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THE HISTORY AND STATUS OF THE HEMLOCK–HARDWOOD FORESTS OF THE ALLEGHENY PLATEAU

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SUMMARY

(1) The post-settlement history of the mixed conifer–hardwood forests of a small area of the Allegheny High Plateau region of Pennsylvania (The Allegheny National Forest) was analysed using published and manuscript sources.

(2) Before settlement, *Fagus grandifolia* (beech) and *Tsuga canadensis* (hemlock) dominated the moister segments of the Plateau. Outliers of the more southern Appalachian oak forest occupied the more xerophytic sites, e.g. upper slopes, stonier soils, and soils with a fragipan.

(3) The disturbance regime of the pre-settlement period, creating small canopy gaps, favoured the ascendancy of the slower growing shade-tolerant beech and hemlock in the understorey and eventually the overstorey.

(4) From 1880 to 1930 the forests of the High Plateau were intensively felled for lumber, tanning material and chemical wood. Since 1930, the forest has suffered from severe overbrowsing by the white-tailed deer. Rapidly growing, shade-intolerant sprouting species, e.g. *Prunus serotina* (black cherry) and *Acer rubrum* (red maple), have been the major beneficiaries of the human-mediated disturbance regime.

INTRODUCTION

Because of its altitude and its rugged topography, the northern portion of the Allegheny Plateau was one of the last areas settled in the north-eastern United States. Early reports suggest that vast forests of *Pinus strobus* (white pine) and *Tsuga canadensis* (hemlock) once blanketed the higher parts of the Plateau in northern Pennsylvania (Sargent 1884). As late as 1890 north-western Pennsylvania still contained the largest remaining body of hemlock timber in the world (Defebaugh 1907). Forty years later the magnificent groves of hemlock and pine were gone. Many authors believed that the area had been reduced to a wasteland (Rothrock 1915; Pinchot 1923). Huge piles of brush and slash alternated with blackened, burnt-over areas, giving rise to the appellation 'the Allegheny brush heap' (Stotz 1973). Some of the above-noted alterations may have been attributed to exaggeration on the part of America's early conservationists. They compared the desolate, cut-over woodlands of the lumberman with an imaginary vision of the stable, productive 'forest primeval' (Raup 1967).

Unfortunately, it is rarely possible to assess the impact of European settlement on North American forests. Records of primary or pre-settlement forests east of the North-west Territory (the site of the first methodical federal land surveys) are poor. Direct comparisons have also been frustrated by the limited amount of quantitative information on the present-day forests. The present study represents an attempt to document the species composition, the environmental deteminants, the areal extent and the disturbance regime of the pre-settlement and post-settlement forests of a part of the unglaciated Allegheny Plateau: the 300 000-ha Allegheny National Forest (ANF).

STUDY SITE

Located in the Allegheny High Plateau section (41°45′N, 79°00′W) of the Appalachian Plateau Province, the ANF is dominated by a series of broad flat-topped ridges separated by deep (120–240 m) V-shaped valleys (Lobeck 1927). The relatively high altitude of the plateau (500–700 m a.s.l.) deflected the Wisconsin Laurentide ice sheet toward lower basins to the east and west (Aguilar & Arnold 1985). Soils in the region reflect the nature of the underlying bedrock. Most are relatively acidic, infertile, moderately fine to moderately coarse-textured soils derived from Mississippian and Pennsylvanian-aged sandstones and shales. Dominant soils in the area include the Hazelton (a typic dystrochrept) and the Cookport (an aquic fragiudult) series formed *in situ* in conglomerates and sandstones and the Gilpin (a typic hapludult) and the Cavode (an aeric ochraquult) series derived from shales (Cronce & Ciolkosz 1983; Cerutti 1985). Proximity to the glacial border also left its mark upon the region's landforms and soils. Large quantities of outwash sands and gravels filled the major drainage channels directly to the south of the ice margin (Lobeck 1927) while intense periglacial activity produced colluvial (solifluction) deposits and boulder fields on lower footslope positions (Aguilar & Arnold 1985).

The climate of the Allegheny High Plateau is cool and humid. Although the altitude is moderate, the region does have somewhat cooler summers (an average of 18·9 °C), less sunshine and more precipitation (1067 mm year^{-1}) than the lowlands to the west (Mason 1936). The growing season (frost-free period) is 100–130 days. Snowfall is generally more than 1500 mm year^{-1} (Bjorkbom & Larson 1977). The orographic lifting of air as it reaches the Plateau probably accounts for the higher precipitation of the region (Shane 1987).

The ANF lies within Braun's (1950) hemlock–white-pine–northern-hardwood (*Tsuga–Pinus–Acer–Betula–Fagus*) region. Küchler (1964) placed most of the High Plateau region in the hemlock–northern-hardwood forest type. Küchler's (1964) map of the potential natural vegetation of the U.S. also shows extensions of the more southern Appalachian oak (*Quercus*) forests penetrating the major river valleys of the area.

NATURE OF THE PRE-SETTLEMENT FOREST

Sources of data

Some investigators (Curtis 1959; Barber 1976) have commented on the importance of the early land-survey records in reconstructing North American pre-settlement forests. Much of the ANF was included in Samuel Dale's 1814–15 survey of approximately 70 000 ha of land for the Lancaster Land Company. Dale's survey was unique in several respects. The survey was completed well before settlement. As late as 1832, the area south-east of the Allegheny River was still "little known . . . scarce explored, and . . . supposed uninhabitable" (Gordon 1832). In many cases, the detail of Dale's survey notes rivals that of the more systematic federal land surveys to the west. The Lancaster Land Company's holdings were subdivided into rectangular tracts or lots of 165 acres (67 ha) and 225 acres (91 ha) (Schenck 1887). Dale ran and marked the north–south and east–west boundaries of each lot, carving the number of every tract on a tree at one of its corners. His field notes contain a wealth of information on the dominant tree species and the disturbances encountered along each of the survey lines. Dale was noted for both the accuracy and the reliability of his surveys (Eaton 1890). One can easily trace his descriptions of the survey lines, e.g. ascending hill, crossing stream, etc., on the same tract or warrant lines which have been overprinted on the U.S. Geological Survey (USGS) 7·5-minute series (7·5′ latitude × 7·5′ longitude) topographic maps for Forest Service use.

Copies of Dale's survey notes were obtained at the ANF surveyor's office in Warren, Pennsylvania. They were supplemented by examining connected drafts (drawings showing the location of the lots) of the early (1793–1819) surveys and warrants of most of the rest of the ANF. The drafts were stored at the ANF surveyor's office and the Warren County Historical Society in Warren, and the Land Records section of the Pennsylvania State Archives in Harrisburg, Pennsylvania.

Tree species abundances and community types

Counts of trees marked at the corner of the lots provide an estimate of the abundance of the various tree species in the pre-settlement forest (Table 1). This table also gives authorities for all tree species', following Fernald (1970). Although the use of witness or corner trees has certain limitations (note Lutz 1930 and Bourdo 1956), most investigators (Curtis 1959; Siccama 1971; Lorimer 1977) believe that the trees satisfactorily reflect the pre-settlement vegetation of the north-east. Lutz (1930) was the first to use the Dale survey data. The results are unsatisfactory as the species' abundance values were based on counts of references to the dominant species encountered along the survey lines (really a frequency value) as well as counts of the marked corner trees.

TABLE 1. Percentage composition of pre- and post-settlement forests of the Allegheny National Forest. Early survey data are based on counts of witness trees. 1973 data are from the U.S. Forest Service timber inventory of ANF based on 149 permanent plots. The number of stems in the 1973 inventory is an estimate of the total number of stems > 13 cm dbh on ANF.

Common name	Scientific name	1793–1819	1973
Ash	*Fraxinus* spp.*	0·8%	2·1%
Aspen	*Populus* spp.†	0·1	4·9
Beech	*Fagus grandifolia* Ehrh.	43·4	6·0
Birch	*Betula* spp.‡	6·3	8·5
Black cherry	*Prunus serotina* Ehrh.	0·8	22·6
Chestnut	*Castanea dentata* (Marsh.) Borkh.	2·8	—
Hemlock	*Tsuga canadensis* (L.) Carr	19·9	5·8
Hickory	*Carya* spp.§	0·9	0·1
Linn	*Tilia americana* L.	0·4	0·7
Red maple	*Acer rubrum* L.	4·7	27·3
Black and scarlet oak	*Quercus velutina* Lam. and *Q. coccinea* Muenchh.	0·6	0·7
Chestnut oak	*Quercus prinus* L.	0·4	0·2
Red oak	*Quercus rubra* L.	0·6	2·3
White oak	*Quercus alba* L.	4·1	2·0
Poplar	*Liriodendron tulipifera* L.	0·2	0·3
Sugar maple	*Acer saccharum* Marsh.	5·3	13·3
White pine	*Pinus strobus* L.	3·1	0·4
Miscellaneous spp.¶		5·4	2·8
Total number of stems		1244	$9{\cdot}64 \times 10^7$

* Spp. indicates species not separated in Dale survey: *Fraxinus americana* L., *F. pennsylvanica* Marsh. and *F. nigra* Marsh. occur in area today.

† Includes *Populus tremuloides* Michx. and *P. grandidentata* Michx.

‡ 6·1% black birch (*B. lenta* L.) and 2·4% yellow birch (*B. lutea* Michx.f.) in 1973 survey.

§ *Carya cordiformis* (Wang.) Koch, *C. ovata* (P. Mill.) K. Koch, *C. glabra* (P. Mill.), and *C. ovalis* (Wang.) Sarg. noted in area today.

¶ Other spp. includes cucumber tree (*Magnolia acuminata* L.), mountain laurel (*Kalmia latifolia* L.), sassafras (*Sassafras albidum* (Nutt.) Nees) and ironwood (*Ostrya virginiana* (Mill.) K. Koch).

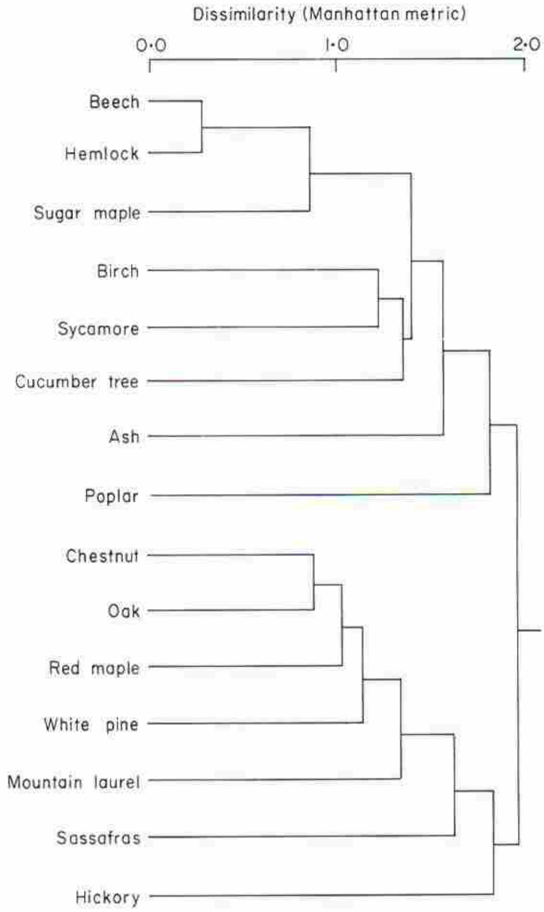

FIG. 1. Dendrogram showing similarity of occurrence of various tree species in the Allegheny National Forest, derived from Dale's survey line descriptions. Species clustered by means of median fusion strategy as applied to Orloci's (1974) derivatative of Manhattan metric. Dissimilarity or distance values range from 0·0 (species occur at same sites) to 2·0 (species show no overlap).

The overwhelming abundance of beech and hemlock (> 60% of all the corner trees) is a particularly noteworthy feature of the pre-settlement period. Although the ANF falls within Küchler's hemlock–northern-hardwood (*Acer–Betula–Fagus*) region, two species—beech and hemlock—dominated the overstorey.

Abundance data provide very little information on the species assemblages of the pre-settlement period. Species associations or co-occurrences were explored by treating each of the survey-line descriptions as a stand. Species dissimilarity values were calculated using the presence/absence equivalent of the Manhattan metric (Orloci 1974). The metric was standardized by the species' totals to give more weight to the rarer species (Greig-Smith 1983, p. 195). The resulting dissimilarity matrix was then converted to a dendrogram utilizing a median fusion strategy (Greig-Smith 1983).

Two distinct clusters of species are evident in the dendrogram based on the species associations noted in survey line data (Fig. 1). Chestnut, oak, red maple, white pine,

TABLE 2. Standardized residuals expressing the degree of association between common species and the various site factor categories (Haberman 1973). The magnitude of the value indicates the species preference (+) or avoidance (−) of that parent material or topography category.

	Acer rubrum	*Acer saccharum*	*Betula* spp.	*Fagus grandifolia*	*Quercus* spp.	*Tsuga canadensis*
Parent material						
Very stony sandstone	1·26	−1·77	−2·02	0·63	1·21	−0·68
Sandstone	1·05	2·16	−1·28	0·30	−1·21	−0·33
Sandstone and shale with fragipan	0·05	1·21	−0·25	1·01	1·46	−1·07
Shale	0·17	1·14	−0·86	−2·01	0·90	0·04
Colluvium with fragipan	−1·77	−0·71	3·18	0·46	−3·32	2·30
Alluvium	−0·89	−1·65	1·86	−0·80	0·13	−0·49
G value	5·95	13·43*	15·51†	5·20	17·78†	5·60
Topography						
Slopes >8%						
Nose (topographic contours convex outward)	0·90	−0·20	−1·48	−0·95	1·10	1·04
Upper side slope	2·52	−1·21	−0·91	−0·24	1·94	−1·25
Lower side slope	−2·89	−0·70	0·84	−0·63	−2·07	2·74
Hollow (contours concave outward)	1·53	0·13	0·79	0·59	−1·99	0·54
Slopes 0–8%						
Plateau top	−1·31	3·05	−0·80	1·96	0·92	−1·40
Terraces and flood plains	−0·99	−2·17	2·39	−1·79	−0·33	0·99
G value	19·24†	16·04†	8·79	7·37	12·72*	10·64

* $P<0·05$; † $P<0·01$.

mountain laurel, sassafras and hickory occur together at one end of a distribution which seems to reflect the moisture gradient. During the pre-settlement period, they represented a somewhat attenuated version of the dry Appalachian oak and chestnut forests to the south. White pine, red maple and extensive areas of ridges forested with mountain laurel were commonly associated with the mixed oak–chestnut type. The second major subdivision of the dendrogram—the hemlock–northern-hardwood type—includes a number of species characteristic of moister sites. Variants of the hemlock–northern-hardwood type included the beech–hemlock community (the most frequently cited type) as well as the beech–sugar-maple community. Moist bottomlands, footslopes and creeks frequently included an admixture of yellow birch, sycamore and ash.

Environmental determinants

The relationship between species distribution and site factors was established by standard contingency table analysis procedures (Strahler 1978). Each corner point was located on 7·5-minute series USGS topographic map and the U.S. Department of Agriculture Soil Conservation Services (USDA SCS) soil map (Cerutti 1985; Churchill 1987; SCS unpublished soil maps for Elk County) and scored for the appropriate site factor category (see Table 2) and the presence and absence of a given species. The presence and absence values of each species summed over the categories (C) for each site factor yielded a $2 \times C$ compartment contingency table. A significant G statistic implied that the species occurrence was related to the factor. The cell frequencies of tables possessing a significant G statistic were then converted to standardized residuals (Haberman 1973) to express the degree of association of the species with each of the site factor categories, i.e. nose, upper side slope, etc. (Whitney 1982). A high positive residual value indicated that the species was more common on that parent material or topography category than might have been expected by chance and similarly a high negative residual indicates that it is less common. Species occurring at less than fifty sites were automatically excluded from further consideration in order to minimize errors associated with small sample sizes (Sokal & Rohlf 1981).

Perhaps the most surprising finding of the species–site relationship study was the ubiquitous occurrence of beech and hemlock. Both spanned the entire range of topography and parent material conditions (note lack of significance in Table 2). Neither was as common or as widespread off the High Plateau. Immediately to the west, for instance, beech was largely confined to the finer-textured tills of the glaciated Allegheny Plateau (Whitney 1982). Hemlock represented less than 1% of the marked corner trees in Crawford County, the county directly to the west of the High Plateau, and here it was limited to the cooler ravines and the edges of swamps (G. Whitney, unpublished data). The cooler and the more humid conditions of the higher elevations have long favoured the widespread persistence of moisture-demanding species like hemlock on the High Plateau (Hough & Forbes 1943; Shane 1987).

Sugar maple and, by implication, the beech–sugar-maple type was strongly associated with the better-drained, coarser-textured, sandstone-derived soils of the flat top of the Plateau (Table 2). Birch (probably primarily yellow birch) occupied the moister colluvial soils of the footslopes with their frangipans and their seasonally perched water-tables (Table 2; Aguilar & Arnold 1985). The preference of oak for upper slope positions may have been due to its relativity xerophytic nature or to its susceptibility to late spring frosts on the lower slopes and the narrower valleys (Perry 1920). The xerophytic oaks also exhibited a preference for stonier soils and soils with an impermeable fragipan. Soils with fragipans tend to be the driest of sites during periods of low summer rainfall (Ward, Berglund & Borden 1966), while stones would have limited the rooting volume and the moisture storage capacity of the soil. Goodlett (1954) also noted that the oak type was confined to the stonier soils of the upper slopes of neighbouring Potter County.

Disturbance regime

Twenty-three of the 1625 survey line descriptions in Dale's field notes contain references to 'windfalls' or 'fallen timber'. As the great majority of the survey lines were roughly equivalent in length (anywhere from 160–220 perches or 800–1100 m long), the maximum percentage of the survey area affected by windfalls was probably less than 1·5% (23 out of 1625 lines).

Assuming that most of the windfalls were still visible fifteen to thirty years after the disturbance (Canham & Loucks 1984; Whitney 1986), the average percentage of the area affected annually was 0·05%–0·10%. Dividing 100 by the average percentage area affected annually yielded a 'return time' or a rotation period of 1000–2000 years. The return time represents the time it takes to disturb an area equal to the size of the region under consideration (Canham & Loucks 1984). Violent windstorms definitely occurred in the area, although their overall impact was relatively low.

References to burns or fires in the field notes were non-existent. Crown fires were probably very rare in the moist hemlock–hardwood forests of the Plateau (Hough 1936; Emerson 1937). There were, however, eleven references to brushy oak (a scrub of regenerating oak) and chestnut ridges in close proximity to the Allegheny River. Several of the brushy ridges occurred in an area that had been hit by a major windstorm in 1795 and had then burned several years later. The area regenerated to a growth of small, scrubby oaks (Schenck 1887). Fire would have stimulated the sprouting of the oaks and the chestnuts, creating a rather brushy appearance. Many of the fires may have been started by the Seneca Indians whose villages were concentrated along the fertile flats of the Allegheny River (Deardorff 1946). Marquis (1975) has even attributed the existence of the fire-resistant oak type along the Allegheny River to Indian-set fires. Cornplanter, a well-known Seneca chief, stated that the Senecas frequently burned the woods to destroy the rattlesnakes which were prevalent along the Allegheny River (Tome 1928).

POST-SETTLEMENT HISTORY

White pine era: 1797–1880

Farming on the High Allegheny Plateau has always been handicapped by a short growing season and rugged terrain (Mason 1936). Lumbering consequently assumed a very important role in the economic development of the region at a very early data. The earliest period of lumbering, the selective or partial cutting era from 1797 to 1880, concentrated on extracting the high-value species from the more accessible sites. The durable, easily worked, lightweight, and thus floatable, white pine was the preferred timber species. The upper reaches of the Allegheny River produced some of the finest 'cork pine' (trees 1–1·5 m in diameter fit for the masts of ships (Cramer 1811; Jennings 1936)) in the U.S.A. The Allegheny River's strategic location—the eastern-most tributary of the Mississippi River within the hemlock–white-pine–northern-hardwood region—ensured its prominence in the early phases of the westward-moving white-pine lumber industry (Kussart 1938). Extensive stands of white pine, termed 'pineries' by the early surveyors, were associated with the coarse-textured outwash terraces of the Allegheny River and its tributary creeks—the Conewango, the Tionesta, the Brokenstraw and the Kinzua (Gordon 1937, 1940; Kussart 1938). By 1831 more than 20 000 000 board feet (*c.* 46 000 m^2) of pine lumber was annually being rafted downriver to Pittsburgh, Cincinnati and other points to the south (Hazard 1831). Most of the pine sent down the Allegheny was from the west side of the river or from New York State (Casler 1973). Scattered pine, an occasional hemlock or a black cherry and small (<10 ha) even-aged patches of white pine, originating after windstorms or fires (Hough & Forbes 1943), formed the bulk of the timber harvested on the Plateau proper. Near the mills, a limited number of the heavier, more valuable hardwoods, e.g. red oak and white ash (*Fraxinus americana*) were also cut (Marquis 1983).

Hemlock and chemical wood era: 1880–1930

Most of the forests on the Plateau remained intact until about 1880 (Marquis 1975). After 1880 both the scale and the intensity of the logging expanded dramatically. A number of technological innovations, e.g. the use of band saws and the development of locomotives designed specifically for railroad logging, made large-scale commercial logging operations feasible. The late nineteenth century ushered in what was probably the most intense period of logging and forest utilization that the temperate world has ever seen (Marquis 1975).

Tanning was a major commercial enterprise of the late nineteenth century in the U.S.A. Leather belting ran the nation's factories while sole leather and harness leather kept the nation's cities and farms running (Hergert 1983). The high tannin content of its bark made

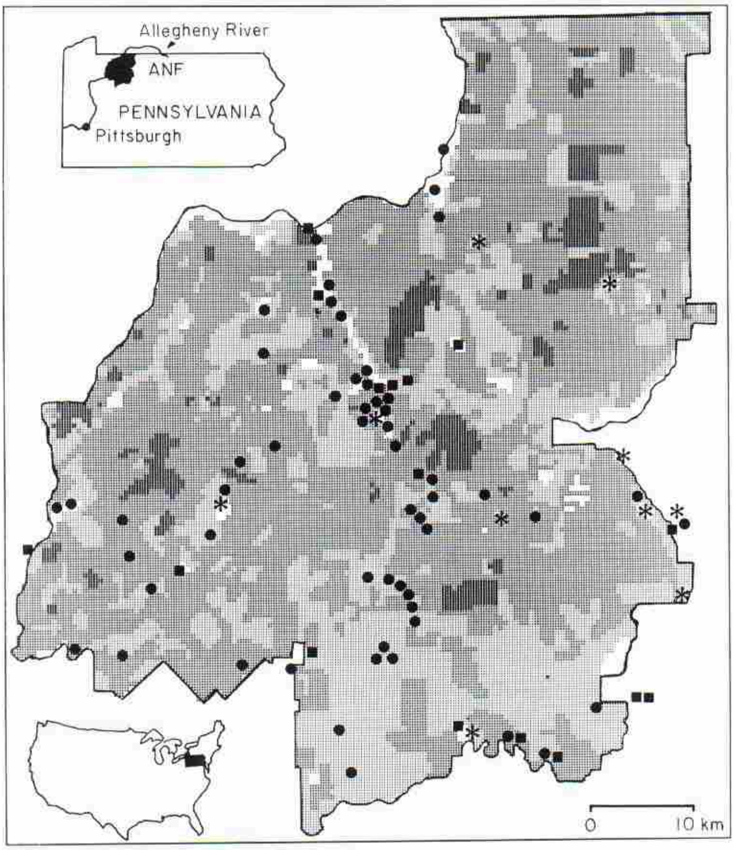

FIG. 2. Map of Allegheny National Forest showing 1936 cover types and location of many early sawmills, tanneries and chemical plants. Shading increases from lightest to darkest as follows: unforested areas, regenerating cover (0–20 years), maturing cover (20–80 years), and old-growth cover (≥80 years). Symbols for industries are as follows: (●) sawmill; (■) tannery; (*) chemical plant. Location of industries based on information in Casler (1973, 1976, 1977), Taber (1974) and Marquis (1988).

hemlock the basic ingredient or raw material of the tanning industry. The prevalence of hemlock on the High Plateau attracted the attention of the commercial leather industry in the mid-nineteenth centry. The large amount of bark required in the tanning process—generally six times the weight of the dry hides (Randall 1968)—made it economical to locate the tanning plants in the woods. By 1880 northern Pennsylvania contained the largest concentration of tanneries in the world (Fig. 2). After 1893 it was the heart of the giant U.S. Leather Company, one of the ten largest companies in the U.S. (Casler 1973). Large tanning firms, like Horton Crary & Company at Sheffield, Pennsylvania, processed up to 600 000 hides annually, consuming upwards of 50 000 cords of hemlock bark in the process (Casler 1973). The cord is a volumetric measure which in this case represents a pile of bark 8′ long by 4′ high by 4′ wide (*c*. 3·6 m^3). Given an average yield of ten cords of bark and 20 000 board feet (*c*. 46 m^2) of logs per acre (0·405 ha) (Walsh 1896), this translated into an annual cut of 5000 acres or 20·2 km^2. It is not surprising that many firms acquired large tracts of land such as the 125 000 acres (*c*. 500 km^2) owned by Horton Crary & Company (Casler 1973).

Initially lumbermen rejected the weak, splintery, coarse-grained wood of hemlock. By the late nineteenth century, however, hemlock represented a cheap alternative to the increasingly scarce, high-priced white pine. By 1899, it formed more than two-thirds of the lumber production of the state of Pennsylvania (Clepper 1934). The U.S. Leather Company even formed a subsidiary company, the Central Pennsylvania Lumber Company, to process the hemlock timber associated with its bark-peeling operations (Casler 1973).

The hemlock bark and saw-log industries complemented each other. Together they financed the construction of the High Plateau's costly logging railroad network. The railroads in turn opened up the more inaccessible regions of the Plateau to logging and encouraged the development of a number of subsidiary industries (Fig. 2). Slabs and edging from the hemlock mills were converted into kindling wood and lath (Casler 1973) while butts and defective hemlocks went into shingles (Defebaugh 1907). Logging railroads also permitted the extraction of the heavier hardwoods at greater distances from the mills. They stimulated the expansion of the hardwood furniture, stave and tool industries (Casler 1976).

The final phase of the harvest operation took most of the remaining hardwoods—those that were either too small or too defective for saw-logs. Before the rise of the petrochemical industry in the 1920s, all important organic chemicals were derived from wood (Baker 1983). Heavy resin-free species like sugar maple and beech made the best chemical wood (Brown 1917). Heated at high temperatures in a retort or an oven, they yielded charcoal, wood alcohol (methanol) and acetate of lime (calcium acetate)—the basic products of the hardwood distillation industry (Brown 1917). An established railroad network, an abundance of hardwoods and a copious supply of fuel in the form of coal and natural gas soon made northern Pennsylvania the centre of the chemical wood industry (Hale 1906; Taber 1975; Casler 1976). Pennsylvania accounted for over 60% of the value of all the products of the wood distillation industry in 1900 (Munroe & Michatard 1902).

Chemical wood plants used enormous quantities of cordwood. The average plant in Pennsylvania in 1922 utilized 10 000 cords of wood a year (Anon. 1923). Trees of all species and sizes were cut, down to a 2–3-inch (5–8-cm) diameter limit (Marquis 1981a). When the plants completed their cutting of the culled old-growth stands, they turned to cutting the resulting 20–40-year-old, even-aged, second-growth stands (Ostrom 1938; Marquis 1981a).

National Forest era: 1923–present

The Weeks Act of 1911 authorized the federal purchase of forest land on the headwaters of navigable rivers with the ostensible purpose of regulating the flow of water (Dana & Fairfax 1980). Concerns about floods downriver in Pittsburgh led to the establishment of the ANF on the upper reaches of the Allegheny River in 1923 (Conarro 1973). Having cut out most of the marketable wood, the larger lumber and chemical wood firms of the area, e.g. the Central Pennsylvania Lumber Company, Wheeler & Dusenberry Lumber Company, T. D. Collins Lumber Company, the McKean Chemical Company and the Day Chemical Company, were more than willing to sell their holdings.

Much of the early research of the U.S. Forest Service in the ANF was devoted to timber stand improvement and studies of the two remaining virgin forests of the area—the 50-ha Heart's Content tract and the 1600-ha Tionesta Natural area (Hough & Forbes 1943). By the 1930s, however, foresters had to contend with a new threat to the health of the forest—

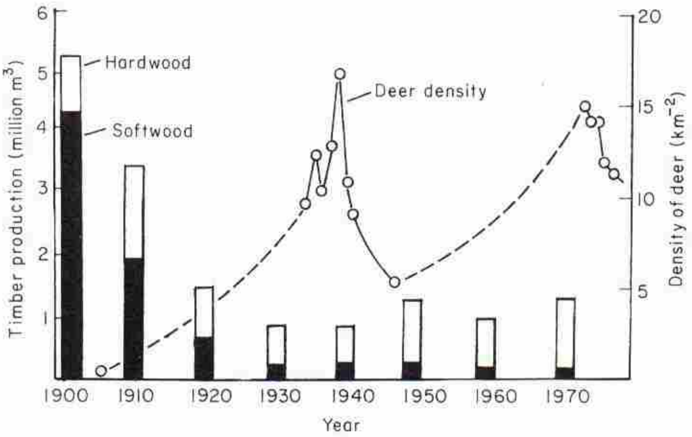

FIG. 3. The relationship between yearly timber production by volume in Pennsylvania since 1900 and estimated deer population densities in the Allegheny National Forest. Broken lines represent periods for which the data are sparse or inadequate. The decline in the 1940s was due to a lack of browse and high winter mortality. Estimates of deer densities were taken from Leopold, Sowls & Spencer (1947), McCain (1941), Hough (1949) and USDA Forest Service (1978), while data on timber production were assembled from Steer (1948) and the U.S. Bureau of the Census (1949, 1962, 1969).

overbrowsing by an expanding deer herd. Market hunting almost eliminated white-tailed deer *Odocoileus virginianus* from Pennsylvania in the late 1800s. Concern over the state's depleted wildlife resources, restrictive hunting legislation, and an increase in the available browse following the logging of 1900–30 favoured the explosive growth of the deer herd (Marquis 1975; Fig. 3). Intense browsing during the last fifty years has created an obvious browse line on the larger trees and eliminated much of the understorey vegetation (Hough 1965; Whitney 1984). White-tailed deer populations should be below eight deer km^{-2} (a figure rarely reached in the last fifty years: see Fig. 3) for the forest to regenerate successfully (B. Nelson, personal communication). Deer are a major factor in many regeneration failures on the Plateau today (Marquis 1981b).

RESULTS OF HUMAN ACTIVITY

Extent of disturbances

Across much of the drier mid-western portions of the U.S., fires starting in the post-logging slash constituted the greatest threat to the regrowth of the forest. Fires were also a problem in some of the cut hemlock stands of the High Plateau (Mason 1936), although it is difficult to determine their exact extent. Records kept by the U.S. Forest Service from 1923 to 1938—a period when lumbering was still in progress in privately owned portions of the forest—indicate approximately 6% of the area burned (McCain & Park 1939). The 6% figure translates into a return time or a recurrence interval of 263 years. Fires created open, poorly stocked, orchard stands of black cherry and the temporary aspen and pin cherry (*Prunus pensylvanica* L.) forest types (Hough 1955; Marquis 1975). However, estimates suggest these fire-dependent forest types never covered more than 12% of the ANF (USDA Forest Service 1986).

The cutting history is somewhat easier to reconstruct. In 1936 the Forest Service prepared a cover type map of the ANF for the purposes of wildlife management (McCain & Park 1939). They subdivided the forest into four major cover types: (i) old-growth,

TABLE 3. Percentage of age classes of trees in Allegheny National Forest. Data from U.S. Forest Service (1986).

Age (years)	Proclamation of forest 1923	Present 1986
0–30	46	5
31–50	39	6
51–70	8	45
71–90	3	38
91–100	0	6
⩾111	4	1

predominantly selectively cut or culled stands ⩾80 years old (6·1% of the total area; (ii) maturing cover, stands 20–80 years old (60·7%); (iii) regenerating cover, cut-over or burned stands 10–20 years old (30·7%); and (iv) unforested areas, small towns and open farmland (2·5%) (Fig. 2). Clearly a majority of the forests post-date 1880, the start of the clear-cutting era. Probably 70% of the ANF has been clear-cut for chemical wood at least once (D. A. Marquis, personal communication). Most of the forest today dates back to the peak cutting period, 50–90 years ago (Table 3).

Changes in composition and areal extent of communities

An intensive analysis of 149 permanently established 800-m^2 plots distributed throughout the ANF permits a detailed comparison of the species composition of the pre- and post-settlement forests (Table 1). Beech and hemlock have shown the major decrease. Their combined representation has fallen from 63% to 12% of all stems greater than 13 cm in diameter. Both sugar maple and red maple increased their representation. Black cherry, however, has increased most, from 1% in the pre-settlement forest to over 22% today.

Changes in area of the various forest types mirror the changes in the species composition (Table 4). The hemlock–northern-hardwood forest type, primarily beech and hemlock, was the dominant forest type in the pre-settlement period. The loss of hemlock and beech and the rise of cherry has converted much of this to the cherry–maple (Allegheny hardwood) type today.

TABLE 4. Pre- and post-settlement extent of various forest types in the Allegheny National Forest. Values are percentage of total land area (207 000 ha). Data from U.S. Forest Service (1986).

	1800	1986
Allegheny hardwood type (black cherry, maple)	6·8	53·0
Hemlock–northern-hardwood type* (hemlock, beech, birch, maple)	83·4	15·8
Oak type (white oak, red oak, chestnut oak)	4·9	18·2
Aspen type	1·0	2·0
Pine type (white pine, some red pine plantations today)	2·0	3·7
Savannah (open stands of black cherry)	2·0	3·7
Open land	—	2·0

* Predominately maple, beech, birch today.

DISCUSSION

Comparison of pre- and post-settlement disturbance regimes

Settlement dramatically altered the disturbance regime of North American forests (Runkle 1985; Whitney 1987). In the process it forced a readjustment of species to more dynamic conditions. In many ways the primary forest of the High Plateau region approximated the stable, self-replicating climax community of Weaver & Clements (1938). Like much of the hemlock–hardwood forests of the north-east, large-scale disturbances, e.g. windthrow and fire, were rare, perhaps occurring once every 1000 years (Lorimer 1977; Canham & Loucks 1984). By way of contrast, small-scale disturbances, i.e. the loss of a single tree here and there due to old age or drought, probably characterized the disturbance regime of the Plateau. Measurements of small-scale canopy gaps in the 1600-ha old-growth Tionesta Scenic and Natural Areas indicate an annual disturbance rate of 0·5% of the land-surface area per year or a return period of approximately 200 years (Runkle 1982, 1985). Small gaps favoured the very shade-tolerant species like beech and hemlock. Their very slow but steady growth in the shaded understorey gave them opportunity to utilize the small but frequently occurring canopy gaps (Kelty 1986; Canham 1988). Many shade-tolerant individuals probably went through several release–suppression cycles before they reached the overstorey (Runkle 1982). Larger-scale disturbances, e.g. windthrows and fires, favoured the less shade-tolerant but more rapidly growing white ash and black cherry (Hough & Forbes 1943). Tolerant species reached the canopy only when they had a head start on their faster-growing competitors (Kelty 1986).

The human-imposed disturbance regime of the nineteenth and twentieth centuries attacked the primary forest at its weakest link—the prolonged suppressed sapling stage. Clear cutting, fires and overbrowsing destroyed the seedling and sapling-size hemlock (Anderson & Loucks 1977; Rogers 1978). Heavy cutting also reduced the proportion of beech in the second and third-growth stands (Ostrom 1938; Hough & Forbes 1943). Occasionally the larger, 20–40-year-old advance growth (i.e. established individuals that represent the next generation of trees) of beech was retained, in which case it forms part of the canopy of today's second-growth stands (Marquis 1981a). Most of the advance growth, however, was either intentionally cut back to the ground or unintentionally broken during the clear-cutting chemical wood operations (Illick & Frontz 1928; Ostrom 1938). Despite the abundant root suckers of beech, few survived to produce new trees (Hough 1937). Species which resprouted vigorously from seedlings and saplings following cutting, e.g. sugar maple and red maple, or shade-intolerant species which grew rapidly, e.g. black cherry, increased their representation in the second-growth stands (Illick & Frontz 1928; Ostrom 1938). Reproduction was rather limited in the first 40–50 years of most second-growth stands because of dense canopy conditions and the lack of mature seed-bearing trees (Illick & Frontz 1928; Westveld 1939). Cutting the immature second-growth stands for chemical wood before they established a seedling layer favoured those species which sprouted vigorously from the stumps. Black cherry again increased its representation in the third-growth stands (Illick & Frontz 1928; Ostrom 1938).

Overbrowsing is the biggest problem confronting foresters and the natural regeneration of the forests today. Woody browse utilization on the ANF is two to ten times higher than that of any other National Forest in the north-east (Stitler & Shaw 1966). Deer have eliminated most of the advance growth less than 2 m high (Whitney 1984), leaving a relatively depauperate understorey composed of very small seedlings of black cherry. Clear-cut areas now regenerate to almost pure stands of cherry (Marquis 1981c).

Three successive attacks on the forest—the selective cutting of the white pine and the hemlock, the clear cutting for chemical wood and overbrowsing by deer—have left their mark. The implementation of a new disturbance regime favoured the meteoric rise to abundance of black cherry. Fortunately black cherry is a very valuable wood, useful for the production of furniture and interior finishes. One may question the value, however, of increasingly converting much of the forest to nearly pure stands or monocultures of black cherry.

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REFERENCES

Aguilar, R. & Arnold, R. W. (1985). Soil–landscape relationships of a climax forest in the Allegheny High Plateau, Pennsylvania. *Soil Science Society of America Journal*, **49**, 695–701.

Anderson, R. C. & Loucks, O. L. (1977). White-tail deer (*Odocoileus virginianus*) influence on structure and composition of *Tsuga canadensis* forests. *Journal of Applied Ecology*, **16**, 855–861.

Anonymous (1923). Chemical wood plants in Pennsylvania. *Forest Leaves*, **19**, 75.

Baker, A. J. (1983). Charcoal. *Encyclopedia of American Forest and Conservation History*, Vol. 1 (Ed by R. C. Davis), pp. 73–77. Macmillan Publishing Company, New York.

Barber, K. E. (1976). History of vegetation. *Methods in Plant Ecology* (Ed by S. B. Chapman), pp. 5–83. Blackwell Scientific Publications, Oxford.

Bjorkbom, J. C. & Larson, R. G. (1977). The Tionesta Scenic and Research Natural Areas. *USDA Forest Service, Northeastern Forest Experimental Station, General Technical Report*, **NE-31.**

Bourdo, E. A. Jr (1956). A review of the General Land Office Survey and of its use in quantitative studies of former forests. *Ecology*, **37**, 745–768.

Braun, E. L. (1950). *Deciduous Forests of Eastern North America.* The Blakiston Company, Philadelphia.

Brown, N. C. (1917). The hardwood distillation industry in New York. *New York State College of Forestry at Syracuse University, Technical Publication No. 5.* Syracuse University, Syracuse, New York.

Canham, C. D. (1988). Growth and canopy architecture of shade-tolerant trees: response to canopy gaps. *Ecology*, **69**, 786–795.

Canham, C. D. & Loucks, O. L. (1984). Catastrophic windthrow in the presettlement forests of Wisconsin. *Ecology*, **65**, 803–809.

Casler, W. C. (1973). *Logging Railroad Era of Lumbering in Pennsylvania*, Vol. 8. *Tionesta Valley.* Lycoming Printing Company, Williamsport, PA.

Casler, W. C. (1976). *Logging Railroad Era of Lumbering in Pennsylvania*, Vol. 9. *Teddy Collins Empire.* Lycoming Printing Company, Williamsport, PA.

Casler, W. C. (1977). *Logging Railroad Era of Lumbering in Pennsylvania*, Vol. 11. *Allegheny Valley Logging Railroads.* Lycoming Printing Company, Williamsport, PA.

Cerutti, J. R. (1985). *Soil Survey of Warren and Forest Counties, Pennsylvania.* USDA Soil Conservation Service, Washington, D.C.

Churchill, N. J. (1987). *Soil Survey of McKean County, Pennsylvania.* USDA Soil Conservation Service, Washington, D.C.

Clepper, H. E. (1934). Hemlock: the state tree of Pennsylvania. *Pennsylvania Department of Forests and Waters Bulletin*, **52.**

Conarro, R. M. (1973). Birth of a National Forest: the labor that produced the Allegheny. *Releases Commemorating Special Fiftieth Anniversary Series of the Allegheny National Forest*, **1.** USDA Forest Service, Warren, PA.

Cramer, Z. (1811). *The Navigator: Containing Directions for Navigating the Monongahela, Allegheny, Ohio, and Mississippi Rivers.* Cramer, Spear & Eichbaum, Pittsburgh.

Cronce, R. C. & Ciolkosz, E. J. (1983). Soils of the Allegheny National Forest. *Proceedings of the Northeastern Forest Soils Conference, Warren, PA* (Ed by L. R. Auchmoody, E. Ciolkosz, K. Cronce & N. Johnson), pp. 8–19. USDA Northeastern Forest Experiment Station, Warren, PA.

Curtis, J. T. (1959). *The Vegetation of Wisconsin*. University of Wisconsin Press, Madison, WI.

Dana, S. T. & Fairfax, S. K. (1980). *Forest and Range Policy*, 2nd edn. McGraw-Hill Book Company, New York.

Deardorff, M. H. (1946). Zeisberger's Allegheny River Indian towns: 1767–1770. *Pennsylvania Archaeologist*, **41,** 2–19.

Defebaugh, J. E. (1907). *History of the Lumber Industry of America*, Vol. II. The American Lumberman, Chicago.

Eaton, S. J. M. (1890). *History of Vernango County, Pennsylvania*, Vol. I. Brown & Runk and Company, Chicago.

Emerson, F. W. (1937). A botanical survey of Big Basin in the Allegany State Park. *New York State Museum Handbook*, **17,** 89–150.

Fernald, M. L. (1970). *Gray's Manual of Botany*, 8th edn. D. Van Nostrand Company, New York.

Goodlett, J. C. (1954). Vegetation adjacent to the border of the Wisconsin drift in Potter County, Pennsylvania. *Harvard Forest Bulletin*, **25.**

Gordon, T. F. (1832). *A Gazetteer of the State of Pennsylvania*. T. Belknap, Philadelphia.

Gordon, R. B. (1937). The botanical survey of the Allegany State Park. *New York State Museum Handbook*, **17,** 23–88.

Gordon, R. B. (1940). The primeval forest types of southwestern New York. *New York State Museum Bulletin*, **321.**

Greig-Smith, P. (1983). *Quantitative Plant Ecology*, 3rd edn. University of California Press, Berkeley.

Haberman, S. J. (1973). The analysis of residuals in cross-classified tables. *Biometrics*, **29,** 205–220.

Hale, H. M. (1906). Wood used for distillation in 1905. *USDA Forest Service Circular*, **50.**

Hazard, S. (1831). *Register of Pennsylvania*, **3,** 333.

Hergert, H. L. (1983). The tannin extraction industry in the United States. *Journal of Forest History*, **27,** 92–93.

Hough, A. F. (1936). A climax forest community in East Tionesta Creek in northwestern Pennsylvania. *Ecology*, **17,** 9–28.

Hough, A. F. (1937). A study of natural tree reproduction in the beech–birch–maple–hemlock type. *Journal of Forestry*, **35,** 376–378.

Hough, A. F. (1949). Deer and rabbit browsing and available winter forage in Allegheny hardwood forests. *Journal of Wildlife Management*, **13,** 135–141.

Hough, A. F. (1955). The long-lasting effects of forest fires on the Allegheny Plateau. *Pennsylvania Forests*, **45,** 36.

Hough, A. F. (1965). A twenty-year record of understory vegetational change in a virgin Pennsylvania forest. *Ecology*, **46,** 370–373.

Hough, A. F. & Forbes, R. D. (1943). The ecology and silvics of forests in the High Plateaus of Pennsylvania. *Ecological Monographs*, **13,** 299–320.

Illick, J. S. & Frontz, L. (1928). The beech–birch–maple forest type in Pennsylvania. *Department of Forests and Waters Bulletin*, **46.** Commonwealth of Pennsylvania, Harrisburg, PA.

Jennings, O. E. (1936). A contribution towards a plant geography of western Pennsylvania. *Trillia*, **10,** 46–81.

Kelty, M. J. (1986). Development patterns in two hemlock–hardwood stands in southern New England. *Canadian Journal of Forest Research*, **16,** 885–891.

Küchler, A. W. (1964). *Potential Natural Vegetation of the Conterminous United States*. (Map.) American Geographical Society, New York.

Kussart, S. (1938). *The Allegheny River*. Burgum Printing Company. Pittsburgh.

Leopold, A., Sowis, L. K. & Spencer, D. L. (1947). A survey of overpopulated deer ranges in the United States. *Journal of Wildlife Management*, **11,** 162–177.

Lobeck, A. K. (1927). Popular guide to the geology and physiography of Allegany State Park. *New York State Museum Handbook*, **1.**

Lorimer, C. G. (1977). The presettlement forest and natural disturbance cycle of northeastern Maine. *Ecology*, **58,** 139–148.

Lutz, H. J. (1930). Original forest composition in northwestern Pennsylvania as indicated by early land survey notes. *Journal of Forestry*, **28,** 1098–1103.

Marquis, D. A. (1975). The Allegheny hardwood forests of Pennsylvania. *USDA Forest Service, Northeastern Forest Experimental Station, General Technical Report*, **NE-15.**

Marquis, D. A. (1981a). Survival, growth, and quality of residual trees following clearcutting in Allegheny hardwood forests. *USDA Forest Service, Northeastern Forest Experimental Station, Research Paper*, **NE-477.**

Marquis, D. A. (1981b). Effect of deer browsing on timber production in Allegheny hardwood forests of northwestern Pennsylvania. *USDA Forest Service, Northeastern Forest Experimental Station, Research Paper*, **NE-475.**

Marquis, D. A. (1981c). Removal or retention of unmerchantable saplings in Allegheny hardwoods: effect on regeneration after clearcutting. *Journal of Forestry*, **79,** 280–283.

Marquis, D. A. (1983). Ecological and historical background: northern hardwoods. *1983 Penn State Forestry Issues Conference: Proceedings of Regenerating Hardwood Stands* (Ed by J. Finley, R. S. Cochran & J. R. Grace), pp. 9–29. School of Forest Resources & Cooperative Extension Service of Pennsylvania State University, State College, PA.

Marquis, D. A. (1988). *Early Sawmills, Tanneries & Chemical Plants of the Allegheny National Forest.* USDA Forest Service, Forestry Sciences Laboratory, Warren, PA.

Mason, C. Y. (1936). The geography of Allegheny State Park. *New York State Museum Circular*, **16.**

McCain, R. (1941). Removing surplus deer by hunting. Allegheny National Forest, Pennsylvania. *Transactions of the North American Wildlife Conference*, **6,** 332–338.

McCain, R. & Park, B. C. (1939). *Initial Report: Carrying Capacity Study for Deer, Allegheny National Forest, 1939.* USDA Allegheny National Forest Supervisor's Office, Warren, PA.

Munroe, C. E. & Michatard, T. (1902). Wood distillation. *12th Census of the U.S.*, Vol. 10. *Manufactures*, Part IV. *Chemicals*, pp. 555–560. U.S. Census Office, Washington, D.C.

Orloci, L. (1974). Revision for the Bray and Curtis ordination. *Canadian Journal of Botany*, **52,** 1773–1776.

Ostrom, C. E. (1938). Clear cutting of young northern hardwood stands. *Journal of Forestry*, **36,** 44–49.

Perry, G. C. (1920). Some effects of frost in northern Pennsylvania. *Forest Leaves*, **17,** 107–108.

Pinchot, G. (1923). The blazed trail of forest depletion. *American Forestry*, **29,** 323–328.

Randall, C. E. (1968). Hemlock: tree of tranquility. *American Forests*, **74,** 24–27, 58–62.

Raup, H. M. (1967). American forest biology. *Journal of Forestry*, **65,** 800–803.

Rogers, R. S. (1978). Forests dominated by hemlock (*Tsuga canadensis*): distribution as related to site and postsettlement history. *Canadian Journal of Botany*, **56,** 843–854.

Rothrock, J. T. (1915). *Areas of Desolation in Pennsylvania.* Herbert & Welsh, Philadelphia.

Runkle, J. R. (1982). Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology*, **63,** 1533–1546.

Runkle, J. R. (1985). Disturbance regimes in temperate forests. *The Ecology of Natural Disturbance and Patch Dynamics* (Ed by S. T. A. Pickett & P. S. White), pp. 17–33. Academic Press, New York.

Sargent, C. S. (1884). *Report on the Forests of North America.* Census Office, U.S. Department of the Interior.

Schenck, C. S. (1887). *History of Warren County, Pennsylvania.* D. Mason & Company, Syracuse, NY.

Shane, L. C. K. (1987). Late-glacial vegetational and climatic history of the Allegheny Plateau and Till Plains of Ohio and Indiana, U.S.A. *Boreas*, **16,** 1–20.

Siccama, T. G. (1971). Presettlement and present forest vegetation in northern Vermont with special reference to Chittenden County. *American Midland Naturalist*, **85,** 153–172.

Sokal, R. R. & Rohlf, F. J. (1981). *Biometry: the Principles and Practices of Statistics in Biological Research.* W. H. Freeman, San Francisco.

Steer, H. B. (1948). Lumber production in the United States, 1799–1946. *USDA Miscellaneous Publication*, **669.**

Stitler, W. M. Jr & Shaw, S. P. (1966). Use of woody browse by white-tailed deer in heavily forested areas of northeastern United States. *Tranactions of the North American Wildlife and Natural Resources Conference*, **31,** 205–212.

Stotz, L. (1973). Crosscut 'n doublebit: timber sales and timber utilization on the Allegheny National Forest. *Releases Commemorating Special 50th Anniversary Series of the Allegheny National Forest*, **7.** USDA Forest Service, Warren, PA.

Strahler, A. H. (1978). Binary discriminant analysis: a new method for investigating species–environment relationships. *Ecology*, **59,** 108–116.

Taber, T. T. III (1974). *Logging Railroad Era of Lumbering in Pennsylvania*, Vol. 10. *Tanbark, Alcohol, and Lumber.* Lycoming Printing Company, Williamsport, PA.

Taber, T. T. III (1975). *Logging Railroad Era of Lumbering in Pennsylvania*, Vol. 7, *Sawmills Among the Derricks.* Lycoming Printing Company, Williamsport, PA.

Tome, P. (1928). *Pioneer Life; or Thirty Years a Hunter, being Scenes and Adventure in the Life of Philip Tome* [Reprint of 1854 edn]. Aurand Press, Harrisburg, PA.

U.S. Bureau of the Census (1949). *1949 Census of Manufactures: Statistics by Industry.* U.S. Government Printing Office, Washington, D.C.

U.S. Bureau of the Census (1962). *1958 Census of Manufactures: Statistics by Industry.* U.S. Government Printing Office, Washington, D.C.

U.S. Bureau of the Census (1969). Lumber production and mill stocks. *Current Industrial Reports.* Series MA-24T (69)-1. U.S. Government Printing Office, Washington, D.C.

USDA Forest Service (1978). *The Deer Issue on the Allegheny National Forest.* USDA Allegheny National Forest Supervisor's Office, Warren, PA.

USDA Forest Service (1986). *Final Environmental Impact Statement: Land and Resource Management Plan, Allegheny National Forest.* Eastern Region, USDA Forest Service, Milwaukee, WI.

Walsh, G. E. (1896). Hemlock for the tanneries. *Garden and Forest*, **9,** 222–223.

Ward, W. W., Berglund, J. V. & Borden, F. Y. (1966). Soil-site characteristics and occurrence of sugar maple canker in Pennsylvania. *Ecology*, **47,** 541–548.

Weaver, J. E. & Clements, F. E. (1938). *Plant Ecology*, 2nd edn. McGraw-Hill, New York.

Westveld, R. H. (1939). *Applied Silviculture in the U.S.* John Wiley & Sons, New York.

Whitney, G. G. (1982). Vegetation–site relationships in the presettlement forest of northeastern Ohio. *Botanical Gazette*, **143,** 225–237.

Whitney, G. G. (1984). Fifty years of change in the arboreal vegetation of Heart's Content, an old-growth hemlock–white pine–northern hardwood stand. *Ecology*, **65,** 403–408.

Whitney, G. G. (1986). The relation of Michigan's presettlement pine forests to substrate and disturbance history. *Ecology*, **67,** 1548–1559.

Whitney, G. G. (1987). An ecological history of the Great Lakes forest of Michigan. *Journal of Ecology*, **75,** 667–684.

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