughout. The stumps consisted of both conifer and hardwood species, including *Castanea dentata* (chestnut) (pers. obs.). There is the possibility that other disturbances (e.g., windthrow and fire) may have also occurred during that time. Past fires in the forest were evident from the presence of fire-scarred trees, typically *T. canadensis*, and soil charcoal. Indeed, a high proportion of the radial growth releases detected by our analysis occurred between 1840 and 1900. Most of the important tree species had peak recruitment during the middle to late 1800s and early 1900s, regardless of their successional class. Therefore, early, middle and late successional tree species apparently benefited from cutting disturbance. Similar observations were made in several remnant old-growth stands that experienced logging in central Pennsylvania (Nowacki and Abrams 1994) and following stand-replacing disturbances in the 1600s at other old-growth stands within the Cook Forest

State Park (Hough and Forbes 1943; Abrams and Orwig 1996).

In the early 1840s, the master ring width index (RWI) chronologies for both *Q. alba* and *T. canadensis* exhibited sharp declines prior to the major releases in the 1850s and 1860s. It is possible that the selective logging in the forest started in the 1840s, and the initial response of residual trees was decreased growth from physiological shock or canopy and bole damage, followed by greatly enhanced growth. Tree growth in the old-growth Pisgah forest in southwest New Hampshire was reduced for five to ten years following the 1938 hurricane due to wind-caused canopy damage, followed by more rapid growth after the tree canopies recovered (Foster 1988). Alternatively, selective logging may have been followed by windthrow events due to enhanced susceptibility of residual trees to wind as the canopy was opened up in this bottomland site (Cho and Boerner 1995) or as a result of lower root to shoot ratios that trees on mesic sites typically possess (Kramer 1983).

The oldest trees in the stand are a cohort of *Q. alba* that are mostly located within the periphery of the stand. Only one *Q. alba* recruited into the stand after 1720, and this was during the major 1855–1930 recruitment episode. It is possible that logging may not have affected *Q. alba* due to this tree's spatial distribution in the forest. In contrast, all of the existing *Q. rubra*

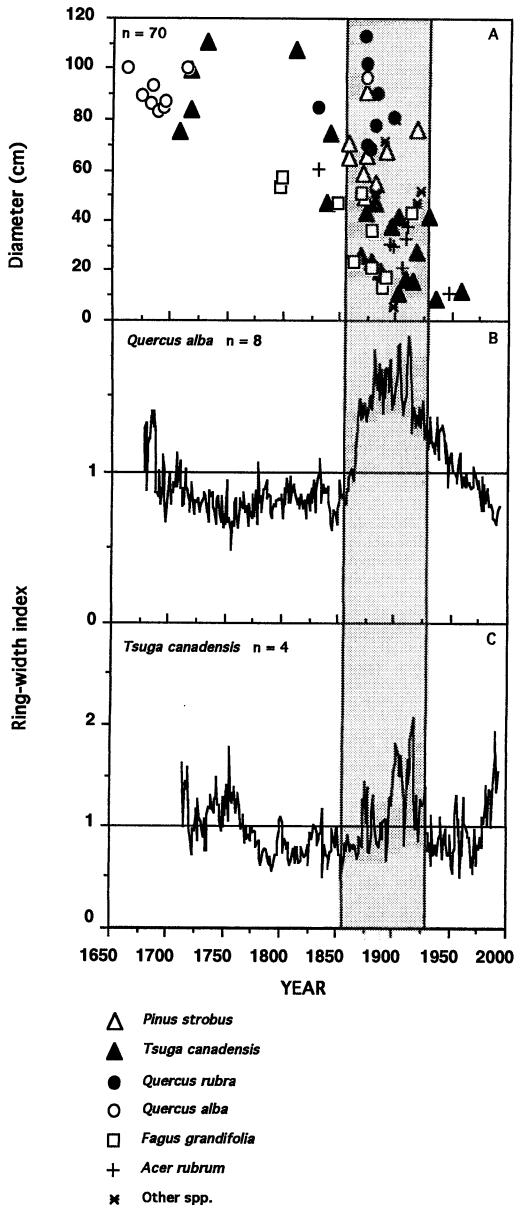


Fig. 3. (A) Age vs. diameter (at 1.37 m) relationships for all cored trees; (B) the mean standardized ring width index for the eight oldest *Quercus alba*; and (C) the mean standardized ring width index for the four oldest *Tsuga canadensis* in the Swamp Forest Natural Area. The shaded area indicates episodic recruitment period.

trees recruited between 1870 and 1900 and have already attained sizes of 70–114 cm dbh, clearly benefitting from the disturbances during or just preceding that time. Throughout the mid-Atlantic and northern regions, *Q. rubra* is one of the primary species that expanded after the original

cutting of northern hardwood-conifer forests and the chestnut blight in the early 1900s (Keever 1953; Siccama 1971; Whitney 1994; Crow 1988; Nowacki et al. 1990; Abrams and Ruffner 1995). In portions of the mid-Atlantic region, *Q. alba* trees have decreased in number from the pre-European settlement to the present-day, and it has been concluded that *Q. alba* did not recover from catastrophic logging and wildfire or fill niches vacated from the chestnut blight as well as some other *Quercus* species (Abrams and Ruffner 1995; Abrams and McCay 1996). This conclusion is consistent with the results of this study, as the *Q. alba* trees have not replaced themselves.

All of the *P. strobus* we aged in the forest became established during the major disturbance period of 1855 to 1930. In studies of nearby upland, old-growth *P. strobus*-*T. canadensis* stands in the Cook Forest, all of the *P. strobus* trees were aged to be 200–350 years old, becoming established after disturbances in the mid- to late 1600s (Hough and Forbes 1943; Abrams and Orwig 1996). In that study, we concluded that *P. strobus* can act as both an early- and mid-successional species following large-scale disturbances. We do not know why the maximum age for *P. strobus* is only 140 years in the swamp stand. It may be that the older individuals were logged or killed by windthrow in the 1800s or that this species has a shorter longevity on bottomland versus upland forests. Nonetheless, the results of this study and previous studies indicate that *P. strobus* can recruit in old-growth forests following disturbance, such as windthrow or fire, that create medium- to large-sized canopy gaps (Lutz 1930; Morey 1936; Hough and Forbes 1943; Heinzelmann 1973; Hibbs 1982; Abrams et al. 1995). Foster (1988) noted that *P. strobus* recruitment in old-growth forests may need a combination of both windthrow and fire for successful establishment. We do not know whether fire occurred in the 1850s or 1860s in the swamp forest, but the possibility does exist as several charred stumps were found in our sampling plots and several large *T. canadensis* snags contained large, v-notched fire scars. In addition, 2 tree cores contained fire scars that were dated to the late 1880s, indicating that fires have probably occurred several times over the last 300 years.

Acer rubrum became established in the stand between 1830 and 1947, although the vast majority of *A. rubrum* recruited between 1885 and 1910, presumably associated with the selective

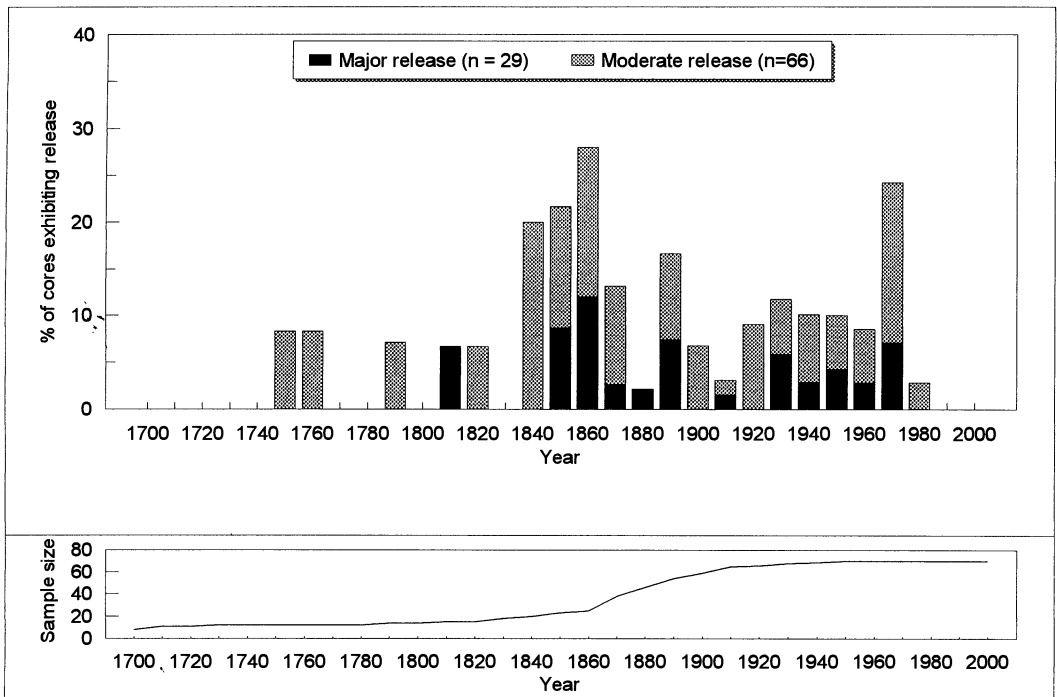


Fig. 4. Decadal distribution of major and moderate releases in 70 cores of the major tree species in the Swamp Forest Natural Area (criteria from Lorimer and Frelich 1989) and the sample sizes for the percentages.

logging. However, the recruitment pulse for this species came 30–40 years after the major releases in the *Q. alba* and *T. canadensis* chronologies, and 25–40 years behind the major recruitment episode for *P. strobus*, *Q. rubra*, and *F. grandifolia*. The reason for this lag in *A. rubrum* is not known, but it may be due to elimination by fires in the mid to late 1800s, variations in seed input, growth rate in the understory, or its facilitation by other tree species (cf. Abrams et al. 1995; Abrams 1998). It is also possible that some *A. rubrum* became established following *C. dentata* salvage logging, as *C. dentata* stumps were observed in the stand. *Acer rubrum* has characteristics of both early and late successional tree species, and thus has the ability to increase in forests after a wide range of disturbances or through successional time during disturbance-free intervals (Abrams 1992; Lorimer et al. 1994; Abrams et al. 1995; Abrams 1998). *Acer rubrum* is considered to be a major opportunistic, replacement species in *Quercus*, *Pinus*, and northern hardwood forests throughout the eastern U.S. (Abrams 1992, 1998).

Most of the *F. grandifolia* recruited into the forest between 1860 and 1915, although two *F.*

grandifolia trees dated back to 1800. We aged this species up to 275 years elsewhere in Cook Forest. Another late-successional species, *T. canadensis*, dominated the swamp forest and the oldest individuals were 275 to 285 years old. This is substantially less than the maximum age of 400–500 years for *T. canadensis* in the region (Morey 1936; Hough and Forbes 1943; Rogers 1978). No *T. canadensis* recruitment was recorded between 1735 and 1815, but continuous recruitment for this species occurred from 1815 to 1960, with peak establishment from 1870 to 1930. Despite their reputation as highly shade tolerant, climax species, both *T. canadensis* and *F. grandifolia* regeneration was stimulated by major disturbance events in the swamp forest.

None of the 70 trees we aged recruited between 1735 and 1800. The absence of *Q. rubra* and *A. rubrum* in that age class may be due to their relatively short longevity, typically less than 200 years, although we have aged *Q. rubra* to 295–325 years and *A. rubrum* to 230 years in upland forests (Abrams et al. 1997; Ruffner and Abrams 1998; Orwig unpubl. data). All other dominant tree species in the stand can live over 300 years. The lack of stem establishment from 1735–1800 may be due to logging of individuals

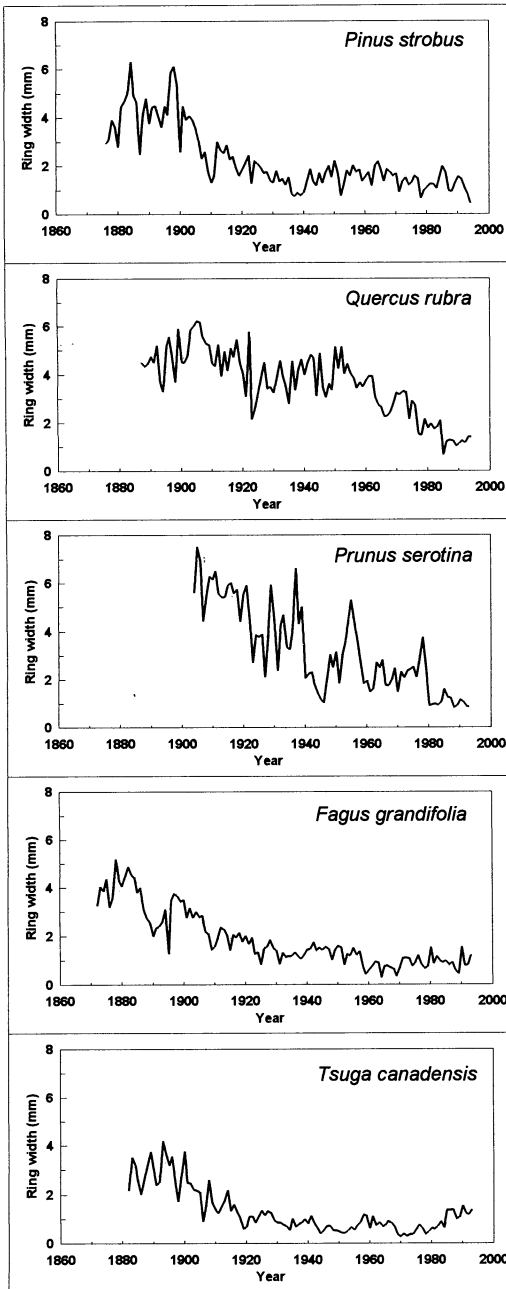


Fig. 5. Representative radial growth patterns of dominant trees that became established during the period of selective logging in the mid- to late 1800s with in the Swamp Forest Natural Area.

in that age class during the middle and late 1800s, although it seems unlikely that all trees within a 65 year age span would have been cut, while leaving many older trees, especially the commercially valuable *Q. alba* cohort. More-

over, age gaps and "mid-life" stem exclusion stages in old-growth forests lasting 30–90 years have been previously documented from natural causes such as following extreme climatic phenomena, post-disturbance recruitment pulses, and intensive mammal browsing (Foster 1988; Abrams and Orwig 1996; Abrams et al. 1997; Ruffner and Abrams 1998). The master RWI chronology for *T. canadensis* shows values well above average between 1735 and 1765, and is coupled with a relatively high number of releases, which may indicate disturbance events in the stand during that time. However, this pattern does not exist in the *Q. alba* master chronology. Therefore, we do not know whether the reason for the 1735–1800 age gap is due to anthropogenic or natural causes, or both.

Since 1930, there has been little tree recruitment within the swamp forest, despite an effort on our part to age a representative number of small diameter trees. A similar finding was reported for another old-growth *P. strobus*-*T. canadensis* stand in the Cook Forest, in which only one tree recruited between 1920 and 1994. The absence of recent recruitment in that forest was attributed to intensive deer browsing. In the swamp forest, we also believe that the lack of recent recruitment is due, at least in part, to deer browsing, although we recognize that a suite of factors can inhibit tree regeneration for protracted periods (Mladenoff and Stearns 1993). For example, the major tree establishment period of 1855 to 1930 may have resulted in canopy closure and near full-site utilization of resources by the new recruits. This could be contributing, along with deer browsing, to the lack of canopy recruitment in the stand after 1930.

We detected profound dendroecological differences in the stand before and after Euro-American settlement in the 1840s. The number of radial growth releases, particularly major releases, was lower before than after 1840. The only species we know that occurred in the stand before 1840 are *Q. alba*, *T. canadensis* and *F. grandifolia*. After 1840, *P. strobus*, *Q. rubra*, *A. rubrum*, *Betula alleghaniensis* (yellow birch), *Prunus serotina* (black cherry) and *Quercus velutina* (black oak) recruited. The lack of some these species before 1840 may be due, in part, to their relatively short longevity, although all of them have the potential to live > 200 years. Moreover, the interpretation of recruitment patterns from static age structure is problematic due to differential mortality among species, age and canopy classes, and stand history events (John-

son et al. 1994). Nonetheless, it seems clear that post-settlement selective logging created an opportunity for increased recruitment by gap-obligate or gap-facultative species, e.g., *P. strobus*, *A. rubrum*, *Q. rubra*, *Q. velutina*, and *B. alleghaniensis*, not present in large numbers before the logging event. The density and wide array of species included in this post-logging cohort has not been observed following natural disturbance events in many other eastern old-growth studies (Mikan et al. 1994; Abrams et al. 1995, 1996; Abrams and Orwig 1995, 1996), and suggests that selective logging had a profound impact on this forest. In addition, species maximum and average growth rates observed after settlement, particularly during 1855–1930, exceeded the growth rates that occurred before settlement. These findings are important for managers interested in using silvicultural techniques to hasten or restore certain old-growth attributes (Runkle 1991; Lorimer and Frelich 1994; Vora 1994; Keddy and Drummond 1996; Trombulak 1996). Although we do not have specific data on the amount and ages of trees that were cut, the age of surviving trees and the presence of large, decayed stumps in this stand (> 50 cm diameter) suggest it was in a mature stage when cut. The actual amount of basal area to cut and the frequency of cutting to achieve desired old-growth attributes in maturing stands is still largely unknown (Lorimer and Frelich 1994), but results from this study suggest that widespread gap creation facilitated the establishment and rapid growth of many species as well as the complex structural attributes.

The high RWI values obtained in the *Q. alba* chronology between 1875 and 1915 have been steadily declining and are now equivalent to the average RWI values of 1700 to 1850, suggesting that the stand in at least some respects may more closely resemble pre-settlement conditions 125 years after the logging (cf. Nowacki and Abrams 1994). RWI values of *T. canadensis* increased significantly in 1875 and again in 1900. Growth then decreased markedly between 1920 and 1930 to levels similar to that before logging, but increased sharply from 1975 to 1994. This recent increase, while not apparent in the *Q. alba* chronology, may be due to release events associated with the 1976 tornado that damaged portions of Cook Forest (cf. Abrams and Orwig 1996) and/or a protracted period of high Palmer Drought Index values (indicative of non-drought conditions) in the region (14 of the 19 wettest years on record since 1895; data not shown).

Similar climatically-induced growth increases were reported for xeric *Pinus rigida* (pitch pine) and *Quercus prinus* (chestnut oak) communities in southeastern New York and west-central Virginia, respectively (Abrams and Orwig 1995; Abrams et al. 1997).

Conclusions. The key features of this bottomland old-growth forest derived from dendroecological analyses are the tree age gap between 1730 and 1800, the large stand-wide growth increases between 1855 and 1920, and the peak recruitment of both late successional and gap phase species between 1855 and 1930. The response to selective logging that apparently occurred in the stand after 1840 differed dramatically from natural gap events that occurred prior to and following the cutting, in which a few trees or a cohort of a single species resulted. Despite the profound impacts of logging, the stand retains many old-growth features, such as large diameter trees (80–115 cm dbh), a wide range of diameter classes and canopy layers, gap formation, abundant coarse woody debris on the forest floor, and large standing dead trees. In addition, the growth rates of many of the oldest trees during the later half of the 20th century have returned to levels similar to or slightly lower than those of the 1700s and early 1800s. While the stand outwardly appears to be in an old-growth condition, it is still being influenced by 19th Century disturbances in terms of species composition and structure. The presence of *P. strobus*, *Q. rubra*, *A. rubrum*, and *P. serotina* apparently resulted from the selective logging in the mid- to late 1800s. In addition, there is a scarcity of new recruits since 1930. Therefore, the future of the forest is difficult to predict because of the impacts of deer browsing and other contributing factors. Deer browsing, in particular, can inhibit the regeneration of *T. canadensis*, *Quercus*, and other northern hardwood species for the long-term (Whitney 1984; Frelich and Lorimer 1985; Abrams 1998). Because of their longevity, *P. strobus*, *Q. rubra*, and *A. rubrum*, along with *T. canadensis* and *F. grandifolia*, should persist in the forest well into the 21st century. However, the original cohort of *Q. alba* is now between 275 and 330 years old, and only one new individual has recruited since that time. Therefore, the dominance of *Q. alba* will most likely wane as the oldest trees die off over the next 50–100 years.

The approach used in this study elucidated the pattern of species recruitment over a 330 year

period, impacts of natural and anthropogenic disturbance events, and growth rates before and after Euro-American settlement. An aim of restoration ecology is the recreation of old-growth attributes in forests logged at varying intensity and timing after European settlement. This study of an old-growth stand that experienced selective logging in the mid-1800s will hopefully serve as an example of how dendroecology can be used to assess the recovery of forests from anthropogenic disturbance. It also points out the need for caution when using silviculture to mimic natural disturbances or to obtain desired attributes such as uneven age or size-class distributions, for it may result in unique assemblages of species that would not establish following small to moderate scale natural disturbances.

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