Eastern White Pine Versatility in the Presettlement Forest

MARC D. ABRAMS

> THIS EASTERN GIANT EXHIBITED VAST ECOLOGICAL BREADTH IN THE ORIGINAL FOREST BUT HAS BEEN ON THE DECLINE WITH SUBSEQUENT LAND-USE CHANGES

One species that typifies the northern forests of the eastern United States in the minds of many ecologists and naturalists is the eastern white pine (*Pinus strobus* L.). Its range includes New England, the Great Lakes region, New York, Pennsylvania, and along the Appalachian Mountains to northern Georgia (Figure 1). The northern limits of its range include southwestern Ontario, above Lake Superior, to southern Newfoundland. In these forests, white pine is the tallest tree, with some individuals reaching a height of 150–175 feet (45–53 m) and a diameter of 40–50 inches (102–127 cm). The great height of white pine makes it an emergent above the upper canopy in many mixed-species forests.

Historically, white pine has been one of the most valuable tree species because of the large volume of standing timber and its multiple uses as a lightweight building material with a straight grain. Intensive logging for the highly preferred white pine started in New England in the 1700s and moved westward to the Great Lake states by the mid-1800s. Indeed, white pine has been called "the tree that built America" and "the tree that won the American Revolution," the latter referring to the outcome when the British Navy could no longer obtain the trees for their ship masts and planks (Harlow et al. 1979). The amount of white pine logged from the northern forests before 1900 measures into the hundreds of billions of board feet (Goodlett 1954, Whitney 1994).

Ironically, white pine was a relatively small component of the pre-European forests of the northeastern United States, compared with the dominance of hemlock (*Tsuga canadensis*), beech (*Fagus grandifolia*), oak (*Quercus*), and sugar maple (*Acer saccharum*) (Lutz 1930a, Whitney 1994, Abrams and Ruffner 1995). Thus, white pine's reputation for great dominance in the original forest was based on inflated estimates to attract settlers as well as on its easy accessibility. Before the railroad era, the earliest logging was concentrated along river systems because of the ease of floating or rafting the logs to sawmills or markets. Early land surveys of the original forest suggest that high concentrations of white pine were mainly found on light, sandy soils along rivers (Whitney 1990, 1994, Cogbill 2000). This location, coupled with its great size and highly valued wood, made white pine an easy target for early logging. However, white pine also dominated sandy outwash deposits prone to burning and dry upland areas affected by frequent blow-down (wind-related tree fall), forming presettlement pineries or pine plains. Various studies (Braun 1950, Whitney 1986, Nowacki and Abrams 1994) suggest that white pine could occupy a range of soil, moisture, and disturbance conditions even wider than those normally associated with this species.

White pine is a major component of five forest cover types recognized by the Society of American Foresters: white pine, white pine–hemlock, white pine–northern red oak (*Q. rubra*),

Marc D. Abrams (e-mail: agl@psu.edu) is Steimer Professor of Forest Science, as well as professor of forest ecology and tree physiology, at the School of Forest Resources, Pennsylvania State University, University Park, PA 16802. His specific research interests are in the long-term temporal and broad spatial changes that have occurred in the northern and central hardwood and conifer forests of the eastern United States.

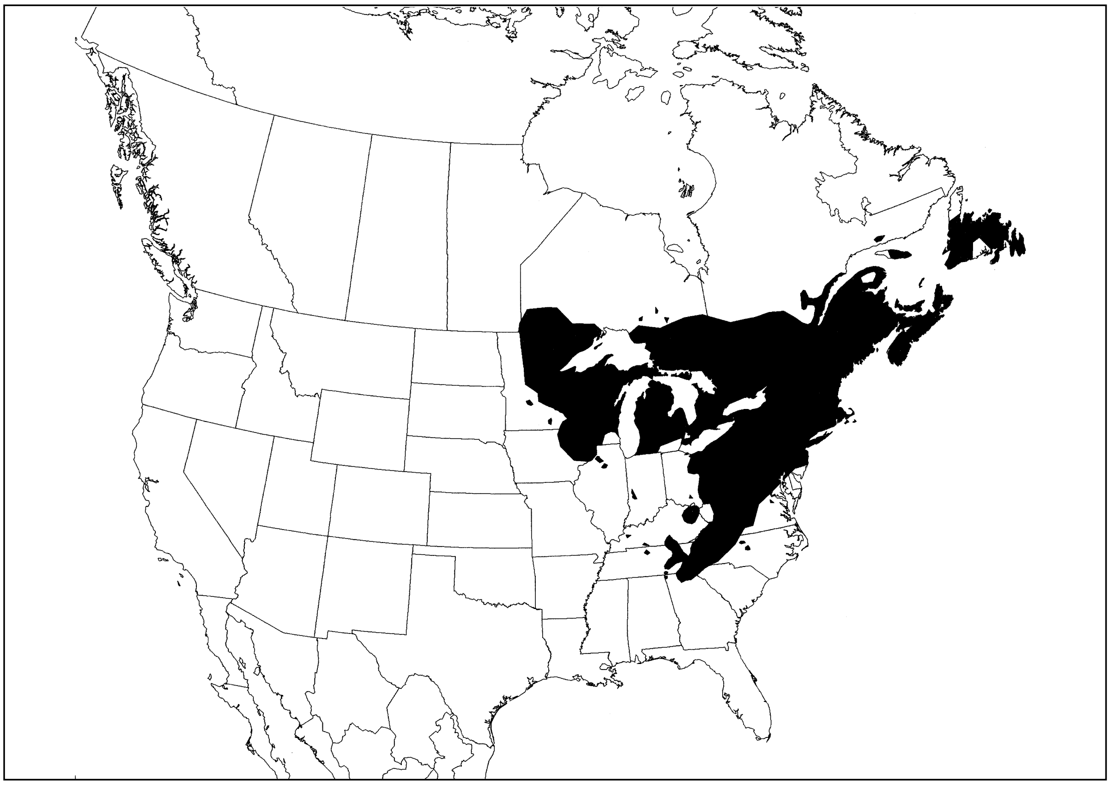

Figure 1. Range map for eastern white pine.

white pine–chestnut oak (*Q. prinus*), and red pine (*P. resinosa*) (Burns and Honkala 1990). Ecologically, white pine is best known for its role in the hemlock–white pine–northern hardwood forest that stretches along the northern tier of the eastern United States and southern Canada (Figures 1 and 2a; Nichols 1935, Braun 1950). Not only is white pine widely distributed and associated with a large variety of species, but it can also persist in various successional stages within these forests. Indeed, white pine has been documented as a pioneer after disturbance, a long-lived successional tree in mature or climax forests, and a physiographic or fire-maintained climax type.

The ecology of white pine was the subject of ecological studies throughout the 20th century, yet these studies did not fully capture the ecological breadth of white pine's role in the eastern forest (Lutz 1930b, Nichols 1935, Hough and Forbes 1943, Hibbs 1982). Early ecologists concluded that it became established after large-scale disturbances, such as agricultural abandonment, fire, and blow-down, and was replaced by shade-tolerant trees during succession. However, this conclusion does not explain its role in highly contrasting forest types, including the presence of multiple-age white pine in old-growth forests that have not been intensively disturbed for 300 or more years (Abrams and Orwig 1996, Abrams et al. 2000). Moreover, many of the ideas formulated about the ecology of white pine during the 20th century lacked dendroecological (tree ring) data. Dendroecological techniques have become an important tool in the study of stand dynamics and ecological history. Studying tree-ring chronologies along with age structure and land-use history can elucidate species recruitment patterns, periodicity and intensity of disturbance, population dynamics, and successional pathways. My students and I used these techniques to study the dynamics of white pine in a variety of old-growth forests of the eastern United States. From these studies, we found a wide array of canopy recruitment patterns and multiple successional pathways for the species.

Information on species' distribution in the original forest and contrasting successional roles in old-growth forests suggests that white pine defies easy classification or pigeonholing. Moreover, white pine has exhibited dramatic changes in forest dominance from presettlement to the present day, with most regions showing a decrease for the species (Whitney 1987, Abrams and Ruffner 1995, Abrams and McCay 1996, Foster et al. 1998). In this article, I explore the ecology of white pine in the pre-European settlement forest by using data from early land surveys (witness trees) and dendroecology (tree ring) studies of a variety of old-growth forests. Dendroecological research of old-growth forests and witness tree data serve as a window to the past and allow for the reconstruction of species' distribution and dynamics during a time that, in general, was under much less anthropogenic pressure than are present-day second- and third-growth forests. The results of this approach should increase our understanding of the complex ecology for this dominant species and shed light on its past, present, and future status, including reasons for the postsettlement decline in this giant of the eastern forest.

Ecophysiological attributes of white pine

White pine is generally considered to be intermediate in shade tolerance and an early-to-middle successional species (Burns and Honkala 1990). Consistent with these ideas, saplings of understory eastern white pine in northwestern Connecticut had 65% survival over a 5-year period, which was intermediate among eight hardwood tree species plus hemlock (Pacala et al. 1996). Black birch (*Betula nigra*) and hemlock had more than 90% survival, whereas white ash (*Fraxinus americana*), red oak, and red maple (*Acer rubrum*) had 20%–38% survival during the same time interval. White pine saplings appear to have very slow radial growth at very low light levels (less than 1% full sun) but intermediate growth in light greater than 10% full sun, as compared with nine other eastern tree species (Pacala et al. 1996). Similarly, a greenhouse study comparing the shoot growth of tree species common to old fields in the Hudson River valley of southeastern New York reported that white pine had much lower growth than sugar maple and red oak in low light (Canham et al. 1996). All species had greatly increased growth with higher light levels. A study of suppressed trees over a 19-year period at Harvard Forest in central Massachusetts rated white pine as tolerant because it had a high survival rate (59%) and one of the highest mean diameter growth rates among nine tree species (Lorimer 1983). These studies suggest that white pine has a slow height growth rate but moderate survival in the understory of second-growth, mixed species forests.

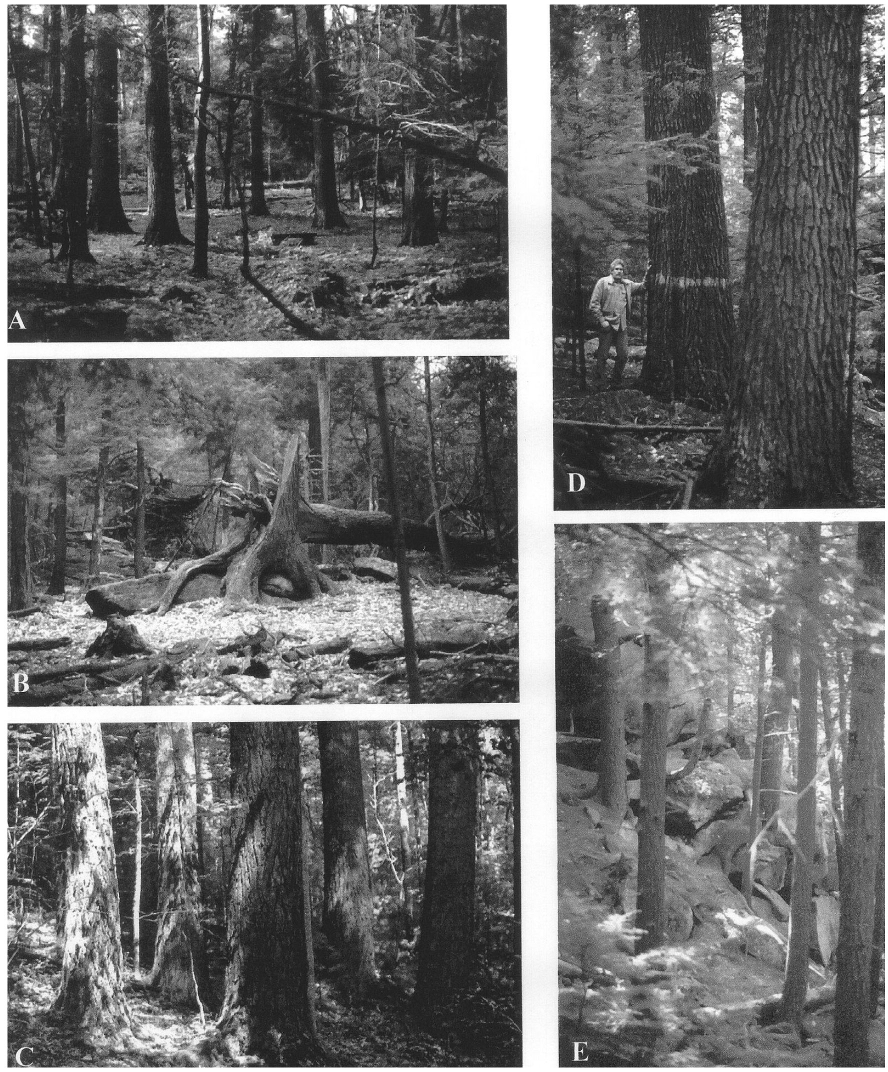

Figure 2. (a) A remnant, old-growth hemlock–white pine–northern hardwood forest at Heart's Content in northwest Pennsylvania, (b) wind-snapped old-growth hemlock (foreground) and white pine in the Cook Forest in northwest Pennsylvania, (c) even-age cohort of white pine in an old gap in old-growth mixed-oak–pine forest in eastern West Virginia, (d) 300-year-old white pine (background) and hemlock in Cook Forest in northwest Pennsylvania, (e) uneven-age white pine and hemlock on the steep rocky slope of Ice Glen Natural Area in southwest Massachusetts.

White pine witness tree data

Land surveys during the period of early European settlement in the eastern United States involved the use of witness (or bearing) trees to identify property corners and other boundaries (Lutz 1930a, Whitney 1994). For many areas, witness trees represent the only quantitative information on presettlement forest composition and, therefore, are an invaluable resource, despite potential biases in tree selection by early surveyors (Whitney 1994). Witness tree data are best viewed as regional rather than stand-level information because of the small number of trees used within any one forest. Moreover, in several instances the land surveyors, particularly in New England and the mid-Atlantic Ridge and Valley Province, listed pine at the genus level, not at the species level. Thus, some of the pine from these regions included pitch pine (*P. rigida*) or red pine along with white pine.

White pine in the pre-European settlement forests of New England ranged from 0% to 22% of the total number of witness trees surveyed (Table 1). It is the first-rank species in only two of the 11 witness tree surveys reviewed here. White pine grew mainly in association with oak and chestnut (*Castanea dentata*) and to a much lesser extent with beech, maple, and hemlock. White pine was widely distributed in colonial forests of central New England, averaging 20% (with a range of 16% to 22%) of the witness trees in the Connecticut River valley, Pelham Hills, central uplands, and eastern lowlands, where it was an important member of the hemlock–

northern hardwood, oak–pine –hemlock, and oak–pine–chestnut forest types (Foster et al. 1998).

In 179 town surveys (48,260 trees) from northern New England and northern New York, pine witness trees (most being white pine) are found in 60% of the townships with an average of only 5% density (Cogbill 2000). White pine was 12% of the presettlement forest in Chittenden County, Vermont, and part of the northern hardwood–hemlock forest that occurred in ravines, slopes, and sandy terraces (Siccama 1971). White pine represented less than 2% of all trees in presettlement surveys of 115 towns in northern Maine, which is consistent with previous work in northeastern Maine (Table 1; Lorimer 1977). Cogbill (2000) concludes that white pine was generally a minor component in the forest of northern New England. It occurred consistently only in special circumstances: on sandy outwash, on rocky ridges, or on the floodplains of large rivers, particularly if they had been burned. Even in these conditions, it was never abundant except on the sandy outwash areas, which were mixed-species areas designated as "pine plains." Indeed, pine had a maximum of 57% forest composition in the Merrimack River valley of New Hampshire, a sandy coastal plain site that most likely had a predominance of pitch pine (Cogbill 2000).

In the mid-Atlantic region, white pine ranged from 0% to 38% of individuals in the presettlement forests (Table 1). It was the first-rank species in only one of 18 witness tree data sets reviewed; it was not listed as a dominant species in nine of these studies. In contrast, beech and white oak were listed as the first-rank species in nine and five of these studies, respectively. White pine was typically associated with northern hardwoods and hemlock in the north and with white oak further south. However, beech–sugar maple–hemlock was a much more common forest association than hemlock–northern hardwood–white pine forest on the Allegheny Plateau. The highest frequency of white pine (38%) among witness trees was recorded with beech, hemlock, spruce, and white oak on the Pocono Plateau of east-central Pennsylvania (Dando 1996).

On the Allegheny High Plateau of northwest Pennsylvania, white pine represented only 6% of the witness trees, and extensive stands of the species were mainly limited to coarse-textured outwash terraces of the Allegheny River and its tributary creeks (Lutz 1930a, Whitney 1990). Old-growth white pine was mainly concentrated on the upper, southeast-facing slope of the Tionesta River valley, growing with hemlock and chestnut on shale-derived soils (Hough and Forbes 1943). In Potter County, white pine grew in "great forests" along many of the river valleys and creeks to the north and on ridge tops and hillsides to the south (Goodlett 1954). In the Allegheny Plateau of western New York, white pine in the original forest was concentrated in the southern counties in a dissected landscape of river drainages, where it formed part of oak–chestnut–pine and pine–beech–hemlock–white oak forests (Seischab 1990). In the Allegheny Mountains of Pennsylvania, white pine represented about 10% of the witness trees and dominated cove forests and, to a lesser extent, stream valleys (Abrams and Ruffner 1995). In eastern West Virginia, white pine dominated mountaintops and southeast-facing slopes; it was not recorded in cove and valley floor forests, suggesting that it occurred at higher elevations at the transition of the central and southern Appalachian Mountains (Abrams and McCay 1996). In the Ridge and Valley Province of central Pennsylvania, white pine mainly occurred with white oak on rich mesic valleys, stream valleys, and mountain coves (Nowacki and Abrams 1992, Abrams and Ruffner 1995).

White pine was rarely a first-rank species in the pre-European forests in the Great Lakes states. But many forests in the region had a white pine component of 5%–35% (Table 1). White pine was associated with hemlock–northern hardwoods or mixed-pine forests on upland sites and with tamarack (*Larix*), cedar (*Thuja*), and spruce (*Picea*) on poorly drained sites. In the Upper Peninsula of Michigan, white pine constituted 10% of the witness trees recorded in well-drained regions and 6% of those recorded in poorly drained regions (Zhang et al. 2000). Hemlock–white pine–northern hardwood forests in northern and lower Michigan had 3% white pine, compared with 19% in mixed-pine forests (Whitney 1987). The highest dominance of white pine (35%) was recorded with red pine, aspen (*Populus*), and birch on dry–mesic, sandy–loam forests in north-central Wisconsin (Nowacki et al. 1990). In northern-lower Michigan, white pine in the original forest occupied a wide range of soils and drainage classes, but it showed a strong association with loam to sandy–loam, ice-contact–derived soils (Whitney 1986). White pine in old-growth forests in Upper Michigan dominated south-facing, excessively drained, sandy–loam soils and exposed rocky ridges (Pregitzer and Barnes 1984).

According to Braun (1950), the hemlock–white pine–northern hardwood forests existed as an alternation of deciduous, coniferous, and mixed-forest communities, with white pine being most characteristic of conifer forests on dry sand plains and ridges. White pine was a part of the mixed-forest type but was subordinate to hemlock and northern hardwoods. Thus, the hemlock–white pine–northern hardwood forest type existed mainly at the regional rather than at the stand level.

These studies suggest that white pine was widely distributed in the presettlement forest and that it occurred in a large range of topographic positions and moisture conditions. White pine occurred mainly on sandy and sandy–loam soils, but it was not limited to these soil textures. White pine was rarely a first-rank dominant at the regional level, but it probably occurred in nearly pure stands in specialized sites such as river valleys and stream valleys, side slopes and ridge tops, and glacial outwash. Therefore, its distribution was somewhat bimodal, with peaks in riparian valleys and dry, nutrient-poor uplands. Sugar maple and beech probably outcompeted white pine on mesic, rich sites, and white pine had to compete with hemlock on cool, moist sites. Pitch pine was probably much more important than white pine on the coastal plain of New England and the northern mid-Atlantic, where white pine may have been limited by climate, soils, and frequent aboriginal burning on the coastal plain (Patterson

Table 1. Percentage composition of witness tree species in pre-European settlement forests in the hemlock–white pine–northern hardwood range.

Region, location	Presettlement forest composition	Reference
New England		
Northeast Maine	Spruce (20%), birch (17%), beech (15%), balsam fir (14%), cedar (12%), **pine** (1%)	Lorimer 1977
Western Maine	Spruce (37%), birch (20%), fir (11%), maple (9%), cedar (6%), **pine** (0%)	Cogbill 2000
Central New Hampshire	Beech (33%), hemlock (22%), spruce (16%), maple (11%), birch (5%), **pine** (5%)	Cogbill 2000
Northern Vermont	Beech (30%), spruce (16%), maple (15%), birch (11%), hemlock (11%), **pine** (1%)	Siccama 1971
Northern Vermont	Maple (24%), birch (16%), **pine** (12%), hemlock (11%)	Siccama 1971
Western Vermont	Beech (34%), maple (20%), ironwood (9%), **pine** (8%)	Cogbill 2000
Northeast Massachusetts	White oak (27%), black oak (26%), **pine** (18%), hickory (9%)	Whitney and Davis 1986
North-central Massachusetts	**Pine** (22%), white oak (17%), chestnut (11%), black oak (9%)	Whitney 1994
North-central Massachusetts		
Upland	**Pine** (22%), oak (21%), hemlock (14%), maple (10%)	Foster et al. 1998
Lowland	Oak (59%), **pine** (17%), chestnut (6%)	Foster et al. 1998
Northwest Connecticut		
Mesic	Beech (40%), hemlock (25%), maple (9%), birch (6%), **white pine** (2%)	Winer 1955
Dry–mesic	Beech (20%), chestnut (14%), hemlock (13%), maple (13%), oak (13%)	Winer 1955
Dry	Oak (28%), chestnut (10%), **white pine** (10%), walnut (10%), maple (9%)	Winer 1955
Mid-Atlantic region		
Allegheny Plateau		
Western New York	Beech (19%), oak (19%), sugar maple (11%), hemlock (11%), **white pine** (11%)	Seischab 1990
Western New York	Beech (47%), sugar maple (22%), **white pine** (2%)	Marks and Gardescu 1992
Western New York, swamps	Black ash (47%), hemlock (9%), tamarack (7%), **white pine** (1%)	Marks and Gardescu 1992
Northwest Pennsylvania	Beech (31%), hemlock (27%), sugar maple (8%), **white pine** (6%)	Lutz 1930a
Northwest Pennsylvania	Beech (43%), hemlock (20%), birch (6%), **white pine** (3%)	Whitney 1990
North-central Pennsylvania	Beech (50%), sugar maple (17%), hemlock (17%), birch (8%), **white pine** (2%)	Goodlett 1954
North-central Pennsylvania	Beech (33%), hemlock (32%), sugar maple (8%), **white pine** (2%)	Abrams and Ruffner 1995
Allegheny Mountains		
Central Pennsylvania	White oak (19%), maple (15%), chestnut (14%), **white pine** (11%)	Abrams and Ruffner 1995
Southern West Virginia	White oak (24%), chestnut (11%), hickory (9%), **white pine** (5%)	Abrams et al. 1995
Eastern West Virginia	Maple (19%), beech (13%), hemlock (10%), basswood (9%), **pine** (0%)	Abrams and McCay 1996
Ridge and Valley		
Southeast New York	White oak (47%), black oak (16%), hickory (12%), **pine** (3%)	Glitzenstein et al. 1990
Central Pennsylvania, valley	White oak (41%), hickory (12%), **pine** (13%), black oak (9%)	Nowacki and Abrams 1992
Central Pennsylvania, mountain cove	Oak (33%, **pine** (27%), hemlock (17%), chestnut (7%)	Nowacki and Abrams 1992
Eastern Pennsylvania	**Pine** (28%), white oak (23%), hemlock (9%), chestnut (7%), maple (6%)	Dando 1996
Eastern West Virginia	White oak (33%), **pine** (16), chestnut oak (8%)	Abrams and McCay 1996
Pocono Plateau, Pennsylvania	**Pine** (38%), beech (12%), hemlock (9%), spruce (7%), white oak (7%)	Dando 1996
Till plain, western New York	Beech (32%), sugar maple (18%), basswood (12%), white oak (11%), **white pine** (2%)	Seischab 1990
Catskill Mountains, eastern NY	Beech (49%), hemlock (20%), sugar maple (13%), birch (7%), **white pine** (< 1%)	McIntosh 1962
Lake States		
North-central Wisconsin		
Mesic	Hemlock (27%), birch (25%), maple (17%), **white pine** (5%)	Nowacki et al. 1990
Dry–mesic	**White pine** (35%), red pine (14%), aspen (12%), birch (10%)	Nowacki et al. 1990
Northern-lower Michigan		
Mesic	Beech (51%), hemlock (20%), sugar maple (17%), **white pine** (3%)	Whitney 1987
Dry–mesic	Red pine (41%), **white pine** (19%), jack pine (18%), white oak (9%)	Whitney 1987
Swamps	Tamarack (30%), cedar (25%), spruce (11%), **white pine** (8%)	Whitney 1987
Mesic	Hemlock (44%), beech (22%), **white pine** (11%)	Palik and Pregitzer 1992
Dry–mesic	Red pine (45%), jack pine (17%), **white pine** (15%)	Palik and Pregitzer 1992
Northern-lower Michigan		
Mesic	Hemlock (32%), **white pine** (26%), red pine (26%)	Kilburn 1960
Dry–mesic	Red pine (40%), white oak (19%), **white pine** (15%), aspen (12%)	Kilburn 1960
Xeric	Jack pine (61%), red pine (27%), **white pine** (4%)	Kilburn 1960
Northern Michigan, swamp	Cedar (41%), tamarack (18%), spruce (9%), birch (8%), **pine** (1%)	Deelen et al. 1996
Northern Michigan		
Well-drained	Beech (14%), sugar maple (14%), **white pine** (10%), hemlock (10%)	Zhang et al. 2000
Poorly drained	Tamarack (23%), white cedar (16%), spruce (14%), hemlock (9%), **white pine** (6%)	Zhang et al. 2000
Eastern Wisconsin	Sugar maple (45%), beech (29%), hemlock (15%), basswood (12%), **pine** (1%)	Ward 1956
Eastern Wisconsin	Beech (36%), sugar maple (20%), hemlock (10%), **white pine** (10%)	Ward 1956
Northern Minnesota	Jack pine (22%), aspen (21%), red pine (19%), **white pine** (13%)	Spurr 1954

and Sassaman 1988). White pine may have reached its greatest distribution on coarse-textured glacial outwash soils in the Great Lake states, which were probably drier and more frequently burned than their counterparts in New England (Whitney 1994, Clark and Royall 1996).

Presettlement versus present-day forests. Comparisons of presettlement versus present-day forest composition of white pine indicate that an overall decline has occurred in the species in northeastern and Great Lakes states forests (Table 2). All eight case studies from the Great Lake region show a decline in white pine percentages from past to present, whereas four of the nine case studies in the Northeast show an increase. In most cases, however, the magnitude of the white pine increases is rather modest. One exception involves the pine plains of Concord, Massachusetts, in which presettlement forests were probably dominated by pitch pine (Whitney and Davis 1986). The dramatic post-European settlement increase in white pine at Concord has been attributed to its prolific seed production and ability to invade abandoned pastureland. Past increases in white pine in the Hudson River valley of New York have also been explained by its invasion of abandoned agricultural lands (Glitzenstein et al. 1990).

The frequency and magnitude of white pine decreases from presettlement to the present day are rather striking. A 35% decrease in white pine composition occurred on dry–mesic sites in north-central Wisconsin (Nowacki et al. 1990). White pine in the Ridge and Valley Provinces of Pennsylvania and West Virginia experienced a 23% and 17% decline, respectively (Abrams and Ruffner 1995, Abrams and McCay 1996). In several cases, white pine has been nearly extirpated. The selective logging of the highly prized white pine in the original forests, resulting in the loss of a local seed source followed at times by catastrophic wildfire, has undoubtedly contributed to the decrease in white pine dominance in many areas (Whitney 1987, Nowacki et al. 1990, Palik and Pregitzer 1992, Frelich 1995). During the 20th century, white pine was faced with a decrease in cutting and fire and an increase in deer browsing, which further exacerbated the decline in white pine dominance in many areas (Abrams and Ruffner 1995, Frelich 1995).

Multiple pathways of white pine recruitment in old-growth forests

During succession, the ecological role of species can be highly variable. Variations in disturbance type and intensity, coupled with complex species reactions and chance events, can result in a multitude of pathways in species recruitment, forest development, and successional changes.

Early and mid-successional white pine. White pine is probably best known for its role in the early successional development of forests. However, the ecophysiological attributes of white pine allow it to exploit periodic disturbances and recruit into the middle successional stages of some forests.

Cook Forest, Pennsylvania. Dendroecological techniques were used to examine the patterns of canopy recruitment in relation to disturbance history for white pine and hemlock at Cook Forest Cathedral Pines, located on the upper slope of

Table 2. Pre-European settlement versus modern forest composition of white pine.[a]

Species	Location	Presettlement (%)	Modern (%)	Reference
	Northeast			
Pine	Champlain Valley, VT	8.5	11.6	Siccama 1971
Pine	Green Mountains, VT	1.4	7.6	Siccama 1971
Pitch pine	Concord, MA	18.5	—	Whitney and Davis 1986
White pine	Concord, MA	0.3	23.3	Whitney and Davis 1986
Pine	Central Massachusetts	19.9	15.2	Foster et al. 1998
Pine	Hudson Valley, New York	3.5	9.2	Glitzenstein et al. 1990
White pine	Allegheny Plateau, Pennsylvania	3.1	0.4	Whitney 1990
White pine	Allegheny Mountains, Pennsylvania	10.5	0.8	Abrams and Ruffner 1995
Pine	Ridge and Valley, Pennsylvania	25.6	—	Abrams and Ruffner 1995
White pine	Ridge and Valley, Pennsylvania	—	2.6	Abrams and Ruffner 1995
Pine	Ridge and Valley, West Virginia	18.2	—	Abrams and McCay 1996
White pine	Ridge and Valley, West Virginia	—	1.4	Abrams and McCay 1996
	Lake States			
White pine	Roscommon County, Michigan	18.0	3.0	Whitney 1987
White pine	Huron, MI	15.3	0.0	Palik and Pregitzer 1992
White pine	Upper Peninsula, Michigan	10.3	3.5	Zhang et al. 2000
White pine	Upper Peninsula, Michigan, swamp	6.0	1.5	Zhang et al. 2000
White pine	Eastern Wisconsin	10.3	3.7	Ward 1956
White pine	North-central Wisconsin			
	Mesic	4.6	0	Nowacki et al. 1990
	Dry–mesic	35.1	0	Nowacki et al. 1990
Red pine/ white pine	Lake County, Minnesota	29.5	5.9	Frelich 1995

a. The pine designation in the presettlement surveys most likely indicates a majority of white pine.

a river valley on the Allegheny Plateau in northwestern Pennsylvania (Abrams and Orwig 1996). This 300-year-old primary stand growing on a stony loam soil is dominated by hemlock (53%), white pine (26%), beech (10%), and yellow birch (*Betula alleghaniensis*, 8%). Hemlock had an extremely high density, averaging more than 11 trees per 0.02-ha plot. In contrast, white pine averaged only two trees per plot but had a high importance value because of the large size of almost all of the existing trees (Figure 2d). White pine recruitment into the tree-size class occurred throughout the initial 110-year period (1690–1800) of the stand history, but it dominated during the first 40 years (Figure 3). Most recruitment of hemlock occurred between 1740 and 1800, although it began as early as 1705 and continued until 1900. Most of the younger trees belonged to several northern hardwood species.

This stand probably experienced a catastrophic disturbance, such as tornado or fire, in the 1690s. Evidence for this disturbance is the absence of any hemlock trees older than 284 years, even though they can exceed 400 years (Hough and Forbes 1943). Furthermore, there was a pulse of white pine recruitment between 1690 and 1730, consistent with many old-growth forest studies in which white pine existed as even-age cohorts that became established soon after large-scale disturbances (Lutz 1930b, Cline and Spurr 1942, Heinselman 1973, Foster 1988a). However, the recruitment pattern of white pine in this study is not consistent with the idea of strictly early-successional, even-age populations, because its initial recruitment was followed by an additional 70 years of concurrent white pine and hemlock recruitment.

White pine also exhibited huge variation in annual tree-ring width. Radial growth in young white pine entering the stand around 1700 grew as much as 4–5 mm annually (Abrams and Orwig 1996). This growth rate dropped to a few tenths of a millimeter in mature trees during decades of suppression, followed by prolonged growth increases up to 2–3 mm after disturbance. This degree of growth plasticity enables white pine to respond to a wide variation in growth conditions during its long life in an old-growth forest.

None of the existing white pine recruited in Cook Forest after 1800 (Figure 3). These results concur with those reported for a former virgin stand of white pine–hemlock–northern hardwoods in the same region, in which white pine recruitment peaked during the initial 80 years of postdisturbance stand development, continued at a lower level for an additional 80 years, and then stopped completely (Hough and Forbes 1943). Thus, white pine can apparently play the role of both early and middle successional species in forests on the Allegheny Plateau. The initial domination of tree recruitment by white pine reflects its faster height growth relative to hemlock rather than differential establishment dates between the two species (Abrams and Orwig 1996). The forest experienced increased hardwood invasion in the early 20th century. However, since 1930 recruitment for all species was practically nonexistent, despite severe storms in the 1950s. Presently, the stand is virtually devoid of an understory because of intensive deer browsing.

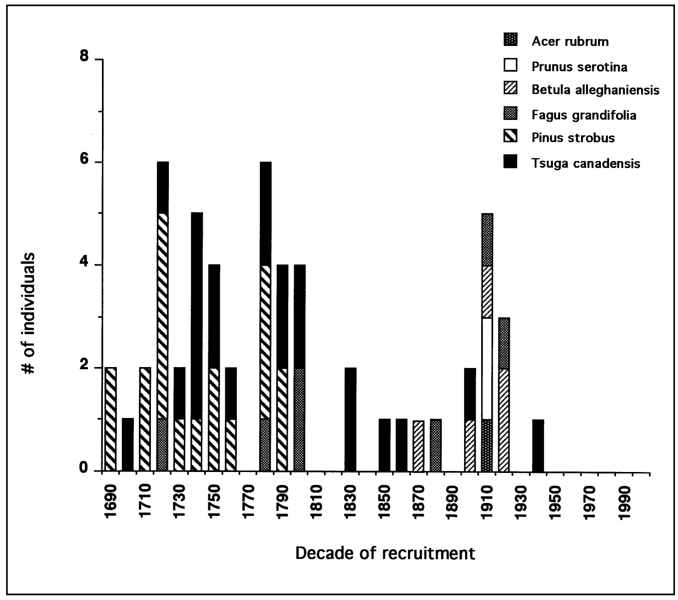

Figure 3. Number of individuals recruiting into the 1.5-m height category by species and decade in an old-growth hemlock–white pine forest at Cook Forest Cathedral Pines in northwest Pennsylvania. Figure adapted from Abrams and Orwig (1996).

Old-growth, old-field white pine. White pine frequently invades abandoned agricultural fields and pastures (called old fields) throughout its range, playing the role of an early-successional, pioneer tree species (Hibbs 1982, Whitney and Davis 1986, Burns and Honkala 1990). Because of the early settlement through much of New England, some old fields have been abandoned for 2 centuries or more. The original white pine that invaded these long-since abandoned fields is now considered to be old growth. In the case of Cathedral Pines near Cornwall, Connecticut, the oldest white pine formed two age classes that were established about 1780 and 1840 (Patterson and Foster 1990). It was considered one of the last remaining stands of old-growth white pine in southern New England. White pine in other forests in central New England dates back to agricultural and pastured fields abandoned in the mid-1800s (Foster et al. 1998). In the case of Cathedral Pines in Connecticut, a severe windstorm in 1989 snapped off or uprooted 90% of the old pine, starting a new cycle of forest succession (Patterson and Foster 1990). Nonetheless, these sites serve as an interesting example of early successional, old-field white pine that formed old-growth forests, given adequate time, and demonstrate the potential effect of windstorms on the dynamics of white pine forest.

Even-age cohorts of white pine in old-growth forests. The range of ages for individual trees of a species can be broad or narrow. A narrow age range often indicates that the trees became established following a marked disturbance event. The age structure of these individuals is generally referred to as an even-age cohort, a condition common to white pine in many forests.

Greenbrier, West Virginia. The species composition, tree ages, diameter structure, and radial growth were studied in a virgin white pine–mixed-oak forest, located on a silt loam, valley floor in the Monongahela National Forest in southern West Virginia (Abrams et al. 1995). The patterns of white pine dynamics in a mixed-oak forest and the effect of fire protection during the last half-century were also evaluated. This uneven-age forest is dominated by white pine (34%), red maple (24%), white oak (*Q. alba*; 13%), northern red oak (7%), and black oak (*Q. velutina*; 6%). White oak and white pine represented most of the oldest and largest trees in the forest, whereas maple, beech, and hemlock were the youngest and smallest (Figure 4). Maximum age was 295 years for white oak and 231 years for white pine. Recruitment of white oak trees was continuous from 1700 to 1900. Most of the white pine recruitment occurred in two pulses (1830–1850 and 1875–1885), both of which were associated with peaks in radial growth of the white pine tree-ring chronology (Figure 4). The peak recruitment of northern red oak and black oak from 1880 to 1900 suggests the possible facilitation of these species by white pine. After the cessation of pine and oak recruitment in 1900, the abundance of maple, beech, and hemlock increased, particularly for red maple.

The results of this study suggest that white pine recruited as even-age cohorts after moderate-scale disturbances (Figure 2c). Similarly, Hibbs (1982) concluded that white pine persists in mixed hardwood forests in New England by group reproduction in small and medium-size gaps. Moreover, white pine in portions of the original forest on the Allegheny Plateau in northwest Pennsylvania was restricted to small, defined areas, having reproduced in even-age cohorts after disturbance (Lutz 1930b). White pine and oak were probably maintained in the Monongahela Forest during the 18th and 19th centuries by periodic disturbance, in particular fire and wind-throw. The lack of recruitment for these species after 1900 and the subsequent increase in later successional tree species indicate the transitional nature of this forest in the absence of fire. Future canopy gaps formed in the forest will most likely be filled with late successional tree species, including red maple, sugar maple, beech, and hemlock, according to their dominance of the overtopped and intermediate canopy classes (Abrams et al. 1995).

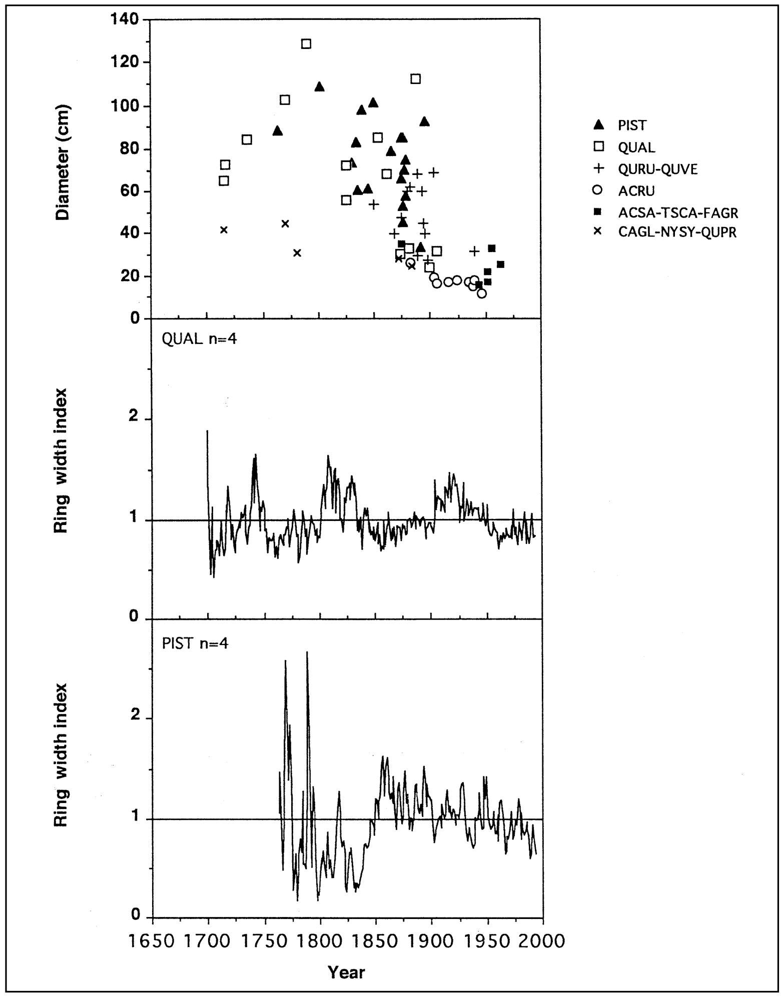

Figure 4. Age-diameter relationships for all cored trees and the mean standardized tree ring index for the oldest **Quercus alba** *and* **Pinus strobus** *in an old-growth forest in eastern West Virginia. PIST,* **Pinus strobus***; QUAL,* **Quercus alba***; QURU,* **Q. rubra***; QUVE,* **Q. velutina***; ACRU,* **Acer rubrum***; ACSA,* **A. saccharum***; TSCA,* **Tsuga canadensis***; FAGR,* **Fagus grandifolia***; CAGL,* **Carya glabra***; NYSY,* **Nyssa sylvatica***; QUPR,* **Q. prinus***. Figure adapted from Abrams et al. (1995).*

Schall's Gap, Pennsylvania. A dendroecological study of an old-growth hemlock forest at Schall's Gap in central Pennsylvania is another example of the disturbance-dependent nature of white pine. The forest is 80%-dominated by hemlock, and it has a small component of white pine and yellow birch. The white pine trees in the forest are strictly even-age, having recruited in a narrow period between 1855 and 1865 (Figure 5). Most of the hemlock was recruited during and shortly after this time. This finding corresponds to a major disturbance in the forest, which increased the hemlock tree-ring growth by 200% shortly after 1855. However, a disturbance of similar magnitude around 1810 apparently did not stimulate a great deal of pine or hemlock recruitment, based on current age structure. The total lack of recruitment for any tree species after 1890 is most likely due to intensive deer browsing, which is characteristic of central Pennsylvania.

Selective logging in old-growth forests. A number of studies reported the formation of even-age cohorts of tree species, including white pine, after selective logging in old-growth forests. For example, partial logging around 1855 in an old-growth hemlock–white pine–hardwoods forest on the Allegheny Plateau in northwest Pennsylvania stimulated a major recruitment period for white pine, red oak, beech, and hemlock (Orwig and Abrams 1999). A similar finding was

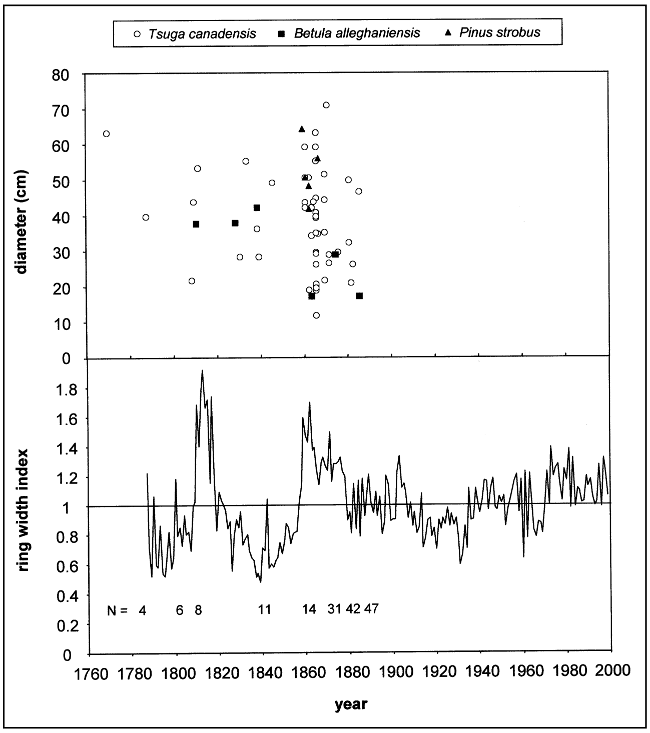

Figure 5. Age-diameter relationships for all cored trees and the mean standardized tree ring index for **Tsuga canadensis** *in an old-growth forest at Schall's Gap in central Pennsylvania. Figure from Black and Abrams, School of Forest Resources, Pennsylvania State University.*

reported for the old-growth forests at Bear Meadows Bog in central Pennsylvania, in which selective logging around 1890 stimulated the establishment and growth of early, middle, and late successional tree species, including white pine, red maple, yellow birch, black spruce (*P. mariana*), and hemlock in the subsequent half-century (Abrams et al. 2001). Selective and more complete logging in old-growth forests at the Alan Seeger Natural Area in central Pennsylvania in the early 1800s greatly increased even-age cohorts of oak, birch, white pine, red maple, and hemlock (Nowacki and Abrams 1994). These studies suggest that tree species representing both gap opportunist, including white pine, and late successional species exhibit large increases in recruitment in canopy openings created by selective logging.

Uneven-age white pine in old-growth hemlock: Ice Glen Natural Area, Massachusetts. The dynamics of an old-growth hemlock–white pine–northern hardwood forest on the extreme slope (65%) at Ice Glen Natural Area in the Berkshire Hills of southwest Massachusetts was studied (Figure 2e; Abrams et al. 2000). The forest grows on a stony, silt loam soil and is dominated by hemlock (60%), white pine (12%), and red maple (10%). Hemlock is the oldest species in the forest, with maximum ages of 305–321 years (Figure 6). The maximum ages for white pine and several hardwood species are 170–200 years old. Recruitment of hemlock trees was continuous from 1677 to 1948. All of the existing white pine recruited from 1800 to 1880, when it formed an uneven-age population within the uneven-age hemlock canopy. This recruitment seemed to be facilitated by a series of moderate disturbances to the stand in the early to mid-1800s (Figure 6). Nearly all of the hardwood species also recruited between 1800 and 1880, but after 1900 recruitment for all species declined dramatically.

The apparent cessation of white pine recruitment after 1880 at Ice Glen may be attributable to the relative intolerance of this species to old-growth understory conditions, including low light, organic seedbed, and high root competition (Cline and Spurr 1942, Abrams et al. 1995). The tree-ring chronology indicates the absence of major standwide disturbances between 1860 and 1945, which may have retarded recruitment of white pine in favor of the later successional hemlock. A lack of tree regeneration and limited overstory re-

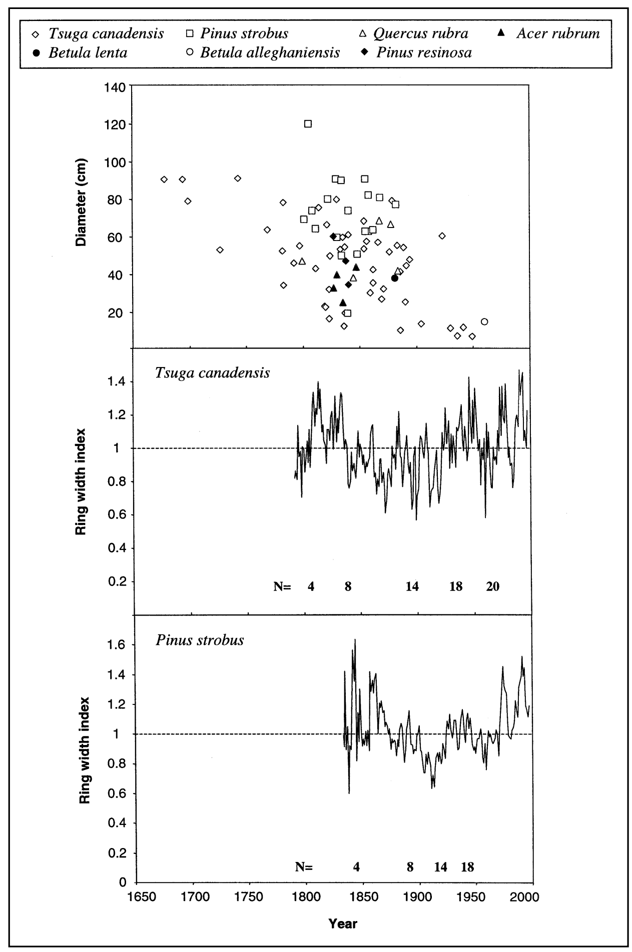

Figure 6. Age-diameter relationships for all cored trees and the mean standardized tree ring index for the oldest 20 **Tsuga canadensis** *and 18* **Pinus strobus** *in an old-growth hemlock–white pine–northern hardwood forest at the Ice Glen Natural Area, southwest Massachusetts. Figure adapted from Abrams et al. (2000).*

cruitment during the 20th century in this forest may be attributable to intensive deer browsing, as observed in many of these old-growth forests.

Scattered individuals of white pine in old-growth oak. Most forests are a mixture of dominant and subordinate species. In addition, many forests contain just a few scattered individuals of a species that appear at random moments in the history of a forest. White pine is known to exist as scattered individuals in forests for many reasons, including severe edaphic or ecological constraints.

Detweiler Run, Pennsylvania. The ecological history of a 326-year-old forest on a steep talus slope was studied in central Pennsylvania (Ruffner and Abrams 1998). The forest is dominated by chestnut oak (39%), red maple (17%), black birch (13%), black gum (*Nyssa sylvatica*; 12%), red oak (9%), and white pine (7%). The witness tree record and wood remains on the site indicate that chestnut used to be an important component of this forest. The forest had fairly continuous recruitment of chestnut oak from 1660 to 1950 (Figure 7). Most of the red maple and red oak recruitment occurred in the early 1900s and was probably associated with chestnut blight mortality. White pine exists as scattered individuals of ages ranging from 30 to 245 years. Three of the most recent recruits at the site are white pine, which may be in response to gypsy moth defoliation and the resulting selective mortality of the oak overstory. White pine is likely to find opportunities for gap capture and will persist as scattered individuals into the foreseeable future, but it is unlikely to become a dominant component on this talus slope forest.

White pine in the oak understory. Substantial white pine regeneration can form under an oak canopy throughout much of the northern forest. White pine saplings had a density of 80–130 stems per ha on transitional mesic and dry–mesic red oak sites in north-central Wisconsin (Nowacki et al. 1990). White pine was the principal sapling species, with 117 stems per ha, in mixed-oak, upland slope forest at the Alan Seeger Natural Area in central Pennsylvania (Nowacki and Abrams 1994). According to Henry David Thoreau's observations of forest succession in Concord, Massachusetts, in the 19th century, white pine invaded the understory of oak forests and oak invaded the understory of white pine forests, allowing for reciprocal replacement of the two species (Whitney and Davis 1986). Hibbs (1982) concluded that white pine could survive and grow through the understory of mixed-hardwood forests in southern New England by group reproduction. Moreover, in mixed-hardwood forests, white pine has the advantage of being an evergreen among deciduous species: It may utilize favorable growth conditions in the nonsummer months when the hardwoods are leafless (cf. Lassoie et al. 1983) and compete with some tree species of similar or lesser understory tolerance (e.g., oak, cherry [*Prunus*], and birch). Nonetheless, for white pine trees to persist over long time periods and to move into the oak forest canopy, they probably need to be released in gaps because of the likelihood that the white pine's shade tolerance will diminish with age.

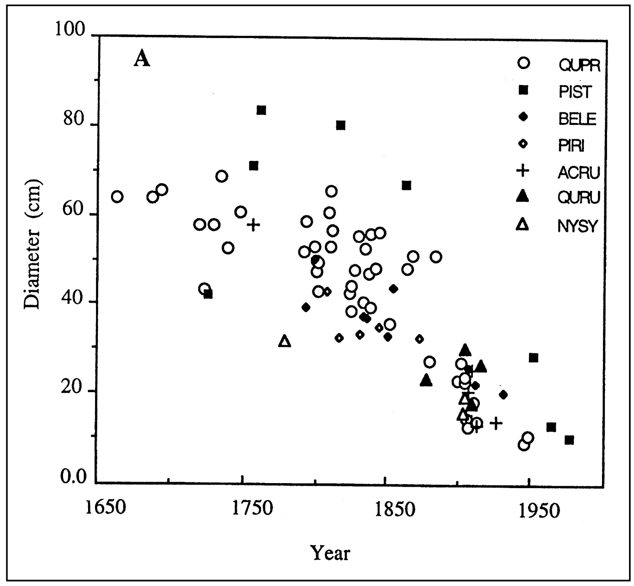

Figure 7. Age-diameter relationships for all cored trees in an old-growth chestnut oak forest on a talus slope at Detweiler Run in central Pennsylvania. QUPR,* Quercus prinus*; PIST,* Pinus strobus*; BELE,* Betula lenta*; PIRI,* P. rigida*; ACRU,* Acer rubrum*; QURU,* Q. rubra*; NYSY,* Nyssa sylvatica*. Figure adapted from Ruffner and Abrams (1998).

White pine as a climax type. The combination hemlock–white pine–northern hardwoods is listed as a climax association in eastern North America by Braun (1950). She questioned the climax status of white pine for much of the range, but she did suggest that it is a climax dominant in the westernmost part of the area, where hemlock is absent. Indeed, a virgin, postfire forest on a lakeshore in west-central Ontario had white pine present in all age classes up to 190 years (Holla and Knowles 1988). Seedlings younger than 10 years had a 63.5% mortality rate per decade. By the time white pine reached the age of 40 years, its mortality dropped to less than 6%. A fire of moderate intensity in the early 1900s contributed to an increase in white pine in that age class. Similarly, white pine was reported to be self-replacing, based on its abundance across all diameter and canopy classes, in old-growth forests on steep, rugged escarpments in east-central Ontario (Quinby 1991). The recruitment of white pine in these forests was most likely facilitated by periodic surface fire, wind-throw, and death of larger individuals. The results of these studies suggest that white pine near its northern limit is self-maintaining, but it certainly benefits from disturbance events. In addition, white pine was reported to be a physiographic climax on ridge tops in New England (Cline and Spurr 1942). However, on better-quality sites outside the northern and western limits of its range, white pine is not a climax species in the traditional sense because of its low-to-moderate shade tolerance. Its recruitment tends to be episodic and linked to disturbance, especially in old-growth forests.

Role of fire and wind. Most studies dealing with the ecology of white pine in the original forest discuss the importance of fire or wind or both in the life history of the species. White pine is known to be particularly sensitive to wind-throw because of its tall stature, often growing as an emergent in eastern forests, and its shallow rooting (Cline and Spurr 1942, Foster 1988b, Patterson and Foster 1990, Foster and Boose 1992). Moreover, ice and snow load may cause frequent canopy pruning and top snapping of white pine. Nichols (1935) concluded that the origin of white pine in the climax forest characteristically dates back to a forest fire or some other calamity. Fire and wind were considered to be common disturbances in the virgin pine–hemlock forests of southwest New Hampshire (Cline and Spurr 1942): Old-growth white pine forests at the Pisgah tract in southwestern New Hampshire formed after a fire in the 1660s and were leveled by a hurricane in 1938; another forest in New England—Cathedral Pine, Connecticut—was blown down by severe winds in 1989 (Henry and Swan 1974, Foster 1988a, Patterson and Foster 1990). Moreover, white pine needs a combination of both extensive wind-throw and fire for successful establishment; wind-throw by itself may not be adequate (Foster 1988a). Indeed, much of the white pine in the original forests of northwest Pennsylvania can be traced back to major fires and tornadoes (Lutz 1930b, Hough and Forbes 1943).

Evidence of fire or blow-down is consistently noted in the early land surveys of northern forests containing white pine (Lutz 1930a, Seischab and Orwig 1991, Marks and Gardescu 1992, Zhang et al. 1999). In the presettlement forest of northeastern Wisconsin, complete canopy wind-throw averaged 4828 ha annually, with an estimated return interval of 1210 years (Canham and Loucks 1984). In northern-lower Michigan, presettlement forests of mixed-pine, pine–oak, and hemlock–white pine–northern hardwoods burned at intervals of 129–258 years, 172–342 years, and 1389–2778 years, respectively (Whitney 1987). However, virgin mixed-pine forests in Minnesota burned at intervals of 10–40 years (Spurr 1954, Heinselman 1973).

Researchers believe that infrequent fire about every 100–200 years maintained oak, white pine, chestnut, and hickory (*Carya*) on upland sites in the precolonial forests of central New England (Foster et al. 1998). White pine and red pine forests in northern Minnesota had a natural fire rotation of about 100 years (Heinselman 1973), whereas white pine forests along a historic travel corridor in southern Ontario burned on average every 15 years between 1721 and 1937 (Dey and Guyette 1996). Paleoecological data also suggest a linkage between fire and white pine perpetuation across the northeastern United States (Clark and Royall 1996).

Conclusion

A review of the witness trees and dendroecological data from old-growth forests indicates a high level of versatility, or ecological breadth, for eastern white pine in the pre-European settlement forest. White pine was widely distributed in northern forests of the eastern United States and grew in densities ranging from nearly pure stands to scattered individuals. At the regional level, its dominance probably did not match that of beech, sugar maple, hemlock, or oak. In present-day old-growth forests, white pine is much more likely to grow with hemlock or oak than with beech or sugar maple. This compatibility may also be true for the presettlement forest, but witness tree data are generally not discernible at that fine a scale. White pine occupied a wide range of sites, including swamps, river valleys, sideslopes, sand plains, and dry, rocky ridges. White pine is also capable of growing on nutrient-poor soils and may be outcompeted by sugar maple and beech on nutrient-rich mesic sites (Burns and Honkala 1990). Thus, white pine grew in some of the wetter and drier nutrient-poor sites in the northern forest, resulting in a quasi-bimodal distribution.

Fire and blow-down are two common disturbing agents associated with white pine in eastern forests. White pine is one of the most susceptible trees to wind-throw because of its height and shallow rooting (Foster and Boose 1992). Its foliage is flammable in both green and dry, brown conditions. Forests dominated by white pine are susceptible to both crown and understory fires, depending on composition, structure, stand age, and climate conditions. Large blow-down areas of pine and hemlock were prone to subsequent burning, a set of conditions that can facilitate a new generation of white pine (Cline and Spurr 1942, Henry and Swan 1974, Foster 1988a). Because young white pine has a thin bark and older individuals have a very thick bark, its tolerance to understory burning will range from low to high, depending on tree age and size.

White pine recruited in a wide range of ecological conditions in old-growth forests. This article has examined examples of white pine that dominated the early and middle stages of succession, forming even-age or uneven-age cohorts or scattered individuals after small to moderate-scale disturbances in uneven-age hemlock and oak canopies, and were self-maintaining in nearly pure stands at the northern limit of its range. This variety of successional pathways gave white pine plenty of opportunities to thrive in the presettlement forest. Once established in the overstory, white pine can live up to 300 years (and occasionally up to 400 years), during which time it can produce large quantities of seed for regenerating in surrounding disturbed areas, both within and outside the immediate stand. Presently, many of the younger white pine stands in eastern forests are the result of the trees' invasion of old fields after agricultural abandonment.

Even though white pine is often a component of late-successional forests, it is not a climax species in the traditional sense. Rather, it is classified as a disturbance-dependent species (Lutz 1930b, Cline and Spurr 1942, Hough and Forbes 1943). In most forests, the amount and duration of white pine recruitment is often directly proportional to the intensity of disturbance. Typical climax species, such as hemlock, sugar maple, and beech, exhibit continuous, long-term recruitment into an uneven-age forest canopy without periodic disturbance. White pine does not have this ability, with the possible exception of stands with extreme latitude or edaphic conditions; however, even these stands are typically subjected to disturbance. Dendroecological studies indicate that the presence of white pine in late-successional hemlock forests is related to its being a long-lived species that established after large-scale disturbance or to its recruitment in the gap phase. Moreover, white pine can be successful in most subclimax forests and disturbed areas across a broad range of soils and sites. However, white pine and oak will most likely be replaced by later successional species in the absence of periodic understory fire, as happened at Greenbrier, West Virginia (Abrams et al. 1995).

White pine was only occasionally listed as a dominant in witness tree records. A major limitation of white pine in the original hemlock–white pine–hardwood forest was the relatively low frequency of fire and catastrophic blow-down in these northern forests. Return intervals of 800–2000 years for large-scale disturbance were not adequate to sustain continuous, large-scale white pine recruitment, and they probably limited its presence to small and medium-size gaps in mature forests (Lorimer 1977, Canham and Loucks 1984, Whitney 1987, Clark and Royall 1996). In contrast, hemlock, sugar maple, and beech prospered in these forests without catastrophic disturbance. Large, persistent areas of white pine in the original forests may have been mainly limited to coarse-textured, fire-prone areas in the Lake States and New England, which were not conducive to late-successional, mesophytic, nutrient-demanding, or fire-sensitive species (Whitney 1994, Cogbill 2000).

Very little of the original eastern forests remain because of intensive cutting over the last two or three centuries. The few extant tracts of presettlement-origin white pine are reaching their maximum longevity. Most comparisons of presettlement versus present-day forest composition indicate an over-all decline in white pine dominance in eastern forests (Whitney 1987, Abrams and Ruffner 1995, Frelich 1995, Abrams and McCay 1996, Foster et al. 1998, Zhang et al. 2000). Some areas saw an increase in white pine because of its invasion of abandoned farmlands. However, the losses in white pine from the original forests are not being fully compensated for by its increase in abandoned pastures or agricultural areas.

The studies reviewed here indicate that most old-growth hemlock–white pine forests have exhibited very little recruitment of new trees over the past 50–100 years, probably because of intensive deer browsing and lack of fire. Large increases in red maple may have further exacerbated the decline in white pine and are likely to continue into the foreseeable future (Abrams 1998). Therefore, these stands are being seriously affected, both directly and indirectly, by anthropogenic factors. If current forest management practices—less cutting and less fire—and high deer pressure continue, the result may well be a continued decline in white pine.

The approach taken in this study—that is, coupling witness tree records with the dendroecology of old-growth forests and land-use history—can be applied to other species and regions in North America. Moreover, the study of old-growth forests in the United States should have high priority, for ecologists and tree-ring scientists have much to learn from the past, and they must do so before the pre-European settlement information contained in the oldest trees is lost.

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