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Historical variation in fire, oak recruitment, and post-logging accelerated succession in central Pennsylvania[1]

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ABSTRACT

Abrams, M. D. and G. J. Nowacki (School of Forest Resources, Ferguson Building, Pennsylvania State University, University Park, PA 16802). Historical variation in fire, oak recruitment, and post-logging accelerated succession in central Pennsylvania. Bull. Torrey Bot. Club 119: 19–28. 1992.—Composition, structure and radial growth patterns were studied in relatively undisturbed, mature mixed-oak (*Quercus*), valley floor forests and in similar forests extensively logged between 1936–1946 in central Pennsylvania. These data were analyzed in relation to presettlement forest composition and historical fire records to investigate temporal variation in *Quercus* recruitment versus accelerated succession of more shade tolerant species following logging. Presettlement valley floor forests in the study area were dominated by *Quercus alba* and *Pinus strobus.* Recurring logging and fire between 1780–1900 associated with charcoal iron furnace activity increased *Quercus* and decreased *Pinus* dominance in second-growth forests established during that period. Between 1908–1989 the total area burned by wildfire throughout Pennsylvania decreased by >99% (from >400,000 ha to <3500 ha per year). The decreased influence of logging and fire this century facilitated recruitment of later successional *Acer* and *Prunus* species in *Quercus* forest understories. Logging of forests in this condition rapidly accelerated the rate of obtaining canopy dominance for *A. rubrum, A. saccharum* and *P. serotina* in area forests. This form of disturbance-mediated accelerated succession should be anticipated in a wide variety of forest types with an overstory dominated by early successional species and an understory comprised mainly of later successional species.

Key words: disturbance, presettlement forests, charcoal production, radial growth analysis, *Acer, Prunus, Pinus,* oak replacement.

Early ecologists recognized to varying degrees the importance of disturbance in North American plant communities (Cooper 1913; Clements 1916; Gleason 1926). Regardless of the emphasis placed on the ecological role of disturbance, it was widely accepted that disturbance sets back succession to some earlier stage (Clements 1916). While this response routinely occurs in nature (White 1979), it is becoming increasingly apparent that disturbance can also accelerate succession to a later stage (Abrams and Scott 1989). In its simplest form, disturbance-mediated accelerated succession involves the destruction of all or part of the dominant pioneer forest overstory, which releases advanced reproduction of later successional species. This process has been documented following a variety of disturbance types, including ice storms, fire, logging, blowdown, and insect and disease outbreaks (Spurr 1956; Carvell *et al.* 1957; Collins 1961; Menges and Loucks 1984; Abrams *et al.* 1985; Glitzenstein and Harcombe 1988; Boerner *et al.* 1988; Abrams and Scott 1989; Veblen *et al.* 1989).

Oak (*Quercus*) species dominate forests in much of eastern North America, and their importance in presettlement forests in the northeast and mid-Atlantic regions has been well documented (Michaux 1853; Bromley 1935; Spurr 1951; Russell 1980; Abrams and Downs 1990). Periodic fire initiated by lightning or early Native Americans seems to be responsible, at least in part, for oak dominance in the original forests (Bromley 1935; Day 1953; Buell *et al.* 1954; Lorimer 1985). Following European settlement, perpetuation or even increases in oak dominance in the region have been attributed to repeated cuttings and slash fires (Lutz 1928; Russell 1980; Whitney 1987; Crow 1988; Nowacki *et al.* 1990). In this scenario, oak maintained its dominance primarily via sprouting following disturbance. However, the understories of many mesic and dry-mesic mature oak forests are presently dominated by later-successional species and contain only a small

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oak component, possibly in response to decreased fire this century (Lorimer 1984; Parker *et al.* 1985; Abrams 1986; Pallardy *et al.* 1988; Nowacki *et al.* 1990; Abrams and Downs 1990). Even when a substantial number of oak seedlings are present in the understory of eastern forests little recruitment of oak into the tree-size classes is expected (Adams and Anderson 1980; Lorimer 1984; Abrams 1986; Host *et al.* 1987; Fralish 1988; Nowacki and Abrams 1991). If this condition persists well into the next century, significant oak replacement by more shade-tolerant species will probably occur routinely on all but the most xeric sites (McCune and Cottam 1985; Host *et al.* 1987; Abrams and Downs 1990). It has also been suggested that the rate of oak replacement will be accelerated by logging (Lorimer 1985; Nowacki *et al.* 1990), although empirical evidence of this phenomenon is lacking (Abrams and Downs 1990).

Mixed-oak forests are prevalent throughout the Ridge and Valley Province of central Pennsylvania. The understories of most forests are dominated by red maple (*Acer rubrum* L.) and black cherry (*Prunus serotina* Ehrh.) (Nowacki and Abrams 1991). In the present study, we examined the response to extensive logging between 1936–1946 of four mesic, mixed-oak forests in central Pennsylvania. We compare the structure and composition of these disturbed forests to four relatively undisturbed, mature forests as well as to presettlement forests, derived from original property maps, in the same area. From radial growth analysis and tree recruitment patterns, we examine the historical disturbance frequency and successional response to logging during periods of increasing then decreasing fire frequency. We hypothesize that logging and subsequent burning of the original oak-pine (*Pinus*) forests following European settlement increased oak dominance, and that recurring fire and logging maintained a high level of oak dominance through the 19th century. A reduction in fire frequency this century allowed the invasion of shade tolerant hardwoods to the oak understory. Logging of oak stands in this condition will accelerate the speed of obtaining dominance for shade tolerant species and the oak replacement process.

Material and Methods. STUDY AREA. Four relatively undisturbed, mature mixed-oak forests ranging in age from 80–160 years and four mixed-oak forests extensively logged between 1936–1946 were used for this study. These stands ranged from 2–6 ha in area and were located in the Nittany Valley of Centre County in central Pennsylvania, USA (40°47′36″N, 77°51′37″W). Disturbed stand 2 and mature stand 4 were adjacent to each other, while disturbed stands 1, 3, and 4 and mature stands 1, 2, and 3 were <3 km apart. Although logging records from the disturbed stands were not available, interviews with the land owners indicated that mostly oak and some pine or hickory (*Carya*) dominated the stands prior to logging in the 1930–1940's. The study area is part of the Ridge and Valley physiographic province, which consists of a series of parallel ridges oriented in a northeast-southwest direction. The forests of the region were originally classified as oak-chestnut (*Castanea dentata* Marsh.) by Braun (1950), although it is now considered a mixed-oak type. *Quercus alba* L. and *Q. velutina* Lam. presently dominate valley floor forests.

The climate of the study area is a composite of a relatively dry continental climate and a more humid climate characteristic of maritime regions of the eastern U.S. (Braker 1981). Average monthly minimum winter temperatures (December–March) range from −5 to −7°C and average maximum summer temperatures (June–August) range from 26 to 28°C. Average monthly precipitation varies from 6.5 to 9.7 cm and total annual precipitation averages 93.4 cm. The average number of frost-free days each year is 170 (27 April–14 October).

Soils in the surveyed stands were part of the Hagerstown-Opequon-Hublersburg association, which formed in limestone residuum (Braker 1981). All soils were either well-drained Typic Hapludalfs or Lithic Hapludalfs with loam/silt-loam surfaces. From a centrally located pit at each site, particle-size analyses were conducted using the Hydrometer method (Bouyoucos 1962). No significant differences were found in percent sand, silt, and clay at the mineral surface, or the 25 and 50 cm depths between mature and disturbed stands (Table 1). Soil pH at three depths was slightly higher on disturbed sites, however these differences were not statistically significant. Mean elevation and percent slope did not differ significantly between the two groups, averaging 350 m and 7%, respectively, for all sites combined.

FIELD METHODS. The point-quarter method was used to sample trees ≥10 cm at 1.37 m (dbh) in all stands (Cottam and Curtis 1956). A total of 20 points were systematically placed 20 or 30 m apart (dependent on stand size) along parallel transects. Transects were restricted to the interior portions of each stand to minimize edge effect. Each point was divided into quadrants and distance to the nearest tree, dbh, species name and canopy position (dominant, codominant, intermediate and overtopped; Smith 1986) were recorded in each quadrant. Two representative trees per point were cored at dbh for age determination. Cores were taken back to the laboratory for age and radial growth analysis. In addition, several large trees not occurring in the point-quarter sample on the disturbed sites were also cored for radial growth analysis.

Seedling and sapling densities by species were recorded at each point within nested circular plots of 5 and 10 m^2, respectively. Seedlings were tree species <1.5 m in height, whereas saplings were individuals ≥1.5 m in height but <10 cm dbh.

PRESETTLEMENT VEGETATION AND FIRE HISTORY. Reconstruction of presettlement vegetation of the Nittany Valley and surrounding valleys was based on maps of single or connected tracts from the Trezilyulny Family Papers housed at the State Archives in Harrisburg, Pennsylvania. Several copies of connected drafts from the book "History of Centre and Clinton Counties, Pennsylvania" were also included (Linn 1883). A total of 263 witness trees, representing 23 individual/connected drafts, were tallied. Dates of the surveys were mainly between 1775 and 1790, but ranged from 1769 to 1817. Fire records for the entire state of Pennsylvania from 1913–1989 were made available by the Bureau of Forestry, Department of Environmental Resources, Harrisburg, PA.

RADIAL GROWTH ANALYSES. Tree cores of the four (stand D1 only) or five oldest individuals within each stand were measured for annual radial growth to the nearest 0.1 mm with a dissecting scope and an ocular micrometer. Individual ring width data from each core were cross dated with other cores and then subjected to linear regression. Division of the measured width by the dated value of the fitted curve derived from regression was used to obtain a ring width index (Fritts and Swetnam 1989). The site chronology or radial growth index was created by averaging year-to-year data from the four or five the oldest tree indices in each stand.

DATA ANALYSES. Tree data were used to calculate species importance value percentages and basal area and density for each stand (importance percentage = [relative density + relative dominance + relative frequency]/3; Cottam and Curtis 1956). Statistical comparisons between mature and disturbed stands were conducted using a one-way analysis of variance for a completely randomized design at $P < 0.05$.

Table 1. Soil texture (%) and pH data ($\bar{x} \pm$ SE) of mature and disturbed mixed-oak forests in central Pennsylvania.[a]

	Mature	Disturbed
Surface		
Sand	30 ± 6	36 ± 5
Silt	54 ± 5	52 ± 4
Clay	16 ± 4	13 ± 1
Soil texture	silt loam	silt loam
pH	4.8 ± 0.2	5.4 ± 0.3
25 cm		
Sand	20 ± 6	19 ± 5
Silt	44 ± 5	49 ± 3
Clay	36 ± 7	33 ± 3
Soil texture	silty clay loam	silty clay loam
pH	4.6 ± 0.1	5.0 ± 0.4
50 cm		
Sand	16 ± 4	18 ± 6
Silt	33 ± 6	41 ± 7
Clay	52 ± 6	42 ± 10
Soil texture	clay	silty clay loam
pH	4.7 ± 0.1	5.3 ± 0.3

[a] Soil texture and pH data differences between mature and disturbed stands were not significant at $P < 0.05$.

Results. The four mature forests were dominated by *Quercus alba, Acer rubrum, Q. velutina,* and *Prunus serotina* (Table 2). In contrast, the disturbed stands had significantly greater *Acer* and lower *Quercus* importance than the mature stands. The increase in *Acer* was due to *A. rubrum* ($P < 0.05$) or *A. saccharum* Marsh in disturbed stands 1–3 and 4, respectively (Table 2). The lower importance of *Quercus* in the disturbed stands was mainly due to a nearly statistically significant decrease in *Q. alba* ($P < 0.07$) and to a lesser extent *Q. velutina*. Stand basal area and tree density were not significantly different between mature and disturbed stands (Table 2).

The dominant and codominant canopy classes in the mature forests were mainly comprised of *Quercus alba* and *Q. velutina* (Table 3). These canopy classes in the disturbed forests were dominated by *Acer rubrum* (or *A. saccharum*) and *Prunus serotina,* with significantly less *Quercus*. The intermediates in mature stands were mainly *Quercus* and *Prunus,* but also included a substantial number of *Carya, Pinus,* and *Acer. Acer,* followed by *Prunus*, dominated the intermediate

Table 2. Importance percentages of principal genera and species and stand basal area (m^2/ha) and tree density (ha^{-1}) in mature (M) and disturbed (D) *Quercus* forests by group ($\bar{x} \pm SE$) and by individual forests in central Pennsylvania. Group means for a species or genus with the same letter are not significantly different at $P < 0.05$.

			Individual stands							
	Mature	Disturbed	M1	M2	M3	M4	D1	D2	D3	D4
Acer	21.3 ± 1.8a	51.5 ± 9.4b	19.3	19.4	19.7	26.7	71.4	37.3	33.6	63.8
A. rubrum	19.9 ± 1.2a	35.6 ± 14.6a	19.3	17.2	19.7	23.1	71.4	37.3	33.6	0.0
A. saccharum	1.5 ± 0.9a	15.9 ± 15.9a	0.0	2.2	0.0	3.6	0.0	0.0	0.0	63.8
Carya spp.[a]	8.3 ± 3.1a	5.8 ± 2.0a	1.2	5.7	15.3	11.0	0.0	7.3	8.4	7.6
Pinus strobus	12.0 ± 5.3a	7.4 ± 4.8a	9.3	25.4	13.4	0.0	9.6	0.0	20.1	0.0
Prunus serotina	14.9 ± 2.8a	21.8 ± 4.5a	13.5	8.1	21.6	16.3	19.0	33.3	23.0	11.7
Quercus	39.8 ± 4.0a	9.7 ± 4.1b	46.7	38.7	29.0	45.0	0.0	19.8	11.4	7.4
Q. alba	23.2 ± 7.7a	4.9 ± 2.5a	37.7	31.3	21.4	2.5	0.0	11.8	2.6	5.3
Q. coccinea	2.2 ± 1.3a	0.0 ± 0.0a	0.0	0.0	4.3	4.4	0.0	0.0	0.0	0.0
Q. rubra	2.0 ± 2.0a	0.8 ± 0.8a	0.0	0.0	0.0	7.9	0.0	3.1	0.0	0.0
Q. velutina	12.5 ± 6.0a	4.0 ± 1.9a	9.0	7.4	3.3	30.2	0.0	4.9	8.8	2.1
Other[b]	3.6 ± 0.4	3.6 ± 2.1	10.0	2.6	1.0	1.1	0.0	2.1	3.2	9.4
Basal area	37.8 ± 3.4a	33.5 ± 3.1a	34.8	40.8	30.0	45.6	32.8	25.2	36.3	39.8
Tree density	519 ± 25a	538 ± 37a	462	557	492	563	464	517	531	638

[a] Includes *C. glabra* and *C. tomentosa.*
[b] Includes *Cornus florida, Sassafras albidum, Populus grandidentata, Fraxinus americana, Amelanchier* spp., *Ostrya virginiana, Juglans nigra, Ulmus* spp., and *Prunus avium.*

canopy class in the disturbed stands. Few overtopped *Quercus* were present in either the mature or disturbed stands; this canopy class was dominated primarily by *Acer* and secondarily by *Prunus* in both stand types.

The seedling layer in mature stands was dominated by *Prunus serotina*, *P. virginiana* L., *Acer rubrum*, and *Quercus alba* (Table 4). The disturbed stands also had a large number of *P. serotina* and *P. virginiana* seedlings, but contained significantly less *A. rubrum*, *Q. alba*, and *Q. velutina* than the mature stands. Disturbed stands 1–3 versus D4 contained 1533 and 775,700 *A. saccharum* seedlings per ha, respectively. The extraordinary number of *A. saccharum* seedlings in stand D4 greatly inflated the mean total seedling density in the disturbed stands, which averaged (±SE) 52,533 ± 9925 in stands D1–D3, a value not significantly different from that of the mature stands. Mature stands had significantly greater total sapling density than the disturbed stands, mainly due to increased *A. rubrum* and *P. serotina* (Table 4). No *Quercus* saplings were recorded in either the mature or disturbed stands.

We mainly attribute episodic increases in radial growth and tree recruitment to logging activity in the mature and disturbed stands, although we recognize that other disturbances such as fire, disease and blowdown may have occurred. One or more disturbance periods were apparent in mature stands 1–3 (Fig. 1). Major recruitment and highest radial growth of the oldest *Quercus* trees in stand M1 occurred at about 1844, presumably the time of extensive logging. A disturbance in 1884 promoted another wave of *Quercus* recruitment and accelerated radial growth of the existing trees. Another disturbance in 1921 stimulated radial growth and a limited amount of recruitment of *Acer*, *Carya*, and *Prunus*. Between 1935–1975, *Acer rubrum* and *Prunus serotina* increased in the tree size classes of this stand. In stand M2, major *Quercus* recruitment occurred during a 40 year period after a major disturbance in 1890. Between 1930–1955, tree recruitment was exclusively from *Acer rubrum*, *Prunus serotina*, and *Pinus strobus*, which included a disturbance in 1942. The oldest *Quercus* trees in stand M3 presumably originated shortly after logging in 1830. A disturbance in 1929 eliminated many of the mature *Quercus*, but promoted the episodic recruitment of all five of the dominant tree genera, including *Acer* and *Prunus*. The oldest *Quercus* in stand M4 originated shortly after logging in 1908, after which

Table 3. Canopy class distribution for trees of the principal genera in mature and disturbed forests in central Pennsylvania. Genus values within a canopy class followed by the same letter are not significantly different at $P < 0.05$. N = number of individuals surveyed in the mature and disturbed stands, respectively.

Canopy class and genera	Relative frequency (%) Mature	Disturbed
Dominant N = 34 and 36		
Acer	8.4a	58.8b
Carya	5.6a	8.8a
Pinus	5.6a	2.9a
Prunus	2.8a	8.8a
Quercus	77.8a	14.7b
Others	0.0a	5.9a
Codominant N = 69 and 117		
Acer	8.7a	55.6b
Carya	8.7a	4.3a
Pinus	8.7a	8.5a
Prunus	8.7a	23.1b
Quercus	63.8a	6.8b
Others	1.4a	1.7a
Intermediate N = 59 and 105		
Acer	11.9a	58.1b
Carya	16.9a	6.7a
Pinus	16.9a	3.8a
Prunus	22.0a	24.8a
Quercus	28.8a	5.7b
Others	3.4a	1.0a
Overtopped N = 155 and 63		
Acer	42.6a	60.3a
Carya	6.5a	7.9a
Pinus	14.2a	1.6b
Prunus	27.7a	20.6a
Quercus	7.1a	4.8a
Others	1.9a	4.8a

no disturbance occurred and recruitment was primarily by *Acer rubrum*, *Prunus serotina*, and *Carya* spp.

The oldest individuals in each of the disturbed stands were *Quercus*, *Carya*, and *Pinus* (Fig. 2), and these species were known to dominate the stands prior to 1936 from eyewitness accounts. Radial growth analysis of these trees and species recruitment patterns indicate one to several disturbance episodes following the stand initiation in the early-to-mid-1800's. Stand D1 was apparently disturbed in 1848. The oak that originated after 1848 was then extensively cut in 1936, which promoted the rapid recruitment of numerous *Acer rubrum* and, to a lesser extent, *Prunus serotina* trees. *Quercus* recruitment in stand D2 occurred following disturbance in 1833. An abrupt release in radial growth was also exhibited by these trees in 1867. Some recruitment of *Acer rubrum* and *Prunus serotina* was associated with

Table 4. Seedling and sapling density ($\bar{x} \pm$ SE per ha) of principal species in mature and disturbed forests in central Pennsylvania. Seedlings and saplings for each species and total means followed by the same letter are not significantly different at $P < 0.05$.

	Seedlings		Saplings	
	Mature	Disturbed	Mature	Disturbed
Acer rubrum	8350 ± 1819a	450 ± 233b	1438 ± 619a	63 ± 24a
A. saccharum	1625 ± 839a	189,650 ± 188,120a	87 ± 55a	125 ± 95a
Carya spp.	975 ± 193a	125 ± 95b	75 ± 75a	0 ± 0a
Fraxinus americana	75 ± 48a	1725 ± 1495a	0 ± 0a	162 ± 162a
Prunus avium	3475 ± 2624a	50 ± 29a	38 ± 38a	0 ± 0a
P. serotina	16,100 ± 4248a	30,525 ± 7508a	850 ± 225a	225 ± 209a
P. virginiana	8475 ± 2439a	9025 ± 1967a	125 ± 66a	288 ± 223a
Quercus alba	6050 ± 2448a	0 ± 0b	0 ± 0a	0 ± 0a
Q. rubra	400 ± 212a	25 ± 25a	0 ± 0a	0 ± 0a
Q. velutina	400 ± 91a	25 ± 25b	0 ± 0a	0 ± 0a
Others	2400 ± 1213a	1725 ± 1269a	275 ± 136a	238 ± 205a
Total	48,325 ± 6656a	233,325 ± 180,928a	2888 ± 450a	1100 ± 298b

an increase in the ring width index in 1916, but major recruitment of these species and *Quercus* occurred after extensive logging in 1936. Only one *Quercus* individual remained in stand D3 in 1990 from the cohort that recruited following a disturbance in 1855. This tree and the four oldest *Pinus*, *Carya*, and *Acer* trees in the stand exhibited an abrupt release in radial growth in 1911, which was associated with widespread recruitment of *Acer rubrum*, *Pinus strobus*, and *Prunus serotina*. Extensive logging in 1946 further accelerated recruitment of *Acer*, *Prunus*, and *Quercus*. In stand D4, the oldest *Quercus* trees recruited in 1830 and 1846. A disturbance at about 1912 caused extensive recruitment of *Acer saccharum*. Subsequent recruitment of *Acer saccharum* and *Pinus strobus* was also associated with logging in 1945. *Acer* and *Prunus* seemingly dominated the understory of all the disturbed stands at the time of extensive logging in 1936–1946 based on recruitment patterns a few years before and immediately after logging.

Thirty-nine percent of the 263 presettlement witness trees tallied in the Nittany Valley and surrounding valleys were *Quercus alba*. *Pinus* (*P. strobus*), *Carya*, and *Q. velutina* represented 25.9%, 14.1%, and 10.6% of witness trees, respectively (Table 5). The remaining 12 species or genera represented only 10.2% of the witness trees. However, the estimated dominance of *Q. alba* in presettlement forests could be somewhat inflated because large individuals in that genus may have been preferred by early surveyors in Pennsylvania (Loeb 1987).

The amount of area burned per year and the average fire size in all of Pennsylvania decreased by 99% and 98%, respectively, between 1908 and 1989 (Table 6). A greater number of fires occurred in the 1920–30's compared to other decades in this century.

Discussion. The ecological status of *Quercus* forests in the study area is intrinsically tied to disturbance. European settlement of Centre County, Pennsylvania started in 1769, at which time the forests were dominated by *Q. alba* and *Pinus strobus*. These species dominated other presettlement forests in the northeast and mid-Atlantic regions, which may be related to periodic fire from lightning or early Native American activity (Spurr 1951; Buell *et al.* 1954; Russell 1980; Loeb 1987; Patterson and Sassaman 1988; Seischab 1990; Abrams and Downs 1990). Indeed, Delaware and Shawanese Indian tribes inhabited Centre County in the 1700's and sold land to the original European settlers (Linn 1883; Wallace 1965). Periodic surface fire may favor *Quercus alba* and *P. strobus* because of the creation of suitable seedbeds for germination, succession to more shade tolerant species is checked and adult individuals have resistant bark (Little 1974; Whitney 1986; Abrams 1988). In addition, *Q. alba* and other eastern oaks can sprout prolifically if top-killed by fire and are resistant to rot after scarring relative to later successional species (Buell *et al.* 1954; Lorimer 1985; Abrams 1985).

In 1774, the first iron producing company started operation in Centre County and by 1792 the first charcoal-fueled iron furnace was erected (Linn 1883). By 1826, there were nine active charcoal iron furnaces and ten forges in the county. Iron production in the region and statewide peaked about 1842 and continued to varying de-

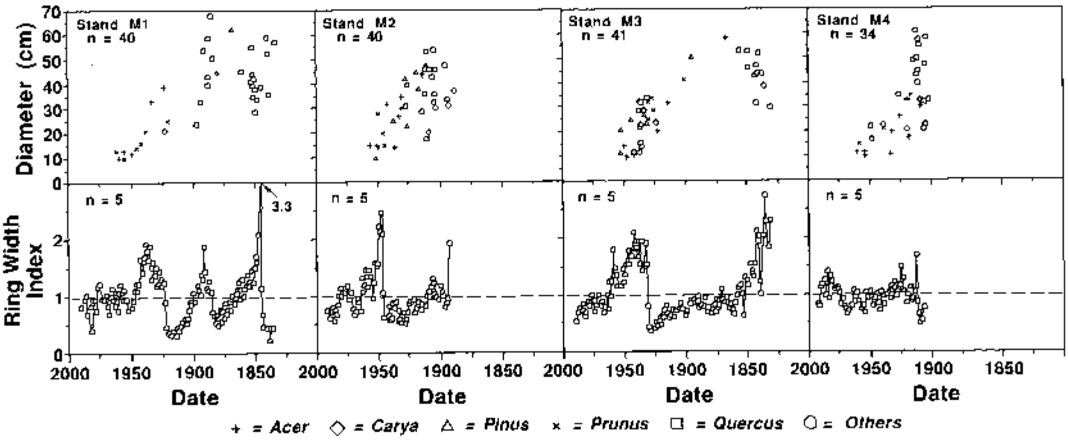

Fig. 1. Tree age-diameter relationships for 34–41 sample trees and ring width index by date for the five oldest trees in four mature mixed-oak forests in central Pennsylvania.

grees until 1911 (Pearse 1876). The iron industry had a profound effect on the vegetation in Centre County. Approximately 120 ha of forests were cleared each year to produce the charcoal needed to fuel a single iron furnace, and forests may have been cut at a 20–30 year interval (Stout 1933). Large and generally uncontrolled wildfires often followed logging activity in the region throughout the 1800's and early 1900's. The oldest trees in Nittany Valley forests established during this period were almost exclusively *Q. alba* and *Q. velutina* (Fig. 1). *Pinus strobus* generally appeared in these stands 20–80 years after the initial oak cohort was established. This temporal sequence in oak versus pine recruitment following disturbance probably relates to the profilic sprouting ability of the former. An increase in oak in former oak-pine or pine forests following post-settlement logging and fire has been previously reported (Whitney 1987; Crow 1988; Nowacki *et al.* 1990; Glitzenstein *et al.* 1990).

Tree recruitment following 1920 in the mature forests in our study area was primarily by *Acer rubrum* and *Prunus serotina*. The importance of *A. rubrum* and *A. saccharum* as shade tolerant understory trees in eastern oak forests and as probably oak replacement species has been widely established (Christensen 1977; Lorimer 1984; Host *et al.* 1987; Nowacki *et al.* 1990; Abrams and Downs 1990). In contrast, *P. serotina* is generally considered intolerant of shade (Spurr and Barnes 1980), and dependent on gaps for canopy recruitment in closed forests (Auclair and Cottam 1971; McCune and Cottam 1985). However,

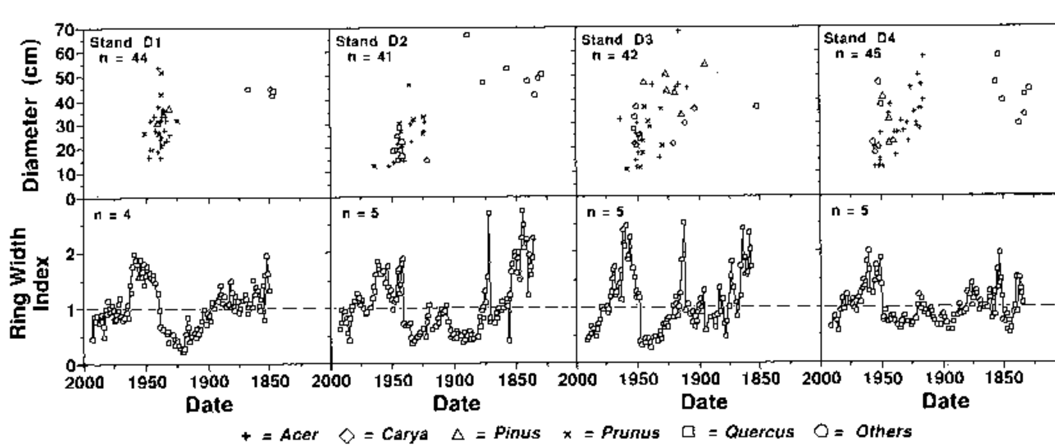

Fig. 2. Tree age-diameter relationships for 41–45 sample trees and ring width index by date for the four (stand D1) or five oldest trees in four mixed-oak forests extensively logged between 1936–1946 in central Pennsylvania.

Table 5. Percent species composition of 263 witness trees in presettlement forests (primarily 1775–1790) in the Nittany Valley of central Pennsylvania.

Species	% composition
White oak	39.2
Pine	25.9
Hickory	14.1
Black oak	10.6
Chestnut	1.9
Spanish oak	1.5
Chestnut oak	1.1
Maple	1.1
Red oak	1.1
Cherry	0.8
Elm	0.8
Ash	0.4
Dogwood	0.4
Ironwood	0.4
Plum tree	0.4
Spruce	0.4

Table 6. Summary of yearly mean forest fire statistics in Pennsylvania.

Year	Number of fires	Hectares burned	Average size (ha)
1908[a]	—	404,700	—
1913–1919	1241	108,155	87
1920–1929	2489	72,378	29
1930–1939	3908	42,049	11
1940–1949	1929	21,158	11
1950–1959	1074	12,784	12
1960–1969	1478	8634	6
1970–1979	1339	3240	2
1980–1989	1431	3388	2

[a] From Banks (1960), number of fires and average size of fires were not reported.

we have found *P. serotina*, as well as *A. rubrum*, growing vigorously in the understory and recruiting well in most mesic oak forests in central Pennsylvania (Nowacki and Abrams 1991). *Acer saccharum* dominance in the overstory and understory is generally restricted to wet-mesic, riparian forests in the study area (Nowacki and Abrams 1991).

Over 400,000 ha burned state-wide in 1908 (Banks 1960), and in 1913, the first year official fire statistics were compiled, 156,322 ha burned. It is probable that early fire records were incomplete and underestimated by 50% or more the actual area that burned each year (Art Creelman, Pennsylvania Bureau of Forestry, personal communication). We believe that the extent and intensity of post-settlement burning peaked in the mid-1800's when charcoal production was at a maximum statewide (Pearse 1876). Based on the composition and structure of our existing forests in Centre County, it is apparent that oak species flourished in a regime of frequent logging and fire. After 1860, when the charcoal iron furnace industry waned, agricultural activity in the Nittany Valley increased (Linn 1883). We attribute the more recent increase in *Acer* and *Prunus* in area forests to a drastic reduction in logging and fire frequency this century.

The increase in later successional *Acer* and *Prunus* in oak understories has made these stands prime candidates for post-logging accelerated succession. Indeed, selective or near-complete logging this century in the disturbed stands has increased recruitment and importance of *A. rubrum*, *A. saccharum* (in stand D4) and *P. serotina* in the upper canopy and, thus, the oak replacement process. Even though some oak recruitment was associated with logging this century in the mature (M3) and disturbed (D2 and D3) stands, their numbers were low relative to that of *Acer* and *Prunus*. Other examples of post-logging accelerated succession in North American forest types include the conversion of *Pinus strobus* and *Thuja occidentalis* L. forests in Michigan to *Acer saccharum* (Whitney 1987; Abrams and Scott 1989), and the episodic recruitment of mixed-mesophytic tree species into the canopy of old-growth *Q. alba* stands in Illinois and southwestern Pennsylvania (Jokela and Sawtelle 1985; Abrams and Downs 1990). Timber harvesting of southern pine forests in Louisiana and Alabama also accelerated a shift to hardwood dominance (Blair and Brunett 1976; Golden 1979).

In conclusion, repeated cutting and burning of the original oak-pine forests following European settlement increased the relative dominance of oak, at least for the short-term. During the 1900's, when disturbances were limited, later successional species increased in the oak understories thus initiating the oak replacement process. While we realize that the influence of other disturbance factors in central Pennsylvania such as white-tailed deer (*Odocoileus virginianus borealis*), gypsy moth (*Lymantria dispar*) and chestnut blight (*Endothia parasitica*) have been prevalent, we attribute the successional progression in oak forests primarily to a drastic reduction of logging and fire this century. For example, gypsy moth grazing in central Pennsylvania has been mainly concentrated on ridge top sites (Kleiner *et al.* 1989), and chestnut was not a dominant in Nittany Valley floor forests (Table 5). Logging of stands with understories dominated by *Acer* and

Prunus accelerated canopy recruitment of these species and the oak replacement process, rather than set back succession to an earlier stage. Accelerated succession following logging and other types of disturbance should be anticipated in a wide variety of forests with overstories dominated by oak or analogous early successional species and understories dominated by later successional species.

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