

COMPOSITION AND STRUCTURE OF AN OLD-GROWTH VERSUS A SECOND-GROWTH WHITE OAK FOREST IN SOUTHWESTERN PENNSYLVANIA

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Abstract: A relatively undisturbed, old-growth *Quercus alba* remnant and a second-growth example of the forest type were surveyed in 1988-89 to investigate the successional status of *Q. alba* in the region. Oaks (*Q. alba*, *Q. rubra*, and *Q. velutina*) totalled 18% importance in the old-growth stand and 30% importance in the second-growth stand. The overstory of the old-growth stand was mainly comprised of *L. tulipifera*, *F. grandifolia*, *Q. alba* and *Nyssa sylvatica*, whereas the overstory of the second-growth stand was mainly *Q. alba* with a relatively minor component of *F. grandifolia*, *A. saccharum*, and *L. tulipifera*. *Acer rubrum*, *A. saccharum*, and *Prunus serotina* were the dominant seedlings in both stands. The younger stand had greater sapling density. Both stands had few *Quercus* individuals in the understory. The oldest and largest trees in both stands were *Q. alba* with ages of 310 years and 148 years in the old-growth and second-growth stand, respectively. However, over 90% of all trees in the old-growth stand were < 120 years-old. Logging of several trees in the 1930's and 40's appears to have accelerated the dominance of the mixed-mesophytic species in the old-growth forest. The radial growth patterns of trees varied with species and canopy position. However, the oldest oak trees had average growth rates of < 0.75 mm/yr and > 1.5-2.0 mm/yr in the old-growth and second-growth stands, respectively. Many of the understory trees had average growth rates of > 1.5-2.0 mm/yr in both stands. We believe these stands represent an early versus late stage of oak replacement by mixed-mesophytic species, a process that seems inevitable in many eastern oak forests.

INTRODUCTION

Oak (*Quercus*) forests dominate much of the eastern deciduous forest biome and have been considered a climax type by early ecologists (Braun 1950, Clements 1936). Indeed, oak presence and dominance was recorded in presettlement forests of the northeast and mid-Atlantic regions (Bromley 1935, Loeb 1987, Russell 1980, Secor 1975, Spurr 1951). Oak dominance prior to European settlement in these regions may be explained, in part, by periodic fire set by early Native Americans and by lightning (Buell et al. 1954, Lorimer 1985). Following European settlement, cutting and slash fires further perpetuated or even

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caused an increase in oaks in many areas (Crow 1988, Lutz 1928, Nowacki et al. 1990, Whitney 1987). However, there now exists substantial documentation that oaks are failing to regenerate under their own canopy, especially on mesic sites, suggesting oak replacement by more shade tolerant species (Abrams 1986, Lorimer 1984, Nigh et al. 1985, Parker et al. 1985). Much of this evidence, however, comes from studies of relatively young forests of generally less than 120-years-old with shade tolerant species confined to regeneration layers. Many eastern oak species can, in fact, live well over 300 years (Fowells 1965). Thus, examples of actual oak replacement with later successional species dominating the canopy of old-growth stands are lacking.

In southwestern Pennsylvania we found a relatively undisturbed old-growth stand with white oak (*Q. alba* (L.)) trees up to 310 years in age. In the same area there also existed an undisturbed second-growth forest on a similar site with white oak trees up to 148 years in age. This paper compares the composition, age and diameter structure, radial growth patterns and regeneration trends in the old-growth stand with that of the second-growth stand to provide evidence that mesic white oak forests in this region are not a true climax type and, thus, are replaced by later successional species. Moreover, the results of this study may indicate whether successional trends apparent in the younger stand actually occurred in the old-growth stand.

METHODS

Study Area

The 3 ha old-growth forest, known as Sophia's Woods, is located within the 270 ha Friendship Hill National Historic Site in Fayette County, in southwestern Pennsylvania. Friendship Hill preserves the country estate of Albert Gallitin, the United States Secretary of Treasury under Presidents Jefferson and Madison. Gallitin purchased this land in 1786 when it was virgin timber. At that time, Gallitin girdled and removed some of the forest for agricultural purposes. By 1880, after Gallitin had sold the estate, 90 ha were cleared for pasture and food crops, while 180 ha were left in mature timber. By 1895, only 80 ha remained wooded.

A 1923 timber cruise of Friendship Hill reported that mature forests on the property were predominantly oaks "of the various species" with ages up to 260 years, and that some trees were of "unusual size" (e.g., the diameter of one white oak was 152 cm). It was also noted that *Carya* (hickory) and *Quercus coccinea* (Muench.) (scarlet oak) were "dying". This report recommended harvesting, but major timber operations were held off until the 1940's and lasted intermittently through the 1950's. Between the 1930's and 1950's the amount of non-forest area within the property had more than doubled.

Physical evidence within Sophia's Woods and growth patterns of the existing trees indicated that this area was selectively cut in the 1930's and 1940's. Several large oak stumps (dbh >

1 m) of low density (about 2 stumps/ha) were irregularly distributed throughout the stand. Fire scarring on trees was lacking and only one uprooted tree was observed. Sophia's Woods is located on an upland bluff over the east bank of the Monongahela River. The stand is gently sloping (3-8%) and is bisected by two small streams. The Monongahela silt loam soil present is deep (1.5-5.0 m) and moderately well-drained. The permeability of this soil is moderately slow due to the presence of a fragipan, normally starting at a depth of 48 cm. The available moisture capacity is high (Kopas 1973).

The 4 ha second-growth stand is located within the 1600 ha Bear Run Nature Reserve, also in Fayette County in southwestern Pennsylvania. This second-growth stand originated after clearcutting and is protected by the Western Pennsylvania Conservancy. No physical evidence of logging or fire since stand initiation was observed. The Bear Run site is located on an upland bluff over the east bank of the Youghiogheny River. The stand is gently sloping to the northwest and traversed by 3 small intermittent streams. The Dekalb soil present is a very stony, sandy loam and is moderately deep (0.6 -1.0 m). The permeability of the soil is rapid and the available moisture capacity can be low (Kopas 1973).

The climate of Fayette County is humid continental. Annual precipitation averages 101 cm per year and is evenly distributed. The mean annual temperature is 12° C (monthly range = -18 to 35° C). The growing season averages about 169 days (Kopas 1973).

Field Methods

Trees (individuals > 10 cm at 1.37 m; dbh) of Sophia's Woods and Bear Run were surveyed during July 1988 and July 1989, respectively, using the point-quarter method (Cottam and Curtis 1956). Twenty sample points located at 20 m intervals along transects were used. Transects were oriented to best include the entire study area and avoid edges. Species name, dbh and distance to the point center of the tree in each of four quadrants closest to the sample point were recorded. These data were used to calculate importance values for each tree species as the sum of relative dominance, frequency and density. The canopy class of each sample tree was rated as dominant, codominant, intermediate, or overtopped (cf. Smith 1986). Sample trees were also cored at 1.37 m for age determination. In Sophia's Woods every sample tree was cored because of the wide range of tree ages. In contrast, only two sample trees from each plot were cored in the younger Bear Run stand. A total of 61 suitable cores from Sophia's Woods were sanded, stained and measured for annual radial growth to the nearest 0.1 mm with a dissecting scope and an ocular micrometer. A total of 37 suitable cores from Bear Run were analyzed using the same technique.

Using the 20 sample points in the tree survey as centers, fixed area plots were established in both stands for regeneration data. Saplings (tree species < 10 cm dbh and taller than 1.37 m) and seedlings (tree species < 1.37 m tall) were counted by species in 10 m² and 5 m² plots, respectively.

RESULTS

In Sophia's Woods, the old-growth stand, *Fagus grandifolia* (Ehrh.) (beech), *Acer rubrum* (L.) (red maple) and *Liriodendron tulipifera* (L.) (tulip poplar) represented 63% of the importance value total (Table 1). White oak, *Quercus rubra* (L.) (northern red oak), and *Q. velutina* (Lam.) (black oak) totalled only 18% importance. The importance of white oak in Sophia's Woods was mainly due to its high basal area from a few large diameter individuals. Bear Run, the second-growth stand, was dominated by white oak, *Acer saccharum* (Marsh.) (sugar maple), red maple and tulip poplar which represented 76% of the importance value.

Table 1.--Relative importance values for trees (> 10 cm dbh) surveyed during 1988 and 1989 in an old-growth (Sophia's Woods) and a second-growth (Bear Run) stand on mesic sites in southwest Pennsylvania. Relative importance value is the sum of the relative dominance, frequency, and density divided by three for each species.

Species	Importance Value	
	Sophia's Woods	Bear Run
<i>Quercus alba</i>	11	27
<i>Quercus velutina</i>	3	1
<i>Quercus rubra</i>	4	1
<i>Acer rubrum</i>	20	12
<i>Acer saccharum</i>	5	25
<i>Liriodendron tulipifera</i>	18	11
<i>Fagus grandifolia</i>	25	7
<i>Betula lenta</i>	4	4
<i>Nyssa sylvatica</i>	4	1
<i>Prunus serotina</i>	2	1
<i>Tilia americana</i>	2	--
<i>Cornus florida</i>	1	4
<i>Carya</i> spp.	1	2
<i>Ulmus</i> spp.	--	4

Prunus serotina (Ehrh.) (black cherry), red maple and sugar maple were the dominant seedlings surveyed in Sophia's Woods and Bear Run, despite the low importance of black cherry trees on both sites (Table 2). Sugar maple and red maple had similar seedling densities at Bear Run, while the density of red maple seedlings was 400% greater than that of sugar maple in Sophia's Woods. Sophia's Woods had greater total seedling density than

Table 2.--Seedling and sapling data (no./ha $\pm$ se) from the 1988 and 1989 survey of an old-growth forest (Sophia's Woods, SW) and a second-growth forest (Bear Run, BR) on mesic sites in southwest Pennsylvania.

Species	Seedlings		Saplings	
	SW	BR	SW	BR
<i>Acer rubrum</i>	23400 $\pm$ 300	7600 $\pm$ 153	50 $\pm$ 2	900 $\pm$ 3
<i>Acer saccharum</i>	5100 $\pm$ 61	7100 $\pm$ 119	100 $\pm$ 3	50 $\pm$ 2
<i>Prunus serotina</i>	11000 $\pm$ 138	14300 $\pm$ 123	50 $\pm$ 2	500 $\pm$ 15
<i>Nyssa sylvatica</i>	4900 $\pm$ 160	600 $\pm$ 18	50 $\pm$ 2	450 $\pm$ 10
<i>Quercus alba</i>	3000 $\pm$ 82	500 $\pm$ 10	0 $\pm$ 0	300 $\pm$ 8
<i>Quercus rubra</i>	2500 $\pm$ 58	800 $\pm$ 22	0 $\pm$ 0	0 $\pm$ 0
<i>Quercus velutina</i>	100 $\pm$ 5	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0
<i>Fraxinus</i> spp.	1500 $\pm$ 27	700 $\pm$ 17	100 $\pm$ 3	150 $\pm$ 5
<i>Fagus grandifolia</i>	1100 $\pm$ 15	300 $\pm$ 8	100 $\pm$ 5	700 $\pm$ 14
<i>Carya</i> spp.	500 $\pm$ 18	900 $\pm$ 25	0 $\pm$ 0	100 $\pm$ 3
<i>Cornus florida</i>	100 $\pm$ 5	900 $\pm$ 25	0 $\pm$ 0	100 $\pm$ 3
<i>Hamamelis virginiana</i>	0 $\pm$ 0	4900 $\pm$ 159	0 $\pm$ 0	600 $\pm$ 16
<i>Crataegus</i> spp.	0 $\pm$ 0	700 $\pm$ 3	0 $\pm$ 0	50 $\pm$ 2
<i>Sassafras albidum</i>	0 $\pm$ 0	600 $\pm$ 15	0 $\pm$ 0	0 $\pm$ 0
<i>Ulmus</i> spp.	0 $\pm$ 0	500 $\pm$ 25	0 $\pm$ 0	50 $\pm$ 2
<i>Asimina triloba</i>	0 $\pm$ 0	400 $\pm$ 12	0 $\pm$ 0	100 $\pm$ 3
<i>Betula lenta</i>	0 $\pm$ 0	100 $\pm$ 5	0 $\pm$ 0	50 $\pm$ 2
<i>Liriodendron tulipifera</i>	0 $\pm$ 0	100 $\pm$ 5	0 $\pm$ 0	50 $\pm$ 2
Total	53300 $\pm$ 874	41000 $\pm$ 744	450 $\pm$ 17	4150 $\pm$ 90

Bear Run and twice the number of species with seedling density > 1000/ha. However, these species (which included *Nyssa sylvatica* (Marsh.) (blackgum), northern red oak, white oak, *Fraxinus* spp. (ash) and beech) had few if any saplings (from 0-100/ha) in Sophia's Woods. At Bear Run these same species had saplings with densities in the range of 150-900/ha (with the exception of northern red oak). Seedlings and saplings of tulip poplar were absent in the sample plots at both sites, but were observed under canopy gaps.

Diameter class distribution in both stands approximated a reverse-J curve typical of an uneven-aged condition (Figure 1) (cf. Smith 1986). In Sophia's Woods the large diameter classes (> 60 cm) were dominated by white oak and beech, whereas the medium classes (35-60 cm) were dominated by tulip poplar and beech with some blackgum. The small diameter classes (< 35 cm) at Sophia's Woods were dominated by red maple, with some sugar maple, beech and tulip poplar also present. White oak and beech dominated the larger and medium diameter classes and sugar maple followed by red maple dominated the smaller diameter classes at Bear Run. Relatively few oak trees were surveyed in the smaller diameter classes at either site. Diameter distribution and tree size was similar in both stands despite the great difference in stand ages.

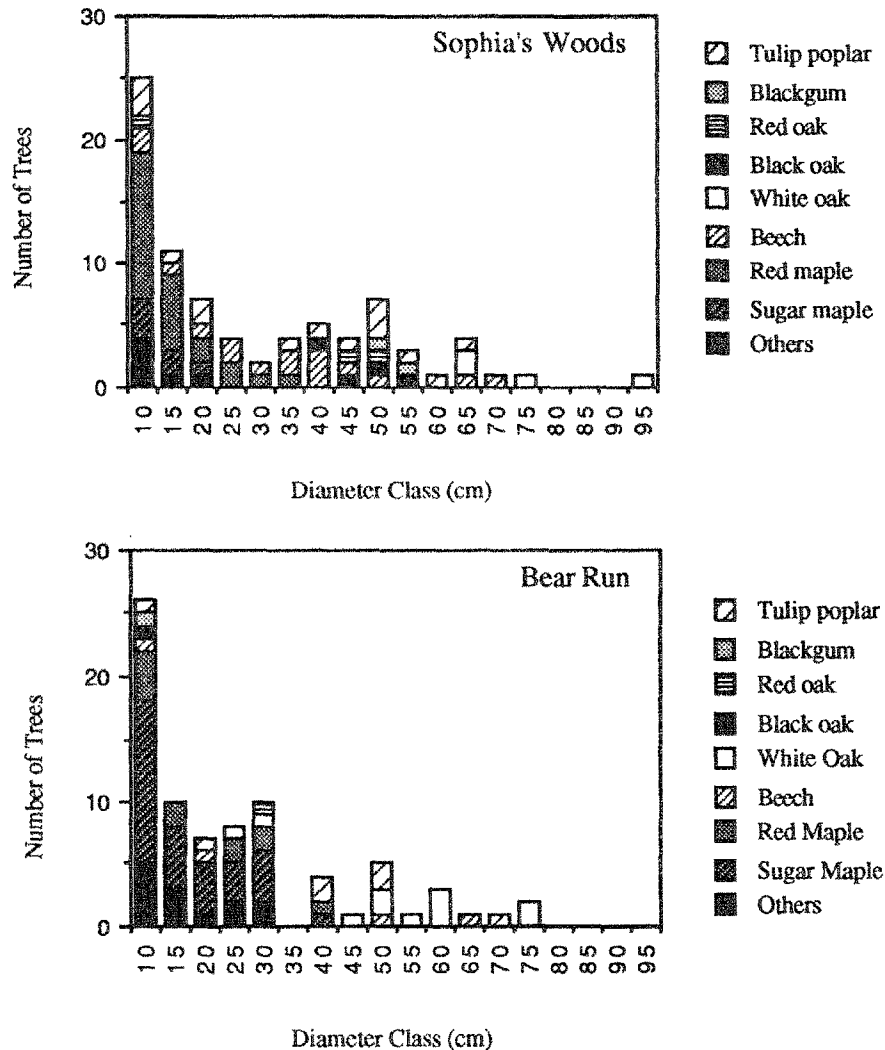


Figure 1. Diameter distribution of tree species in an old-growth oak forest (Sophia's Woods) and a second-growth oak forest (Bear Run) in southwestern Pennsylvania. Other species include *Betula lenta*, *Prunus serotina*, *Tilia americana*, *Cornus florida* and *Aesculus* spp. in Sophia's Woods and *Betula lenta*, *Prunus serotina*, *Cornus florida*, *Carya* sp. and *Ulmus* spp. in Bear Run. The Bear Run distribution excludes a white oak tree surveyed in the 125 cm class.

Table 3.--Canopy and diameter class distributions among the surveyed trees at Sophia's Woods (SW) and Bear Run (BR), old-growth and second-growth stands, respectively, in southwest Pennsylvania, surveyed in 1988 and 1989. N=number of individuals. Large, medium and small diameter classes are dbh >60, 35-60 and <35 cm, respectively.

Canopy Class	Species	N		Diameter Class	
		SW	BR	SW	BR
Dominant:	<i>Liriodendron tulipifera</i>	5	1	Medium	Large
	<i>Fagus grandifolia</i>	4	1	Large	Large
	<i>Quercus alba</i>	3	3	Large	Large
	<i>Quercus velutina</i>	1	0	Medium	-----
	<i>Nyssa sylvatica</i>	1	0	Large	-----
	<i>Tilia americana</i>	1	0	Medium	-----
Codominant:	<i>Liriodendron tulipifera</i>	2	3	Medium	Medium
	<i>Fagus grandifolia</i>	2	1	Medium	Medium
	<i>Nyssa sylvatica</i>	1	0	Medium	-----
	<i>Betula lenta</i>	1	0	Medium	-----
	<i>Quercus alba</i>	0	8	-----	Medium
	<i>Acer saccharum</i>	0	2	-----	Medium
	<i>Acer rubrum</i>	0	1	-----	Medium
Intermediate:	<i>Fagus grandifolia</i>	6	0	Medium	-----
	<i>Liriodendron tulipifera</i>	4	1	Small	Medium
	<i>Acer rubrum</i>	2	3	Small	Small
	<i>Acer saccharum</i>	0	9	-----	Small
	<i>Quercus rubra</i>	2	0	Medium	-----
	<i>Quercus velutina</i>	1	0	Medium	-----
	<i>Carya</i> spp.	0	2	-----	Small
	<i>Ulmus</i> spp.	0	2	-----	Small
	<i>Prunus serotina</i>	0	1	-----	Small
Overtopped:	<i>Acer rubrum</i>	22	8	Small	Small
	<i>Acer saccharum</i>	6	18	Small	Small
	<i>Fagus grandifolia</i>	7	2	Small	Small
	<i>Liriodendron tulipifera</i>	2	2	Small	Small
	<i>Betula lenta</i>	2	3	Small	Small
	<i>Carya</i> spp.	1	0	Small	-----
	<i>Prunus serotina</i>	2	0	Small	-----
	<i>Quercus rubra</i>	1	1	Small	Small
	<i>Quercus alba</i>	0	1	-----	Small
	<i>Quercus velutina</i>	0	1	-----	Small
	<i>Cornus florida</i>	1	4	Small	Small
	<i>Ulmus</i> spp.	0	1	-----	Small
	<i>Nyssa sylvatica</i>	0	1	-----	Small

Canopy position of trees in Sophia's Woods and Bear Run was closely related to their respective diameter class (Table 3). However, species composition within canopy classes differed between the old-growth and second growth stands. More dominant beech and tulip poplar were surveyed at Sophia's Woods versus Bear Run. Eight codominant white oaks were surveyed at Bear Run compared to none at Sophia's Woods. Sugar maple and red maple were overstory codominants at Bear Run but not at Sophia's Woods. Sophia's Woods had a greater number of dominant overstory species, which included blackgum, black oak, and *Betula lenta* (L.) (black birch), not present at Bear Run. Overtopped trees in Sophia's Woods were primarily red maple, beech and sugar maple, while at Bear Run more overtopped sugar maple and less beech and red maple were present.

Two white oaks were estimated to be > 300 years-old at Sophia's Woods (Figure 2). However, greater than 90% of all sampled trees were less than 120 years-old, including many beech, tulip poplar and red maple, but few oaks. Several beech and tulip poplar were in the canopy despite their relatively young ages (Table 3). At Bear Run, white oak, with a maximum age of 148 years, and to a lesser extent beech, dominated the higher age classes. A greater number of 90-148 year-old white oaks were surveyed at Bear Run compared to Sophia's Woods. Sugar maple was much more dominant in the younger age classes at Bear Run compared to Sophia's Woods. Relatively few individuals in the 20-year class were observed at either site.

Radial growth patterns of the surveyed trees varied with species and canopy position in both stands (Figures 3 and 4). Several cores of Sophia's Woods showed release in the 1930's and 40's which coincided with reported logging activities (Figure 3D, E, F, G, and H). Many trees in Bear Run also exhibited periodic release, such as intermediate white oak, red maple and sugar maple, presumably in response to natural gaps (Figure 4B, D, G). A codominant sugar maple in Bear Run had high but decreasing growth with age, suggesting it had originated in a gap and had no accelerated growth after reaching the canopy (Figure 4C) (cf. Lorimer et al. 1988). A dominant white oak in Sophia's Woods exhibited this same pattern (Figure 3C). An understory northern red oak at Bear Run had early growth of 5.0 mm/yr and a decrease to < 1.0 mm/yr probably as a result of gap closure (Figure 4H). A codominant beech at Bear Run (Figure 4E) displayed moderate, low, then high radial growth, suggesting that it grew during the opening and closing of a gap and then was released upon reaching the canopy. Tulip poplar exhibited the highest average growth rate of any species in both stands (3.0 mm/yr), with no extended periods of suppression.

Differences in radial growth between stands were apparent when comparing the oldest oaks. At Sophia's Woods a 310 year-old white oak and a 240 year old black oak averaged < 0.60-0.75 mm/yr radial growth (Figure 3A, B). In contrast, the oldest white oaks of Bear Run averaged > 1.5-2.0 mm/yr radial growth (Figure 4A, B). Younger trees of all species at both sites, in general, had average growth rates exceeding 1.5-2.0 mm/yr.

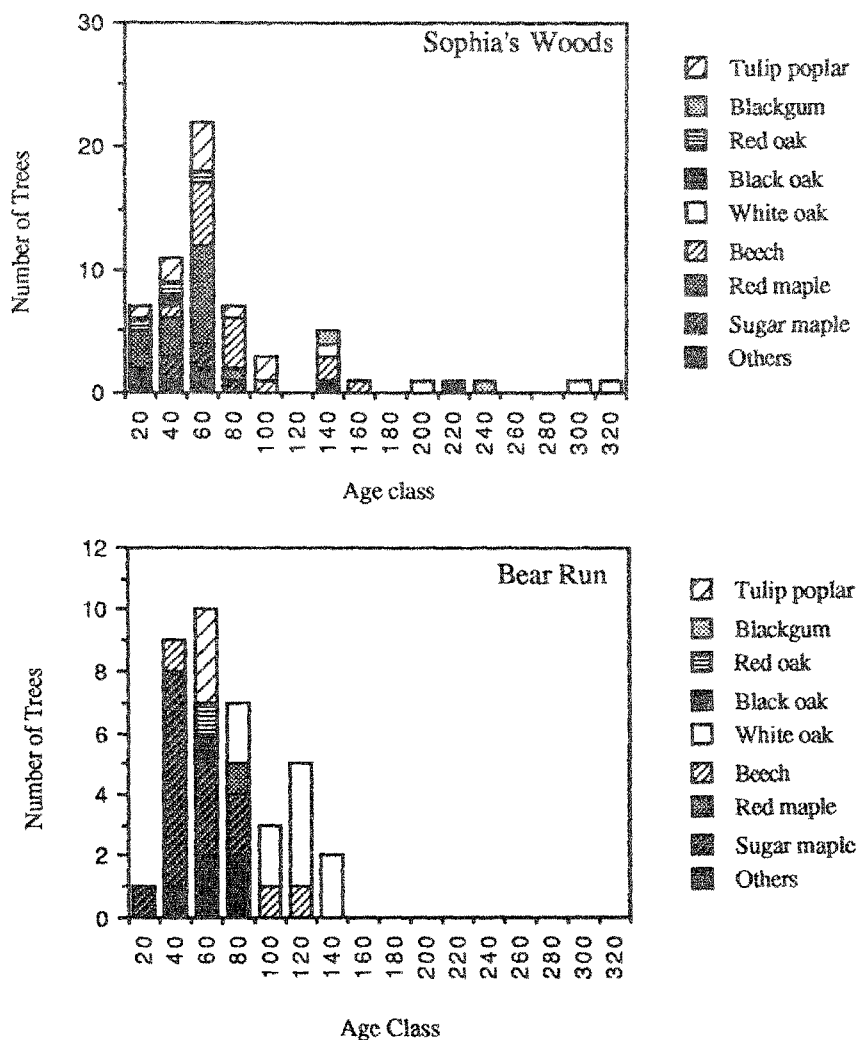


Figure 2. Age distribution of tree species in an old-growth oak forest (Sophia's Woods) and a second-growth oak forest (Bear Run) in southwestern Pennsylvania. Other species include *Betula lenta*, *Prunus serotina*, *Tilia americana*, *Cornus florida* and *Aesculus* spp. in Sophia's Woods and *Prunus serotina*, *Carya* spp. and *Ulmus* spp. in Bear Run.

DISCUSSION

Presettlement forests of southwestern Pennsylvania were dominated by white oak (Braun 1950, Jennings 1927). Beech may have been a codominant with white oak in the original forests (Braun 1950), and at Friendship Hill one beech and two white oak were among five trees present in a 1787 survey of the property corners. The age of beech trees relative to white oak in the original forests is unknown, but they were distinctly younger than the white oaks in Sophia's Woods, despite that beech can live over 300 years. Periodic fire by Native Americans and lightning seems to be responsible, at least in part, for the predominance of oak

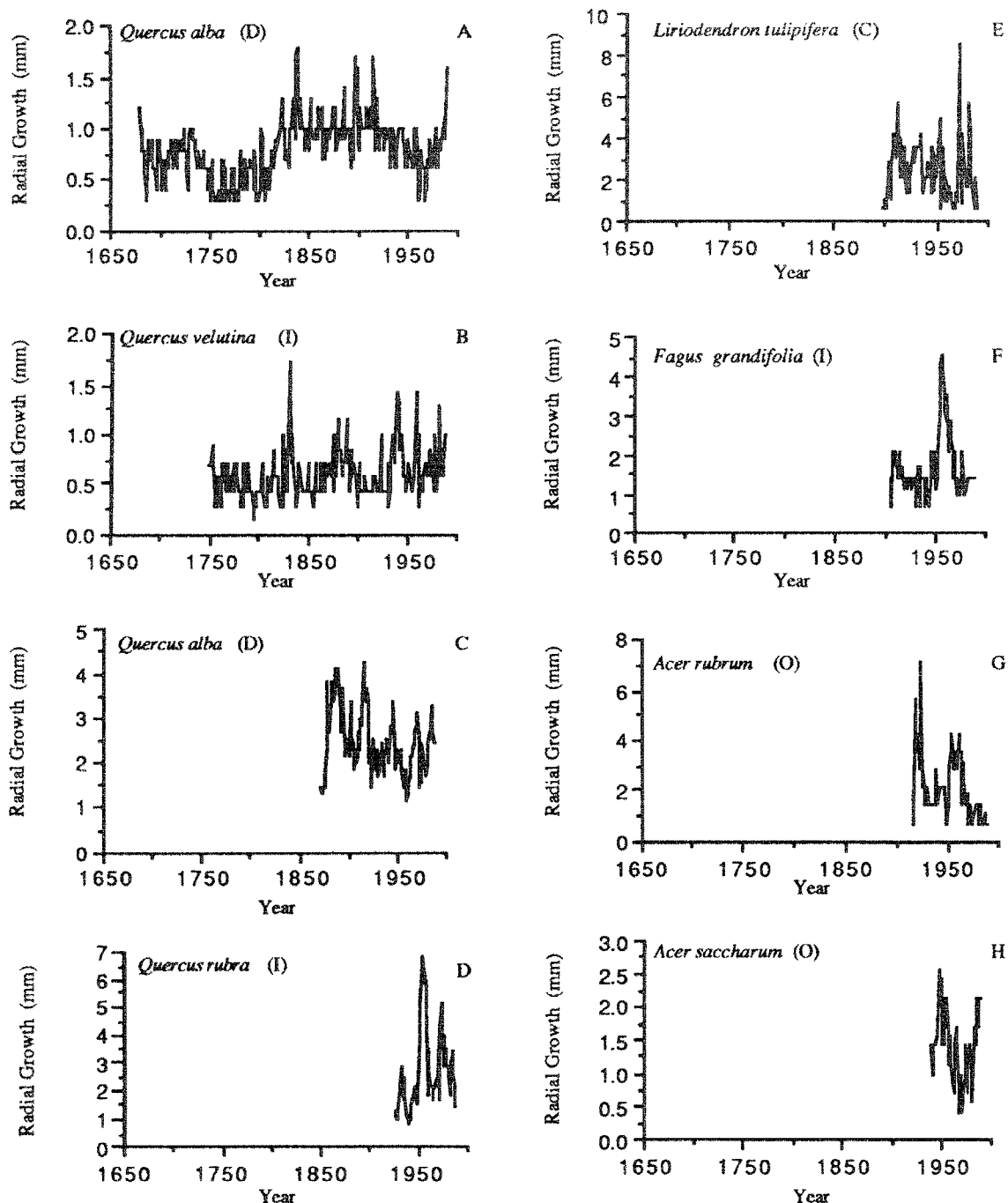


Figure 3. Radial growth of representative trees in an old-growth white oak forest (Sophia's Woods) located in southwestern Pennsylvania. Letters in parentheses indicate canopy class as follows: D = dominant, C = codominant, I = intermediate, O = overtopped (cf. Smith 1986).

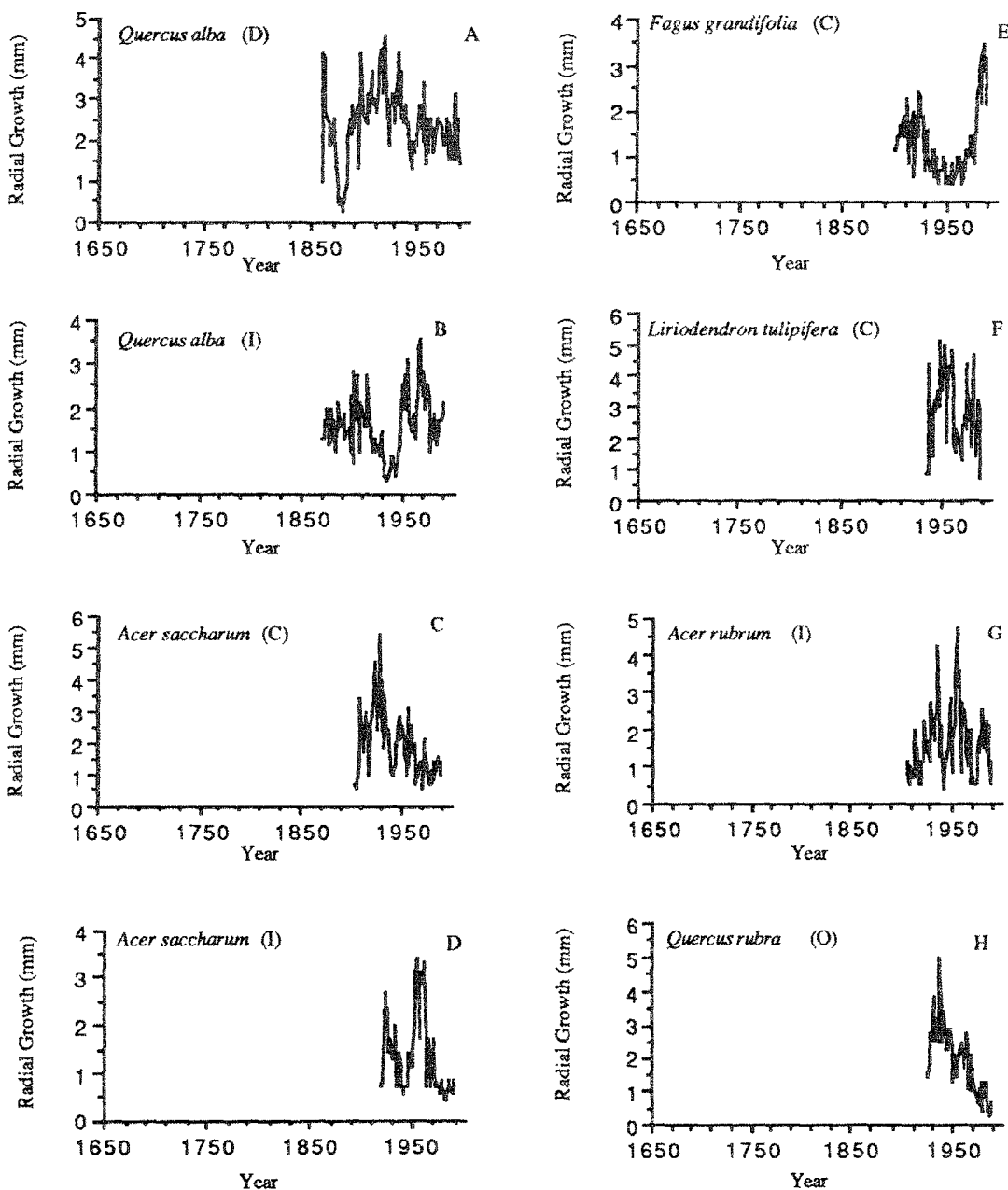


Figure 4. Radial growth of representative trees in a young-mature white oak forest (Bear Run) located in southwestern Pennsylvania. Letters in parentheses indicate canopy class as follows: D = dominant, C = codominant, I = intermediate, O = overtopped (cf. Smith 1986).

in the region prior to European settlement (Buell et al. 1954, Lorimer 1984). Not surprisingly, however, fire scarring on trees was not observed at Sophia's Woods, which has been a country estate for the last 200 years. Sophia's Woods was probably dominated by white oak in the 1600-1700's. Five trees (four oak and one blackgum) in the stand were over 195 years and the two oldest trees were white oak of over 300 years.

All of the older trees surveyed at Sophia's Woods exhibited slow radial growth of approximately 0.60-0.75 mm/yr. The specific reason for slow growth of the oldest white oak is unknown, but may be related to growing up in small gaps of an uneven-aged forest, or to the differential survival of slow growing individuals in an even-aged oak cohort. In contrast, the white oak of Bear Run originated directly after logging and exhibited high growth rates (> 1.5-2.0 mm/yr) probably in response to growing in high light. Likewise, many present-day northeastern, Lake States and Central Plains oak forests have an even-aged cohort of oak that originated either directly after large-scale disturbances, such as logging and fire, or the cessation of prairie fires and exhibited relatively high growth rates (Abrams 1986, Knox 1984, Lorimer 1981, Nowacki et al. 1990, Oliver and Stephens 1977). The younger northern red oaks in Sophia's Woods had much higher radial growth than the older white oaks and black oaks, suggesting that these individuals benefited from greater understory light conditions created by periodic logging or other gap-creating events. Relatively high growth rates with little or no periods of prolonged suppression were also exhibited by younger trees of beech, tulip poplar, red maple and sugar maple at Sophia's Woods, which matched the growth rates of those species at Bear Run. The general scarcity of trees > 195 years and the consistently high growth rates of younger individuals in Sophia's Woods suggest the occurrence of selective logging not reported in the historical record.

Oaks at both study sites were represented almost exclusively in the older age and middle to larger diameter classes, with the slight exception of northern red oak. Northern red oaks were also present in the smaller diameter classes of two virgin hemlock-pine forests in northwestern Pennsylvania (Morey 1936a), and were able to maintain a minor place in the forest canopy by infrequent gap capture in a southern Appalachian hardwood forest (Barden 1981). A scarcity of young oak trees is typical of many forests in eastern North America, and this has been used as evidence for predicting oak replacement by more shade tolerant species (Abrams 1986, Adams and Anderson 1980, Fralish 1988, Host et al. 1987, Lorimer 1984, Nowacki et al. 1990, Parker et al. 1985).

In both Sophia's Woods and Bear Run, beech, tulip poplar, red maple and sugar maple dominated the smaller and middle tree classes. In addition, many beech and tulip poplar and some blackgum, *Tilia americana* (L.) (basswood) and black birch also dominated the upper canopy at Sophia's Woods. This contrasted with the predominance of white oak at Bear Run and suggests that Sophia's Woods is in a later stage of oak replacement. Red maple and sugar maple trees at Sophia's Woods were generally smaller in diameter and height than the other mesophytic hardwoods, but showed every indication of becoming a codominant in the canopy in the near future. Red maple and sugar maple were present as codominants and dominated as understory trees at Bear Run. Thus, a pattern of decreasing oak and increasing sugar and red maple importance was also apparent in this stand. The more advanced status of maples at Bear Run versus Sophia's Woods may be due to the more extensive or complete

logging of that stand. We were somewhat surprised at the higher importance of sugar maple at Bear Run which has soil with lower moisture holding capacity than that at Sophia's Woods. Other studies reported higher red maple than sugar maple in drier oak forests (Host et al. 1987, Nowacki et al. 1990).

A pattern of gradual decreasing oak and increasing tulip poplar, beech and some red maple trees in Sophia's Woods was apparent before the selective logging in the 1930-40's. However, peak recruitment of these species and sugar maple occurred during and shortly after logging. Thus, this stand seems to have experienced accelerated succession of mixed-mesophytic hardwoods following logging (cf. Abrams and Scott 1989, Lorimer 1985). Similarly, gaps created by oak wilt or gypsy moth in eastern and Lake States forests became dominated by sugar maple or red maple (Collins 1961, Menges and Loucks 1984, Tryon et al. 1983). Beech has been reported to grow slowly as saplings beneath overstory conifers or hardwoods and then extend to the canopy following subsequent disturbance (Foster 1988, Spurr 1956). The small number of younger trees (in the 20-year age class) and saplings in both stands may be due to monopolization of resources (e.g. from canopy closure) by older, shade tolerant or gap-specialist trees.

Red maple was a dominant seedling at Sophia's woods and Bear Run, which was consistent with its importance as an understory tree at both sites. Red maple is the dominant seedling in many eastern and Lake States oak forests (Christensen 1977, Host et al. 1987, Lorimer 1984, Nowacki et al. 1990). Beech was poorly represented as seedlings at both sites which contrasts with its reputation of forming a dense seedling layer even in heavily shaded understories (Curtis and Rushmore 1958, Fowells 1965). However, beech seedlings were also scarce in many southeastern Pennsylvania hardwood forests, where reproduction of this species occurs mainly from root suckers (Keever 1973). Regardless, beech was present in most age classes in both stands. Tulip poplar also dominated the overstory but was not surveyed in the seedling layer at either site. Tulip poplar is intolerant of shade, but is a component of old-growth forests because it is an aggressive gap-phase species that often dominates its own gaps, and because trees of this species obtain great size and age (Buckner and McCracken 1978). Northern red oak and white oak were well represented as seedlings at Sophia's Woods, but they were poorly represented at Bear Run. Northern red oak has had some recruitment into the tree size class over the last 80 years in Sophia's Woods whereas white oak has not. Oak recruitment in closed stands may be limited to whether or not a substantial number of oak seedlings are present (Abrams 1986, Nowacki et al. 1990).

Black cherry seedlings dominated at Bear Run and were second in abundance to red maple at Sophia's Woods, despite the presence of only a few black cherry trees in both stands. The adults in Sophia's Woods were only about 20-years-old, which suggests that black cherry invaded the stand relatively recently. Black cherry recruitment in response to canopy gaps has been reported for oak woods in Wisconsin (Auclair and Cottam 1971, McCune and Cottam 1985), and has been observed in mesic white oak stands in central Pennsylvania (Nowacki and Abrams, unpublished data). We anticipate a gradual increase of black cherry into the canopy of Sophia's Woods and Bear Run.

In conclusion, Sophia's Woods is a remnant white oak forest in a late stage of oak replacement. Presettlement white oak forests in the region were probably maintained by periodic fire. Younger mixed-oak forests in the region are most likely a direct response to wide-spread cutting and subsequent fire in the mid-to late-1800's (Powell and Considine 1982). Sophia's Woods has been a part of a country estate since the late 1700's, during which time fire frequency was most likely reduced and a succession from white oak to mixed-mesophytic species has occurred. No white oaks under 130-years-old were surveyed, whereas numerous beech, tulip poplar, red maple, and sugar maple trees less than 120 years-old were present. A succession toward these mixed-mesophytic species was also apparent at Bear Run, but because of the relatively young stand age white oak still dominated. Replacement of oaks on undisturbed sites is relatively slow due to their longevity, but the results of this and previous studies of second growth oak forests indicate the inevitability of this process in many eastern forests.

LITERATURE CITED

- Abrams, M. D. 1986. Historical development of gallery forests in northeast Kansas. *Vegetatio* 65:29-37.
- Abrams, M. D., and M. L. Scott. 1989. Disturbance-mediated accelerated succession in two Michigan forest types. *For. Sci.* 35:42-49.
- Auclair, A. N., and G. Cottam. 1971. Dynamics of black cherry (*Prunus serotina* Ehrh.) in southern Wisconsin oak forests. *Ecol. Monog.* 41:153-177.
- Adams, D. E., and R. C. Anderson. 1980. Species response to a moisture gradient in central Illinois forests. *Am. J. Bot.* 67:381-392.
- Barden, L. S. 1981. Forests development in canopy gaps of a diverse hardwood forest of the southern Appalachian Mountains. *Oikos* 37:205-209.
- Braun, E. L. 1950. *Deciduous forests of eastern North America*. MacMillan Pub. Co., New York, 596 p.
- Bromley, S. W. 1935. The original forest types of southern New England. *Ecol Monog.* 5:61-89.
- Buckner, E., and W. McCracken. 1978. Yellow-poplar: A component of climax forests? *J. For.* 76:421-423.
- Buell, M. F., and H. F. Buell, and J. A. Small. 1954. Fire in the history of Mettler's Woods. *Bull. Torrey Bot. Club.* 81:253-255.

- Christensen, N. L. 1977. Changes in structure, pattern, and diversity associated with climax forest maturation in Piedmont, North Carolina. *Am. Midl. Nat.* 97:176-188.
- Clements, F. E. 1936. Nature and Structure of the climax. *J. Ecol.* 4:252-284.
- Collins, S. 1961. Benefits to understory from canopy defoliation by gypsy moth larvae. *Ecology* 42:835-838.
- Collins, B. S., and S. T. A. Pickett. 1982. Vegetation composition and relation to environment in an Allegheny hardwoods forest. *Am. Midl. Nat.* 108:117-123.
- Cottam, G., and J. T. Curtis. 1956. The use of distance measures in phytosociological sampling. *Ecology* 37:451-460.
- Crow, T. R. 1988. Reproductive mode and mechanism for self replacement of northern red oak (Quercus rubra) -A review. *For. Sci.* 34:19-40.
- Curtis, R. O., and F. M. Rushmore. 1958. Some effects of stand density and deer browsing on reproduction in an Adirondack hardwood stand. *J. For.* 56:116-121.
- Foster, D. R. 1988. Disturbance history, community organization and vegetation dynamics of the old-growth Pisgah Forest, south-western New Hampshire, U. S. A. *J. Ecol.* 76:105-134.
- Fowells, H. A. (ed.) 1965. Silvics of forest trees of the U.S. U.S. Dept. of Agric., Agric. handb. 271, Washington, DC, 762 p.
- Fralish, J. S. 1988. Predicting potential stand composition from site characteristics in the Shawnee hills Forest of Illinois. *Am. Midl. Nat.* 120:79-101.
- Host, G. E., K. S. Pregitzer, D. W. Ramm, J. B. Hart, and D. T. Cleland. 1987. Landform-mediated differences in successional pathways among upland forest ecosystems in northwestern Lower Michigan. *For. Sci.* 33:445-457.
- Husch, B. 1965. The regeneration of Prunus serotina in northwestern Pennsylvania following cutting. *Ecology* 35:11-17.
- Jenning, O. E. 1927. Classification of the plant societies of central and western Pennsylvania. *Proc. Penn. Acad. Sci.* 1:23-55.
- Keever, C. 1973. Distribution of major forest species in southwestern Pennsylvania. *Ecol. Monog.* 43:303-327.
- Knox, R. G. 1984. Age structure of forests on Soldiers Delight, a Maryland serpentine area. *Bull. Torrey Bot. club* 111:498-501.

- Kopas, F. A. 1973. Fayette County Soil Survey. U.S. Dept. of Agriculture Soil Conservation Service, 200 p.
- Loeb, R. E. 1987. Pre-European settlement forest composition in eastern New Jersey and southeastern New York. *Am. Midl. Nat.* 118:414-423.
- Lorimer, C. G. 1981. Survival and growth of understory trees in oak forests of the Hudson Highlands, New York. *Can. J. For. Res.* 11:689-695.
- Lorimer, C. G. 1984. Development of the red maple understory in northeastern oak forests. *For. Sci.* 30:3-22.
- Lorimer, C. G. 1985. The role of fire in the perpetuation of oak forests. In Proceedings, Challenges in oak management and utilization, J. E. Johnson (ed.). Coop. Extension Service, University of Wisconsin, Madison, WI, p. 8-25.
- Lorimer, C. G., L. E. Frelich, and E. V. Nordheim. 1988. Estimating gap origin probabilities for canopy trees. *Ecology* 69:778-785.
- Lutz, H. J. 1928. Trends and silvicultural significance of upland forest succession in southern New England. Yale University School of Forestry and Environmental Studies, Bulletin 22, 68 p.
- McCune, B., and G. Cottam. 1985. The successional status of a southern Wisconsin oak woods. *Ecology* 66:1270-1278.
- Menges, E. S., and O. L. Loucks. 1984. Modeling a disease-caused patch disturbance: Oak wilt in the midwestern United States. *Ecology* 65:487-498.
- Morey, H.F. 1936a. A comparison of two virgin forests in northwestern Pennsylvania. *Ecology* 17:43-55.
- Morey, H. F. 1936b. Age-size relationships of Hearts Content, a virgin forest in northwestern Pennsylvania. *Ecology* 17:251-257.
- Nigh, T. A., S. G. Pallardy, and H. E. Garrett. 1985. Sugar maple-environment relationships in River Hills and central Ozark Mountains of Missouri. *Am. Midl. Nat.* 114:235-251.
- Nowacki, G. J., M. D. Abrams, and C. G. Lorimer. 1990. Composition, structure and historical development of northern red oak stands along an edaphic gradient in north-central Wisconsin. *For. Sci.* 36: 276-292.
- Oliver, C. D., and E. P. Stephens. 1977. Reconstruction of a mixed-species forest in central New England. *Ecology* 58:562-572.

- Parker, G. R., D. J. Leopold, and J. K. Eichenberger. 1985. Tree dynamics in an old-growth, deciduous forest. *For. Ecol. Manage.* 11:31-57.
- Powell, D. S., and T. J. Considine. 1982. An analysis of Pennsylvania's forest resources. USDA For. Serv. Resour. Bull. NE-69, 97 p.
- Russell, E. W. B. 1980. Vegetational change in northern New Jersey from precolonization to the present: a palynological interpretation. *Bull. Torrey Bot. Club* 107:432-446.
- Secor, R. 1975. Pennsylvania 1776. Pennsylvania State University Press, University park, PA, 300 p.
- Smith, D. M. 1986. The practice of silviculture. John Wiley and Sons. New York 32:544-549.
- Spurr, S. H. 1951. George Washington, surveyor and ecological observer. *Ecology* 32:544-549.
- Spurr, S. H. 1956. Natural restocking of forests following the 1938 hurricane in central New England. *Ecology* 37:443-451.
- Tryon, E. H., J. P. Martin, and W. L. MacDonald. 1983. Natural regeneration in oak wilt centers. *For. Ecol. Manage.* 7:149-155.
- Whitney, G. G. 1987. An ecological history of the Great Lakes forest of Michigan. *J. Ecol.* 75:667-684.