RESEARCH ARTICLE

Disturbance History of Two Natural Areas in Wisconsin: Implications for Management

James E. Cook

College of Natural Resources
University of Wisconsin–Stevens Point
Stevens Point, WI 54481 USA
jcook@uwsp.edu

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ABSTRACT: A thorough understanding of the changes in a disturbance regime caused by European settlement of North America can contribute to better management of natural areas. Using multiple information sources, I investigated the disturbance regimes, since the time of overstory establishment, in two Wisconsin natural areas. The objectives of the study were to determine if significant changes had occurred and to assess the relative importance of natural and anthropogenic disturbances. The two areas differ in overstory composition—one is white pine and oak dominated, whereas the other is largely composed of northern red oak and sugar maple. The current overstories became established over a 60+-year period beginning in the mid-1800s, prior to extensive settlement. A series of low- to moderate-intensity disturbances created canopy openings that led to recruitment of present canopy members. In New Hope Pines, the white pine/oak forest, a combination of logging, low-intensity fire, and natural disturbances resulted in peak establishment between 1891 and 1911. In the northern red oak/sugar maple forest, Haskel-Noyes Memorial Woods, all disturbances since 1850 were probably natural but did not include fire. A moderatly intense disturbance, probably wind, initiated the northern red oak cohort that currently dominates the overstory. Accordingly, fire suppression this century has not affected Haskel-Noyes, whereas its exclusion from New Hope Pines has reduced pine and oak establishment and allowed red maple to increase dramatically. The rate of canopy gap formation appears to have accelerated recently, though median gap sizes are relatively small—30 m^2 at New Hope Pines and 48 m^2 at Haskel-Noyes. Given the disturbance history of these two areas, it is highly probable that the current composition and structure will not persist under the current disturbance regimes. White pine and oak dominance at New Hope Pines could be maintained by judicious use of prescribed fire in conjunction with creation of canopy openings. Size class distributions suggest a strong successional trend toward sugar maple at Haskel-Noyes. A moderately intense disturbance that creates gaps greater than about 0.3 ha will be required to keep northern red oak at its current level of abundance. This study demonstrates the value of using many information sources to reconstruct and describe disturbance regimes and thereby provide valuable information to natural area managers.

Index terms: age structure, disturbance regimes, maple, northern red oak, white pine,

INTRODUCTION

Natural areas are commonly established to preserve representative communities, especially threatened ones, and to provide areas where natural processes and changes can be studied (e.g., Hunter and Swisher 1983, Nowacki and Abrams 1994). In Wisconsin, "natural area" is defined as "an area of land or water which has education-al or scientific value, or is important as a reservoir of the state's genetic or biologic diversity" (95-96 Wisconsin Statute 23.27). Given these purposes, it is crucial to be able to identify the factors that led to cur-rent community composition and to anticipate vegetation changes that are likely to occur in natural areas.

Forest ecosystems are dynamic entities and rarely reach a state that would be considered equilibrium (e.g., Sousa 1984, Reice 1994). One of the primary driving forces of the temporal changes in terrestrial communities is disturbance (Pickett and Thompson 1978, White 1979, Attiwell 1994, Reice 1994). The primary characteristics of disturbances that determine their precise effects are size, intensity, frequency, and the length of time since the last disturbance (Pickett and Thompson 1978, White 1979, Pickett and White 1985, Perry 1994). A change in the dominant type of disturbance or in its frequency can lead to a different successional pathway, that is, a different community (Abrams et al. 1985, Keane et al. 1990, Cook 1996). Even for Beres in which community-level parameters (biomass, basal area, richness, etc.) stay relatively constant, the abundance and/ or frequency of species can change greatly in response to different frequencies, types, and intensities of disturbance (Attiwell 1994).

Two studies from Pennsylvania clearly illustrate the effects of a changing disturbance regime on the composition of natural areas. Logging and fires in oak-pine forests in central Pennsylvania during the settlement era led to increased oak *(Quercus* spp.) dominance (Abrams and Nowacki 1992). A de-crease in the frequency of these disturbance types during the twentieth century has facilitated widespread establishment of late-successional species such as red maple *(Ater rubrum* L.) and sugar maple *(A. saccharum* Marsh.). Thus, the change in disturbance regime from the 1800s to 1900s is leading to an overstory composition quite different from that of the presettlement forest (Abrams and Nowacki 1992). In the other natural area, an old-growth mixed pine-hardwood forest, eastern white pine *(Pinus strobus L.),* yellow poplar *(Liriodendron tulipifera L.),* and oaks became more abundant in the canopy, whereas maples, yellow birch *(Betula alleghaniensis* Britton), and eastern hemlock *(Tsuga canadensis [L.]* Can.) recovered very slowly from settlement-era disturbances (Nowacki and Abrams 1994).

In the Great Lakes Region fire was an integral part of the disturbance regimes of white pine or white/red pine (P. *resinosa* Ait.) forests before European settlement. Stand-replacing fires occurred once every 120–250 years (Frissell 1973, Heinselman 1973, Ahlgren 1976, Grimm 1984, Whitney 1986, Loope 1991, Frelich 1992). In contrast, in sugar maple dominated communities the return interval for stand-replacing fires was greater than 1,000 years (Whitney 1986, Frelich and Lorimer 1991). The frequency of large-scale, intense, wind-generated disturbances was 1/1,200 years, or longer, for both community types (Canham and Loucks 1984, Whitney 1986). Therefore, the vast majority of pine-dominated forests present at the time of European settlement are thought to have originated from intense fire (e.g., Heinselman 1973, Cwynar 1977), whereas only a small percentage of sugar maple stands extant at that time could be attributed to large-scale disturbance events (Canham and Loucks 1984, Frelich and Lorimer 1991).

In the Great Lakes Region, the disturbance regime changed greatly after European settlement. Settlement brought new disturbances (e.g., harvesting, clearing) and altered the frequency and intensity of fire (Stearns 1992, Johnson 1995, Pyne et al. 1996). The post-European settlement disturbance regime has not affected all species equally; at a regional level it led to a significant decrease in some species (e.g., white pine, Stearns 1992), whereas other species have become more abundant (e.g., sugar maple, Lorimer 1985a).

Given the disturbance history of the region, we would expect white pine dominated forests to be affected by fire suppression more than sugar maple forests. However, the disturbance regimes in these types *of* forests included at least two types *of* disturbance, and we do not know if the disturbances interacted. In addition, human activities (e.g., harvesting, firewood cutting) could produce a similar or different successional pathway than that produced by the natural disturbance regime. Thus, it is important for biologists and land managers to have, whenever possible, comprehensive, site-specific information about the disturbance regimes *of* the natural areas they manage. To illustrate how this site-specific information can be obtained, a case study approach was unclertaken in central Wisconsin to (1) de-scribe and characterize the disturbance regime of two natural areas—one pine-oak dominated and the other a northern red oak–sugar maple forest; (2) compare the disturbance regime of each community during the time of establishment to that of the post-establishment period (pre- versus post-settlement); and (3) evaluate the roles of natural and anthropogenic disturbances in producing the current composition and structure of the two natural areas.

METHODS

Study Areas

The two natural areas in central Wisconsin selected for intensive study were chosen for two reasons. In each area, a recent baseline inventory provided data on the current structure and composition of the forest (Leitner 1988, Cook 1990). I also chose them because I hypothesized that the two natural areas had responded differently to European settlement-induced change in their disturbance regimes.

New Hope Pines

This 71-ha natural area is a white pine dominated Northern Dry-Mesic Forest (sensu Curtis 1959) located in Portage County, the approximate geographic center of Wisconsin. Other species found in the overstory include red pine, white oak *(Q. alba L.),* northern red oak *(Q. rubra L.),* and bigtooth aspen *(Populus grandidentata* Michx.) (Table 1) (Cook 1990). The midstory is dominated by red maple. The forest is located on the rolling topography of a ground moraine from the Wisconsin glaciation. The soil is a sandy loam over sandy glacial till. The last significant harvest, which was primarily of broad-leaved species, occurred in 1938. Only limited, selective harvesting for firewood occurred between 1939 and 1983, when the forest was designated a state natural area. Tesch (1982) described the presettlement vegetation of this general area as a "zone of intermingling between an oak community and a white-red pine community. Possible white-red pine intrusions into the oak community may have occurred." In the 1840s, before significant European settlement, the area to the west was dominated by oak savanna (Finley 1976). Pollen analyses from bogs in eastern and east-central Wisconsin indicate that pines and oaks dominated the landscape from the hypsithermal (approximately 8,000 years BP) to the early 1800s, and oak savannas were probably present (West 1961, Schweger 1966).

Haskel-Noyes Memorial Woods

This natural area comprises 27 ha, of which 21 ha is Southern Mesic Forest (sensu Curtis 1959). Only the Southern Mesic Forest was included in this study. Haskel-Noyes is located approximately 100 km southeast of New Hope Pines in Fond du Lac County. The overstory is composed primarily of northern red oak and sugar maple, but seven other species are present that exceed 10 cm dbh (diameter at breast height) (Table 1) (Leitner 1988). The midstory is dominated by sugar maple. As with New Hope Pines, this forest sits on a moraine—specifically an

Table 1. Site, disturbance history, and disturbance characteristics of two state natural areas in Wisconsin.

	New Hope Pines	Haskel-Noyes
Overstory composition	WP[a], WO, RO, RP	RO, SM
Midstory dominant	RM	SM
Size (ha)	71	21
Surface soil texture	Sandy loam	Loam, silt loam
Logging history	Selective logging, 1800s, 1938	Never logged
Fire history	Low intensity, mid 1800s through approx. 1930	No fire for at least 200 years
Overstory establishment period	1848–1941	1846–1921
Median overstory age	Pine = 87, Oak = 85	RO = 113, SM = 96
Dominant gap origin, 1982–1991	Standing dead	Wind snapped
Median gap size (m^2), 1982–1991	30	48
Annual gap formation rate, 1982–1991	0.5%	0.8%
Percent of gaps multiple age	38%	42%
Pit and mound density (#/ha)	3	1.5

[a] Species abbreviations: WP = eastern white pine, RP = red pine, WO = white oak, RO = northern red oak, RM = red maple, SM = sugar maple

interlobate moraine between the Green Bay and Lake Michigan Lobes from the Wiscon-sin glaciation. The soils are barns and silt barns with a high percentage of gravel. The forest has never been logged, not even se-lectively, except perhaps for a 2-ha patch in the north end (C. Smith, former land man-ager of Haskel-Noyes, pers. corn.). This purported lack of harvesting is supported by two reports. The "Appraisal Report," filed on January 9, 1947, stated that the "tract resembles a virgin hardwood forest." An inspection report from 1966 says: "This near climax hard maple-red oak forest was pur-chased in 1947 to prevent its imminent de-struction by logging" (records on file, Bu-reau of Endangered Resources, Madison, Wisconsin). Furthermore, the land managers and state records attest to a complete absence of fire this century (C. Smith, pers. corn.). Thus, all evidence that existed prior to this study indicated that this forest was "virgin" in the sense that it had not been logged or burned by Euro-Americans. Ac-cording to Finley (1976), this general area supported a maple-basswood-oak forest be-fore European settlement.

Field Methods

The disturbance regimes of the two areas since the mid-1800s were determined using a variety of indicators and types of information (after Lorimer 1985b): (1) tree diameter distributions, (2) age structure and composition of overstory and midstory, (3) diameter growth rate patterns, (4) fire scar analysis, (5) charcoal presence in the top soil, (6) visible (current) canopy gaps, and (7) abundance of pit-and-mound topography. The basic tenet behind this approach is to use as many sources of information as possible, because each has its limitations and collectively they pro-vide a clearer picture of the disturbance regime than just one or two sources pro-vide (Lorimer 1985b). Accordingly, I also used three other sources: (1) aerial photo-graphs from 1938, 1968, and 1979 (New Hope only); (2) diameter-age relationships; and (3) autecological differences among dominant tree species.

Overstory Composition and Structure

A standardized (Wisconsin Department of Natural Resources, Bureau of Endangered Resources, Natural Areas Program, Mad-ison) baseline vegetation inventory was conducted at each site. All stems greater than 10 cm were recorded by species and diameter in twenty 10-m x 25-m plots. The plots were systematically distributed over each natural area from a random starting point along a base line.

Transects: Canopy Gaps and Pit-and-Mound Topography

Ten meter-wide belt transects, distributed systematically (30–50 m apart) following a random start, were used to collect data on gap size and frequency, on cause of gap formation, and on the number of pit-and-mound pairs. At New Hope Pines, 16 north–south belt transects totaling 4,115 m were inventoried. This equates to a sample intensity of 7.1%. Eleven transects oriented east–west were sampled at Haskel-Noyes. The total transect length was 1,925 m, or 9.7% of the forest. These transects were oriented perpendicular to the prevailing morainal ridges. To exclude edge-induced effects, transects were not sampled in a 30-m buffer along all natural area boundaries. The transects were sampled between July and October of 1991.

All overstory gaps that intersected the belt transects were measured. A gap was de-fined as an opening in the upper canopy, and gap size was determined from two perpendicular diameters measured from crown edge. The cause of each gap was recorded as snapped tree, windthrow, light-ning, or died in place (standing dead) due to no obvious cause. This latter class in-cluded any disease or insect-caused mor-tality. Some gaps formed over several years and thus spanned two of the age classes established (see below). These gaps are referred to as multiple-age gaps.

Previous work with down trees (coarse woody debris) has indicated that certain taxa fragment and deteriorate structurally at reasonably consistent rates (Harmon et al.1986, Chueng and Brown 1995). Be-cause the finer components of coarse woody debris (leaves, twigs, small branch-es, and bark) fragment much faster than the bole of a tree (Harmon et al. 1986), these components have been used to assign down logs to decay classes (Hunter 1990). I therefore utilized the expected patterns of fragmentation, supplemented by my observations over a three year period (1990–1992), to establish the age class-es shown in Table 2.

Little work has been done with fragmentation of coarse woody debris in the eastern United States (Harmon et al. 1986). How-ever, the data available (silver maple *[Ater saccharinum* L]. from Chueng and Brown [1995] and yellow poplar from Harmon et al. [1986]) are consistent with the loss rates of bark and small branches incorporated into the scheme in Table 2.

Age and Fire Scar Inventory

All overstory trees in the transects, and a few oaks outside, were carefully examined for fire scars, following the criteria of Lorimer (1985b) and Barrett and Arno (1988). On all trees with external evidence resembling a fire scar, two cores were taken at approximately 30 cm above ground, following the recommendation of Sheppard et al. (1988). The diameter of the cored trees ranged from 25 to 91 cm (n=30, New Hope Pines) and from 23 to 54 cm (n=18, Haskel-Noyes). An additional 42 (New Hope) and 5 (Haskel-Noyes) trees were aged without recording diameter. These data were collected in the fall of 1991.

Table 2. Down-tree characteristics and corresponding age classes used to estimate the age of canopy gaps at New Hope Pines and Haskel-Noyes natural areas, Wisconsin.

Characteristics of Gap Maker	Gap Age Class (years)
Foliage or all fine twigs present	< 1
Most fine twigs present; bark on branches breaking up	1–2.5
All or most fine twigs gone; some bark on smaller part of bole gone	3–4.5
Virtually all bark gone from bole; no crown structure except large (>–10 cm) branches	5–6.5
All bark gone; surface of wood starting to soften; all branches in crown gone	7–9

Charcoal in Soil

I used a systematic inventory to search for charcoal in the soil. After a random start, I located a series of 8-cm x 8-cm quadrats throughout each natural area. At each quad-rat the leaf litter was carefully removed and the humus layer (the soil horizon in which organic matter is being incorporated into the mineral soil) was meticulously examined for charcoal fragments. The quadrat was then excavated with a trowel to a depth of 5 cm. This 5-cm slice was sifted carefully and examined for charcoal fragments. In addition, at least two walls of the pit were inspected for evidence of a charcoal layer. The intensity of this inventory was approximately one quadrat per hectare. These data were collected during the fall of 1996.

Analyses

Tree Cores

All cores were sanded and examined in the laboratory under a binocular scope. The diameter growth rate patterns were utilized to derive an estimate of the frequency of release presumed to follow gap formation, from 20 years after establishment until 1980. The first 20 years were excluded because the trees (seedlings and saplings at that time) may have been in a moderately open environment, or, if they were in the shade of small trees, the death of a midstory tree could result in a marked increase in growth rate. Lorimer (1985b) proposed a 10-year growth increase of at least 100% as a criterion to indicate a release event. This criterion seems too conservative given the fact that the majority of gaps in temperate forest are small (< 200 m^2) (Runkle 1982, Webb 1989, Cho and Boerner 1991, Clinton et al. 1993; but see Romme and Martin 1982), and thus would fill in rather quickly by expansion of adjacent trees (Hibbs 1982, Webb 1989). Therefore, my criterion was a 5-year growth increase of at least 50%, which is slightly more stringent than that used by Henry and Swan (1974). To decide when a release event had occurred, each 5-year growth rate (beginning with an age of 25) was compared to the rate in the previous 5 years. Thus, a 10-year period of growth was involved in each determination. There-fore, it is possible, but highly unlikely, that weather produced the growth pattern used to indicate a release. See Appendix for examples of growth rate patterns.

Gap Formation Rates, 1982–1991

An approximation of the aerial extent of canopy gap formation for the 1982–1991 period was calculated from the median gap size, the average number of gaps formed each year, and the total area of the transects. These data were used in two ways. Each gap was assigned to an age class using the estimated age of the gap makers (see Table 2); for multiple-age gaps, the gap was assigned to its oldest age class. This approach provided a way to look for changes in recent gap formation rates, and a way to compare the two disturbance regimes. The second purpose for collecting these data was to estimate the annual rate of gap formation over this 10-year period. The percent of canopy opened up annually during this period was calculated from data for the 10-year period using the following formula: (average number/year x median size) 1 area of transect (Romme and Mar-tin 1982).

Statistical Analyses

A chi-square test was employed to test between the two natural areas for differences in rates of canopy gap formation between 1982–1991 and causes for the gaps. The relationship between age and diameter of overstory trees was explored graphically for each forest, and then tested for a significant relationship with linear regression. Because sample sizes were unequal and relatively small, I used a Mann-Whitney U-test to determine if the median ages of the overstory northern red oak differed from those of overstory sugar maple in Haskel-Noyes Natural Area. The ages were compared to determine if there was significant temporal separation in time of establishment between these two over-story dominants. A similar comparison was

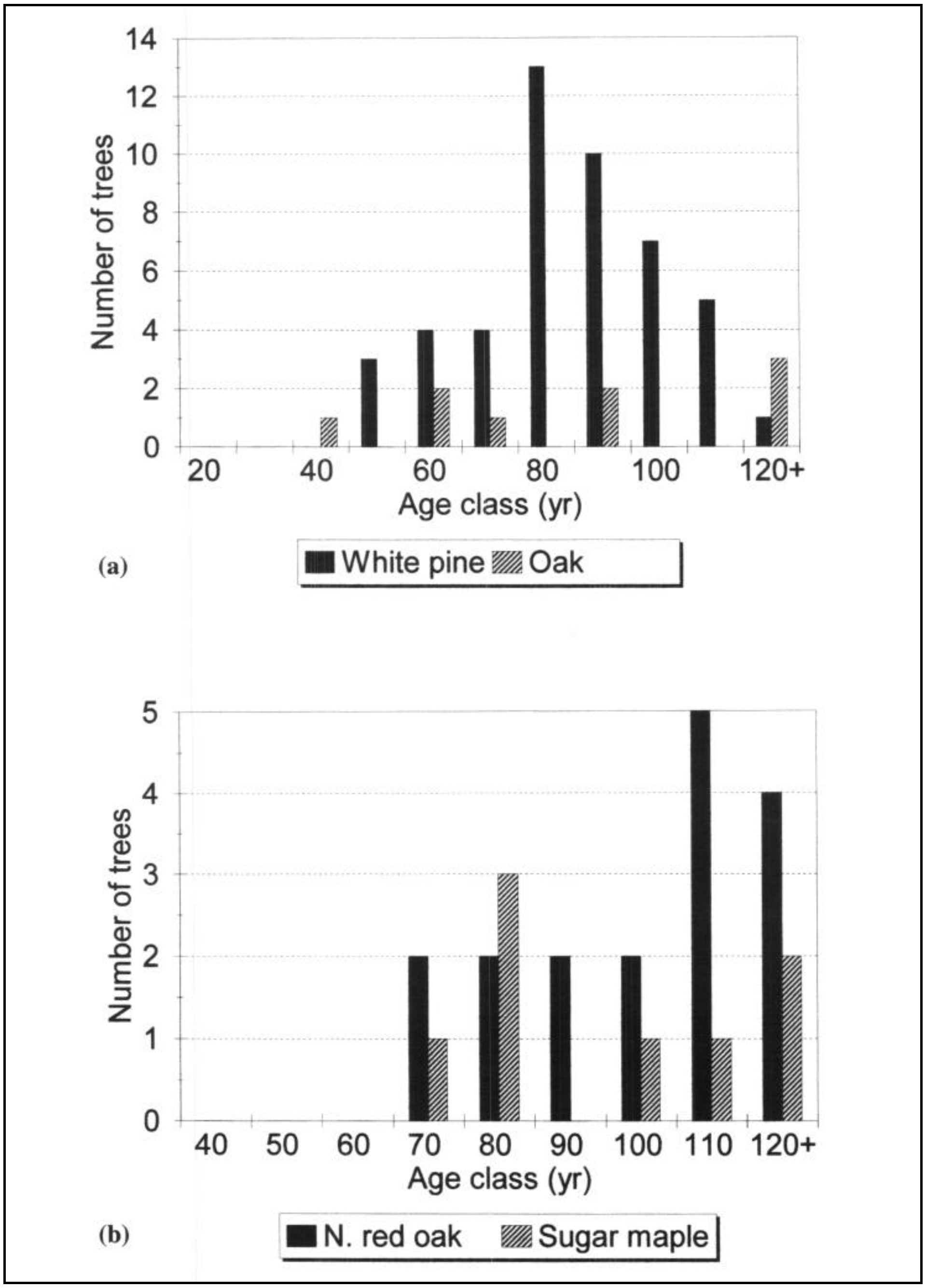

Figure 1. Age structure in 1991 of the overstory dominants at two natural areas in Wisconsin. (a) Structure for white pine and oaks at New Hope Pines Natural Area, Portage County. (b) Structure of northern red oak and sugar maple at Haskel-Noyes Memorial Woods, Fond du Lac County.

not made for New Hope Pines because the age range data for the oaks and pines were very similar (see Results/New Hope Pines below). A relationship, pattern, or test was considered significant if the p-value was < 0.10.

RESULTS

New Hope Pines

Overstory Establishment Period (1848–1941)

The percents of the total basal area of trees greater than 10 cm for each of the major species were as follows: white pine—49.3%, red pine—5.0%, white oak—11.2%, northern red oak—7.0%, and red maple—14.0% (Cook 1990).

The age (at 30 cm) range of the overstory (trees > 10 cm) at New Hope Pines was 58–143 years, with median ages of 87 and 85 years for the pine and oak, respectively (Table 1). The oaks had a greater age range (63–143) than the pines (58–120), but white pine dominated the upper stratum of the forest. Based on these age data, the overstory establishment period lasted from 1848 until 1941. For white pine, the peak period of recruitment was 1881–1911 (the 80–100 year age classes, Figure IA), whereas the oaks did not exhibit any distinct pattern. The two oak species were considered collectively because they have similar requirements for establishment and because they are expected to respond similarly to disturbance (e.g., Abrams and Nowacki 1992).

None of the cores showed any characteristic evidence of fire scars. However, distinct, clearly identifiable charcoal fragments within 5 cm of the surface were found in 11% of the quadrats. An additional 7% of the quadrats had very small fragments that were probably charcoal. The quadrats with charcoal were not clustered in one section of the natural area.

Post–Overstory Establishment Period (1942–1991)

The rate of canopy gap formation was moderately high from 1982 through 1991 (Table 3A). Gaps caused by insects, pathogens, and/or natural senescence dominated (44/69, 64%), and those caused by snapped trees (26%) were the second most common during this decade (Table 3B).

A total of 69 gaps were encountered at New Hope Pines; the median size was 30 m^2 (Table 1) and the range was 1.2–170 m^2. For the period 1982–1991, the median amount of canopy opened up annually was 0.5% (Table 1).

Evidence Spanning Both Periods

There was apparently no temporal pattern in canopy gap formation through 1970,

Table 3. Number of gaps classified (A) by time of gap formation and (B) by origin, at New Hope Pines and Haskel-Noyes Memorial Woods natural areas, Wisconsin, for the period 1982—1991. Chi-square tests indicated no significant difference by time period (0.75 >p > 0.50), but the origin of the gaps was significantly different between the two natural areas (0.10 > p > 0.05).

A.

	Years before 1991 Inventory					
Natural Area	**< 1**	**1–2.5**	**3–4.5**	**5–6.5**	**7–9**	**Total**
New Hope	2	24	16	19	8	69
Haskel-Noyes	3	13	7	5	3	31

B.

		Gap Origin		
Natural Area	**Windthrow**	**Snapped**	**Standing Dead**	**Total**
New Hope	7	18	44	69
Haskel-Noyes	3	16	12	31

though the sample size was small. More gaps were detected in the 1930s and 1950s than in other decades (Table 4). The number of pit-and-mound pairs encountered on the transects was 15 at New Hope Pines, or approximately 3 ha-' (Table 1).

The diameter distribution of all stems greater than 10 cm closely approximates the classic, reverse-J shape of all-aged forests (Figure 2) (Hett and Loucks 1976, Lorimer and Krug 1983). However, it is the diameter distributions of species or groups of species that are most informative. The oaks have their peak concentration in the 23—38 cm size range, with limited representation in the larger size classes. White pine is well represented in all size classes greater than 18 cm and clearly dominates the size classes greater than 38 cm. This latter characteristic reflects the large age range in the overstory, as noted above (Lorimer and Krug 1983). Red maple, the midstory dominant, exhibits an exponentially declining distribution with strong domination of the two smaller size classes. This species ranged in age from 31 to 60 years (median = 46 years).

There was a weak but statistically significant (p 0.05) relationship (coefficient of determination = 0.19) between age and diameter for the overstory dominants, white pine and oak (Figure 3). The pattern for each species was examined individually and no substantial difference was noted. Furthermore, no nonlinear patterns were suggested and the two taxa showed a similar amount of variation around the regression line. This was expected because they have a similar shade tolerance and response to canopy gaps (Crow 1988, Stearns 1992).

Haskel-Noyes

Overstory Establishment Period (1846—1921)

For all species in the overstory, the age range was 76—145+ years; the median for northern red oak (113 years) is significantly greater ($p < 0.05$) than the median (96 years) for sugar maple (Table 1). The overstory age structure included two decades with above-average representation: 1871—1881 (110 year age class) and 1861—1871 (120+ year age class), but some recruitment by northern red oak occurred every decade (Figure 1B).

None of the cores showed any characteristic evidence of fire scars and no charcoal was found in the upper 5 cm of the soil.

Post—Overstory Establishment Period (1922—1991)

The canopy gap formation rate during the period 1982—1991 increased toward the end of the decade. Snapped trees created the majority (16/31, 52%) of the canopy gaps, and gaps of biological origin made up 39% (12/31, Table 3). The median gar was 48 m^2 (Table 1) and the range was 2.3—418 m^2. The median amount of canopy opened up annually was 0.8%.

The pattern of canopy gap formation prior to 1970 included a concentration before 1920 with only one recorded between 1951—1970 (Table 4). The number of pit-and-mound pairs encountered on the transects was three at Haskel-Noyes, whicl equates to approximately 1.5 ha-'.

Table 4. Number of gaps formed per decade, based on diameter growth rates (see Methods), at New Hope Pines and Haskel-Noyes Memorial Woods natural areas, Wisconsin. Numbers in parentheses are percent of total within each natural area. The number of cores examined were 30 (New Hope) and 18 (Haskel-Noyes).

Natural Area	Pre 1910	1911–20	1921–30	1931–40	1941–50	1951–60	1961–70	Total
New Hope	1 (5.9)	1 (5.9)	2 (11.8)	4 (23.5)	1 (5.9)	5 (29.4)	3 (17.6)	17
Haskel-Noyes	3 (27.3)	3 (27.3)	1 9.1)	1 (9.1)	2 (18.2)	0 (0)	1 (9.1)	11

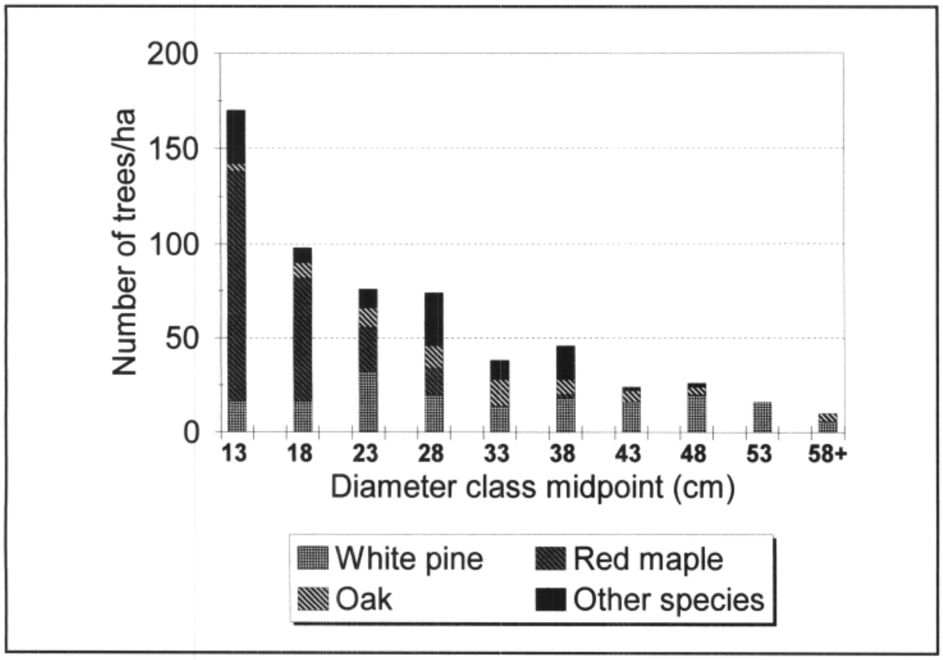

Figure 2. Diameter distribution for all trees (> 10 cm dbh) and for the three dominant taxa at New Hope Pines Natural Area, Portage County, Wisconsin.

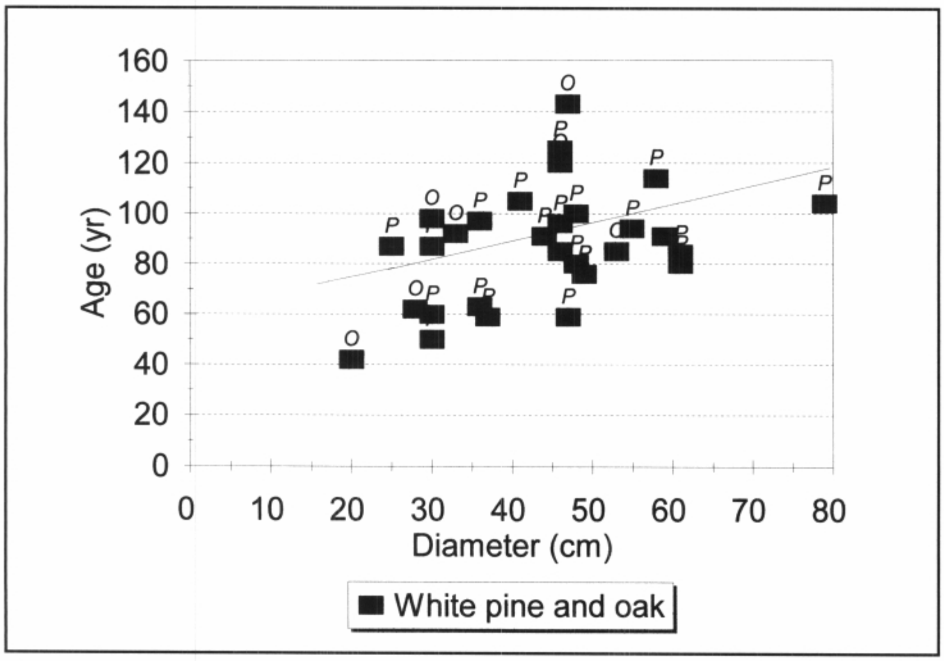

Figure 3. Relationship between age and diameter for white pine and the oaks at New Hope Pines Natural Area, Portage County, Wisconsin. Each data point for white pine is labeled with a P and those for the oaks with an O. The least squares, linear regression estimate of this relationship is age = 53.17 + **0.844 x diameter;** R^2 **= 0.19,** $p < 0.05$**.**

Evidence Spanning Both Periods

The diameter distribution for all overstory stems (Figure 4) is either a shallow negative exponential or a compound distribution (Lorimer and Krug 1983). This is a result of the two dominants having distinctly different distributions: sugar maple has a reverse-J shape, whereas the distribution of northern red oak is unimodal and centered around 38—43 cm. This probably reflects autecological differences between the two species, in particular their shade tolerance (Peet and Loucks 1977, Crow 1988, Canham 1988).

There was a moderately strong and statistically significant ($p < 0.10$, coefficient of determination = 0.44) linear relationship between age and diameter for sugar maple stems > 10 cm (Figure 5A); in contrast, northern red oak did not exhibit a significant ($p > 0.10$) relationship between age and diameter (Figure 5B). No nonlinear patterns were suggested.

Comparisons between Natural Areas

The current overstory in each forest was established over a very long time frame, though it was approximately 20 years longer for New Hope Pines Natural Area (Table 1). In addition, the period of greatest establishment, which later led to canopy recruitment, occurred more recently at New Hope (Figures IA, 1B).

The number of gaps by age class did not differ significantly ($p > 0.50$) between forests, and a larger proportion occurred between 1988 and 1990 than during any other period (Table 3A). The proportion of multiple-age gaps, out of the total found, was very similar (38% and 42%, Table 1).

The frequency of gap-origin processes differed significantly ($0.10 > p > 0.05$) between the two natural areas because "standing dead" origin gaps dominated at New Hope, whereas "wind-snapped" origin gaps were most common at Haskel-Noyes (Table 3).

DISCUSSION New

Hope Pines

Overstory Establishment Period (1848—1941)

Several lines of evidence indicate that this pine-oak forest did not originate from an intense fire or from heavy logging. The strongest evidence supporting this conclusion is the 93-year span of ages (50—143) for the overstory pines and oaks. This is twice as long as any other situation in the Great Lakes states in which white pine

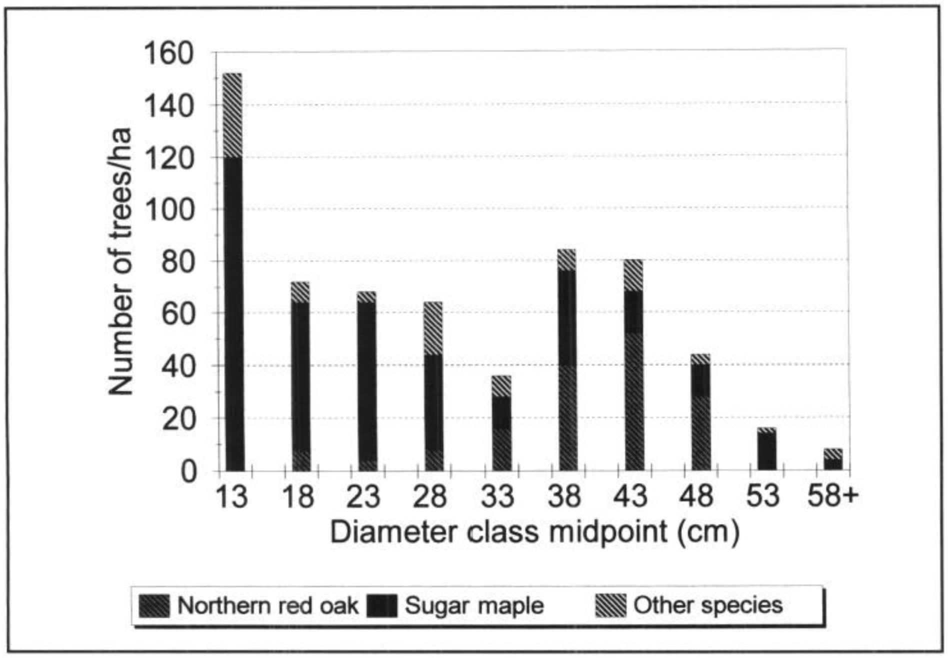

Figure 4. Diameter distribution for all trees (> 10 cm dbh) and for the two dominant species at Haskel-Noyes Memorial Woods, Fond du Lac County, Wisconsin.

came in after a "heavy disturbance" (Fre-lich 1992). Second, the lack of a charcoal layer and the scattered presence of char-coal in the upper 5 cm of soil indicate that no high intensity fires occurred in the past few hundred years. And third, the weak relationship between age and diameter of the current overstory trees suggests that these stems grew under a wide range of light conditions rather than the relatively uniform conditions found immediately after an intense disturbance.

The "extended establishment period" is probably a function of a series of low- to moderate-intensity disturbances between the mid-1800s and 1940. The exact inten-sity (degree of overstory destruction) of individual disturbances cannot be deter-mined, but almost certainly they were not small-scale events such as selective logging of individual trees (Crow and Metzger 1987) or windthrow/snapping of single trees (Crow 1988, Cho and Boerner 1991). Each gap would need to be approximately 0.4 ha or larger to produce a significant change in the microenvironment (radiation, temperature, etc.) in the middle of the gap (Phillips and Shure 1990) and thus provide the conditions suitable for the recruitment of the pines and oaks (Ross et al. 1982, Crow 1988, Cho and Boerner 1991, Abrams and Nowacki 1992, Stearns 1992).

Given the land use history of this area (Stearns 1992, Johnson 1995), it is likely that two or three logging episodes con-tributed to this extended recruitment peri-od. It is also equally probable that one or more natural events played a key role. Though the supporting information is not extensive (Bruederle and Stearns 1985, Attiwell 1994), an ice storm is unlikely. In contrast, wind events of low- to moderate-intensity are relatively common (e.g., Stearns 1949, Runkle 1982, Webb 1989. Frelich and Lorimer 1991), and thus the disturbance is more likely to have been of this type. The dominance of 80- and 90-

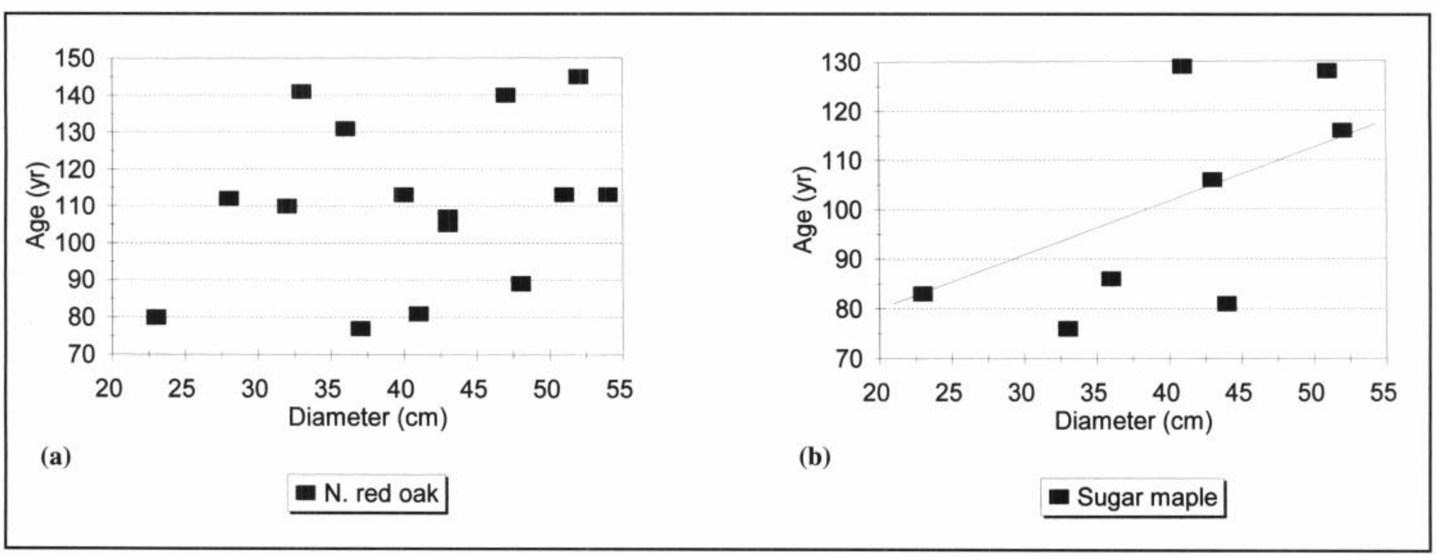

Figure 5. Relationship between age and diameter for northern red oak and sugar maple at Haskel-Noyes Memorial Woods, Fond du Lac County, Wisconsin. (a) The relationship was not significant (p > 0.10) for northern red oak. (b) The relationship was significant (p = 0.07, R^2 = 0.44) for sugar maple. The linear regression estimate of this relationship is Age = 39.04 + 1.525 * diameter.

year age classes suggests that more extensive disturbance (logging or multiple types) that impacted the overstory occurred from about 1891 to 1911. For example, after a harvest there may have been an increasing incidence of wind damage or windthrow among trees contiguous with the gaps created; such interactions have been noted in several temperate forests (Foster and Reiners 1986, Tanaka and Nakashizuka 1997).

The charcoal found in the soil at this site suggests that the establishment of at least some of the overstory stems was enhanced by litter layer reduction as a result of fire. This latter scenario is consistent with other studies in the region that showed that fire is helpful to pine regeneration (e.g., Maissurow 1935, Heinselman 1973, Ahlgren 1976, Whitney 1986). Also, we know that fires occurred frequently during the latter half of the nineteenth century in other parts of the Great Lakes Region (Heinselman 1973, Loope 1991). However, the disturbance regime in the vicinity of New Hope in the mid-1800s differed from that of most in the region (Frelich 1992) in that high-intensity fire was not involved and fire apparently played a secondary role. The absence of any red maple older than 60 years also suggests that fire occurred during the establishment period (Lorimer 1985a, Walters and Yawney 1990).

The youngest age class of overstory white pine matches the time of the last known "widespread" timber harvesting in this forest. Aerial photographs from 1938 show two portions of the forest with a small but significant amount of open canopy; one of these portions is the section that now contains most of the aspen in the forest (Cook 1990), and the other has a concentration of pine (1968, 1979 aerial photographs). The 1968 and 1979 aerial photographs indicate an even and high degree of canopy cover, but with small gaps scattered throughout the forest. All of these indications point to a substantial effect from logging in 1938. This evidence is consistent with the conclusion that logging events in the 1800s contributed to today's forest composition.

In summary, the disturbance regime that produced the current forest at New Hope Pines Natural Area was complex; it probably involved three or more types of low-to moderate-intensity disturbances and some interaction among the different types. However, the types of disturbance contributing to the regime changed during this time period (1849–1941). It is not possible to separate anthropogenic and natural disturbances, but the relative intensity and temporal pattern of these events are clear.

Post–Overstory Establishment Period (1942–19.91)

Settlement and fire suppression by the state excluded fire from New Hope after approximately 1930 (Mecozzi 1994), which greatly limited further establishment of white and red pine (Maissurow 1935, Heinselman 1973, Ahlgren 1976, Whitney 1986). The relatively infrequent occurrence of pit-and-mound topography suggests that windthrow was uncommon from 1930 (and possibly earlier) to 1980; however, the frequency of canopy openings appears to have fluctuated substantially through the decades (Table 4). Nonetheless, the general openness of the overstory was approximately equal in 1938, 1968, and 1979. The release events that occurred during this time, as confirmed by diameter growth rate patterns, could have been due to natural mortality (dying in place), wind snapped trees, firewood cutting, or a combination of these sources.

Toward the end of this period, the forest appears to have experienced an accelerated rate of canopy gap formation, with approximately 5% of the canopy opened up by natural events between 1982 and 1991. This increase probably reflects the maturation of the canopy, but could also have been triggered or exacerbated by the drought (Clinton et al. 1993) of 1985–1988 (Naber-Nox 1993). This trigger mechanism may also explain why trees dying in place dominated gap formation at New Hope. Given the coarser soil, the below-average precipitation probably stressed the trees, making them more susceptible to pathogen and insect-induced mortality (Castello et al. 1995).

Haskel-Noyes

Overstory Establishment Period (1846–1921)

Any forest in the Upper Great Lakes Region that contains moderate amounts of sugar maple in the overstory will have greater representation by maple as the time since last intense disturbance increases (Stearns 1949, Auclair and Goff 1971, Peet and Loucks 1977, Whitney 1986, Frelich and Lorimer 1991, Frelich and Graumlich 1994). Therefore, the domination of the larger diameter classes by northern red oak, which is not shade tolerant (Lorimer 1985a, Crow 1988), is evidence of a moderately intense disturbance. As discussed above for New Hope Pines Natural Area, it was probably a wind event similar in in-tensity to that noted by Webb (1989) in the pine-fir community at Itasca State Park, Minnesota. The significantly greater median age of northern red oak confirms that the earlier cohort was dominated by north-ern red oak.

The oldest red oaks were established at about the time that logging began in Wisconsin. The age range among the overstory northern red oaks confirms that the forest was not clearcut or harvested heavily in the mid-1800s. During the early phases of logging, pine was selectively harvested (Curtis 1959, Johnson 1995). Given this and the location (not near a major river and on a moraine), it is probable that no commercial harvesting occurred during the period when the older cohorts of the cur-rent overstory were established. If trees were cut between 1900 and 1920, some of the stumps would have been evident in the 1940s when this forest was inventoried by public foresters. Therefore, I conclude that this forest was not harvested in the 1800s and is indeed "virgin" as noted in the Methods section. The absence of charcoal in the soil and of fire scars on the trees indicate that fires have not been part of the disturbance regime for several hundred years (Henry and Swan 1974).

In summary, the "establishment period" disturbance regime at Haskel-Noyes consisted of a series of events, with the first of greater intensity than the rest. The initial event resulted in moderately large gaps throughout the forest and led to the establishment of a large northern red oak cohort. Compared to New Hope, the disturbance regime is simpler and involved less interaction among types of disturbance. It is highly probable that no anthropogenic influences contributed directly during this period.

Post–Overstory Establishment Period (1922–1991)

The lack of fire at Haskel-Noyes since 1921 represents a continuation of the typical situation for this relatively mesic forest (e.g., Whitney 1986, Frelich and Lorimer 1991). Fires in forests dominated by deciduous angiosperms are not frequent because of several characteristics of the vegetation and potential fuel they produce. The chemical composition of angiosperm litter is such that it does not ignite readily. Furthermore, the litter layer of a broad-leaved forest compacts more than conifer litter and thus holds more moisture. These characteristics work against a fire starting in and/or carrying through a mesic forest such as Haskel-Noyes (Pyne et al. 1996).

The diameter growth rate patterns and the rarity of recent pit-and-mound topography indicate that very few canopy openings were formed between 1920 and 1982. The fact that the majority of overstory trees were young during this period is probably the primary reason for the lack of openings. In the early stages of stand formation, the trees are generally small crowned, windfirm, and not susceptible to ice build-up (Bruederle and Stearns 1985, Webb 1989). Thus, gaps are not formed often, and when they do they are quite small and less likely to release a tree in the understory (Hibbs 1982, Webb 1989). It is during this period, however, that many of the small-diameter sugar maples were recruited into the midstory. Even shade-tolerant species such as sugar maple typically need one or more release events for canopy recruitment (Canham 1988, Frelich and Lorimer 1991). The very infrequent (Table 4), small-scale, low-intensity disturbances during this period appear to have strongly limited canopy recruitment (Figure IB).

The amount of canopy opened up for the decade 1982–1991 was 8%, which is significantly greater than the amount of previous decades. The larger median gap size in this community (relative to that of the New Hope Pines area) indicates that larger crowned trees are creating the openings. These "gap makers" are probably some of the older northern red oaks (Crow 1988) and/or the few really large sugar maples (Figure 4). The amount of canopy opened up during this decade is the same recorded for old-growth hemlock-hardwood forests of the Upper Great Lakes Region (Frelich and Lorimer 1991), lower than the average for mature/old-growth mesic forests of the Appalachian region (Runkle 1982), but higher than two old-growth oak-maple-beech forests in Ohio (Cho and Boerner 1991). Though information does not permit a direct comparison, the data suggest that this mature forest has a canopy gap formation rate similar to the rate we would expect in the old-growth stage.

Implications and Comparisons

Because one of the primary purposes of natural areas in Wisconsin is to preserve particular plant communities and the associated biotic resources, any widespread or long-term change in the disturbance regime of an area is usually relevant to its management. The Bureau of Endangered Resources' records clearly indicate that it was the pine-oak-dominated forest at New Hope that merited saving. This objective is warranted given the surveyors' records of the county (Tesch 1982), pollen analyses of the region (West 1961, Schweger 1966), and the composition of the older trees. Thus, a major reduction in the abundance of pine and oak would largely negate the purpose for establishing and protecting the natural area. The exclusion of fire at New Hope, and perhaps the absence of logging, are causing a shift in the composition to-ward more and more red maple. There-fore, the change in disturbance regime is working against the objectives of the natural area. However, this situation appears to be manageable. That is, because small to moderate canopy openings and fire played a key role during the establishment period, this type of disturbance regime could easily be re-created. The openings can be created, if needed, by girdling trees or felling them and leaving them in place. It would also be possible to reintroduce fire into the system through prescribed burning. An active approach to restoration and maintenance of the community type seems warranted because of the pervasive red maple midstory, which probably did not exist in the mid-1800s.

The arboreal composition of Haskel-Noyes Memorial Woods appears to be shifting to much greater abundance of sugar maple (Figure 4). This compositional shift has also probably resulted in some vertical structure changes. The current mix of northern red oak and sugar maple in the overstory was determined by a particular intensity or frequency of disturbance(s), which has not occurred in about 100 years. If this (these) disturbance(s) were wind and/or ice, they are unpredictable (e.g., Bruederle and Stearns 1985) and are totally outside the influence of the natural area manager. Periodic monitoring of the rate of gap formation and of the density of northern red oak less than 18 cm will en-able the managers to know if further domination by sugar maple has occurred. In the absence of a moderately intense natural disturbance, or several large gaps per hectare formed regularly over a couple of decades, active measures will be required to maintain the northern red oak and other less shade-tolerant species at their current levels of abundance.

Based on typical longevities for the species of concern, compositional changes in the next few decades will determine the future biological value of these natural areas. Based on the rates of canopy gap formation for 1982–1991, each decade will result in an additional amount of the over-story being replaced—5% at New Hope and 8% at Haskel-Noyes. In both communities, it is likely that maple will be the most abundant recruit. Though this projected change in overstory composition is an extrapolation of my data, it provides managers with a general idea of how long it will take for a specific amount of change in the current overstory.

CONCLUSION

This study has demonstrated how many information sources can be combined to describe the disturbance history of a natural area, and to pinpoint changes in the disturbance regime over time. When this information is combined with autecological information and vegetation data, the dynamics of the natural area are elucidated. Though it was not always possible to separate natural and human disturbance events in this study, it was clear that human influence has been of paramount importance at New Hope Pines but not at Haskel-Noyes. It is probable that active management in both natural areas will be necessary to maintain the plant communities of interest.

James Cook is Professor of Forest Ecology at the University of Wisconsin–Stevens Point. His research interests range from population processes such as regeneration and pollination, to community level phenomena such as succession and disturbance. Secondary successional patterns in the blast zone of Mount St. Helens are his newest research effort.

LITERATURE CITED

Abrams, M.D. and G.J. Nowacki. 1992. Historical variation in fire, oak recruitment, and post-logging accelerated succession in central Pennsylvania. Bulletin of the Torrey Botanical Club 119(1):19-28.

Abrams, M.D., D.G. Sprugel, and D.I. Dickmann. 1985. Multiple successional path-ways on recently disturbed jack pine sites in Michigan. Forest Ecology and Management 10:31-48.

Ahlgren, C.E. 1976. Regeneration of red pine and white pine following wildfire and logging in northeastern Minnesota. Journal of Forestry 74:35-40.

Attiwell, P.M. 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. Forest Ecology and Management 63:247-300.

Auclair, A.N. and F.G. Goff. 1971. Diversity relations of upland forests in the western Great Lakes area. American Naturalist 105:499-528.

Barrett, S.W. and S.F. Arno. 1988. Increment-borer methods for determining fire history in coniferous forests. General Technical Report INT-244, U.S. Department of Agri-culture, Forest Service, Intermountain Re-search Station, Ogden, Utah.

Bruederle, L.P. and F.W. Stearns. 1985. Ice storm damage to a southern Wisconsin mesic forest. Bulletin of the Torrey Botanical Club 112(2):167-175.

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

Canham, C.D. and O.L.Loucks. 1984. Catastrophic windthrow in the presettlement forests of Wisconsin. Ecology 65:803-809.

Castello, J.D., D.J. Leopold, and P.J. Smallidge. 1995. Pathogens, patterns, and processes in forest ecosystems. BioScience 45(1):16-24.

Chueng, N. and S. Brown. 1995. Decomposition of silver maple *(Acer saccharinum* L.) woody debris in a central Illinois bottom-land forest. Wetlands 15(3):232-241.

Cho, D.S. and R.E.J. Boerner. 1991. Canopy disturbance patterns and regeneration of *Quercus* species in two Ohio old-growth forests. Vegetatio 93:9-18.

Clinton, B.D., L.R. Boring, and W.T. Swank. 1993. Canopy gap characteristics and drought influences in oak forests of the Coweeta Basin. Ecology 74:1551-1558.

Cook, J. 1990. New Hope Pines State Natural Area. Unpublished report of baseline data acquisition, Wisconsin Department of Natural Resources, Natural Areas Program, Madison.

Cook J.E. 1996. Implications of modern successional theory for habitat typing: a re-view. Forest Science 42:67-75.

Crow, T.R. 1988. Reproductive mode and mechanisms for self-replacement of north-em red oak *(Quercus rubra):* a review. Forest Science 34:19-40.

Crow, T.R. and F.T. Metzger. 1987. Regeneration under selection cutting. Pp. 81-94 *in* R.D. Nyland, ed., Proceedings: Managing Northern Hardwoods. College of Environmental Science and Forestry, State University of New York, Syracuse.

Curtis, J.T. 1959. Vegetation of Wisconsin. University of Wisconsin Press, Madison.

Cwynar, L.C. 1977. The recent fire history of Barron Township, Algonquin Park. Canadian Journal of Botany 55:1524-1538.

Finley, R.W. 1976. Original vegetation cover of Wisconsin (map). U.S. Department of Agriculture, Forest Service, North Central Experiment Station, St. Paul, Minn.

Foster, J.R. and W.A. Reiners. 1986. Size distribution and expansion of canopy gaps in a northern Appalachian spruce-fir forest. Vegetatio 68:109-114.

Frelich, L.E. 1992. The relationship of natural disturbance to white pine stand development. Pp. 27-37 in R. Stine and M. Baugh-man, eds., Proceedings: White Pine Symposium. Publications NR-BU-6022, Minnesota Extension Service, St. Paul.

Frelich, L.E. and L.J. Graumlich. 1994. Age-class distribution and spatial patterns in an old-growth hemlock-hardwood forest. Canadian Journal of Forest Research 24:1939-1947.

Frelich, L.E. and C.G. Lorimer. 1991. Natural disturbance regimes in hemlock-hardwood forests of the upper Great Lakes region. Ecological Monographs 6:145-164.

Frissell, S.S., Jr. 1973. The importance of fire as a natural ecological factor in Itasca State Park, Minnesota. Quaternary Research 3:397-407.

Grimm, E.C. 1984. Fire and other factors con-trolling the Big Woods vegetation of Minnesota in the mid-nineteenth century. Ecological Monographs 54:291-311.

Harmon, M.E., J.F. Franklin, F.J. Swanson, P. Sollins, S.V. Gregory, J.D. Lattin, N.H. Anderson, S.P. Cline, N.G. Aumen, J.R. Sedell, G.W. Lienkaemper, K. Cromack Jr., and K.W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15:133-302.

Heinselman, M.L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. Journal of Quaternary Research 3:329-382.

Henry, J.D. and J.M.A. Swan. 1974. Reconstructing forest history from live and dead plant material: an approach to the study of forest succession in southwest New Hampshire. Ecology 55:772-783.

Hett, J.M. and O.L. Loucks. 1976. Age structure models of balsam fir and eastern hem-lock. Journal of Ecology 64:1029-44.

Hibbs, D.E. 1982. Gap dynamics in a hemlock-hardwood forest. Canadian Journal of Forest Research 12:522-527.

Hunter, M.L., Jr. 1990. Wildlife, Forests, and Forestry. Prentice Hall, Englewood Cliffs, N.J.

Hunter, N.B. and K.J. Swisher. 1983. Arboreal composition of a Pennsylvania natural area: past, present and future. Bulletin of the Torrey Botanical Club 110:507-518.

Johnson, J.E. 1995. The Lake States region. Pp. 81-128 *in* J.W. Barrett, ed., Regional Silviculture. 3rd Ed. John Wiley and Sons, New York.

Keane, R.E., S.F. Arno, and J.K. Brown. 1990. Simulating cumulative fire effects in Ponderosa pine/Douglas-fir forests. Ecology 71:189-203.

Leitner, L. 1988. Haskel-Noyes Memorial Woods Natural Area. Unpublished report of baseline data acquisition, Wisconsin Department of Natural Resources, Natural Areas Program, Madison.

Loope, W.L. 1991. Interrelationships of fire history, land use history, and landscape pattern within Pictured Rocks National Lakeshore, Michigan. Canadian Field-Naturalist 105(1):18-28.

Lorimer, C.G. 1985a. The role of fire in the perpetuation of oak forests. Pp. 8-25 *in* J.E. Johnson, ed., Proceedings: Challenges in Oak Management and Utilization. University of Wisconsin Extension, Madison.

Lorimer, C.G. 1985b. Methodological considerations in the analysis of forest disturbance history. Canadian Journal of Forest Research 15:200-213.

Lorimer, C.G. and A.G. Krug. 1983. Diameter distributions in even-aged stands of shade-tolerant and midtolerant tree species. American Midland Naturalist 109:331-343.

Maissurow, D.K. 1935. Fire as a necessary factor in the perpetuation of white pine. Journal of Forestry 33:373-379.

Mecozzi, M. 1994. It started with fire: the origins of forestry in Wisconsin. Publication FR-079-94, Wisconsin Department of Natural Resources, Madison.

Naber-Nox, P. 1993. Monthly precipitation from North Pelican weather station. State Climatology Office, Madison, Wis.

Nowacki, G.J. and M.D. Abrams. 1994. Forest composition, structure, and disturbance history of the Alan Seeger Natural Area, Huntington County, Pennsylvania. Bulletin of the Torrey Botanical Club 121:277-291.

Peet, R.K. and O.L. Loucks. 1977. A gradient analysis of southern Wisconsin forests. Ecology 58:485-499.

Perry, D.A. 1994. Forest Ecosystems. Johns Hopkins University Press, Baltimore, Md.

Phillips, D.L. and D.J. Shure. 1990. Patch-size effects on early succession in southern Appalachian forests. Ecology 71:204-212.

Pickett, S.T.A. and J.N. Thompson. 1978. Patch dynamics and the design of nature reserves. Biological Conservation 13:27-37.

Pickett, S.T.A. and P. White (eds.). 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York.

Pyne, S.J., P.L. Andrews, and R.D. Lavens. 1996. Introduction to Wildland Fire. 2nd Ed. John Wiley and Sons, New York.

Reice, S.R. 1994. Nonequilibrium determinants of biological community structure. American Scientist 82:424-435.

Romme, W.H. and W.H. Martin. 1982. Natural disturbance by tree falls in old-growth mixed mesophytic forest: Lilley Cornett Woods, Kentucky. Pp. 367-383 *in* R.N. Muller, ed., Proceedings of the Fourth Central Hard-woods Conference, Lexington, Kentucky, March 5-6, 1982.

Ross, M.S., T.L. Shank, and D. W. Smith. 1982. Age-structure relationships of tree species in an Appalachian oak forest in southwest Virginia. Bulletin of the Torrey Botanical Club 109:287-298.

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

Schweger, C.E. 1966. Pollen analysis of Iola bog and paleoecology of the Two Creeks interval. M.S. thesis, University of Wisconsin, Madison.

Sheppard, P.R., J.E. Means, and J.P. Lassoie. 1988. Cross-dating cores as a nondestructive method for dating living, scarred trees. Forest Science 34:781-789.

Sousa, W.P. 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics 15:353-392.

Stearns, F.W. 1949. Ninety years change in a northern hardwood forest in Wisconsin. Ecology 30:350-358.

Stearns, F.W. 1992. Ecological characteristics of white pine. Pp. 10-18 *in* R. Stine and M. Baughman, eds., White Pine Symposium Proceedings. Publication NR-BU-6044, Minnesota Extension Service, St. Paul.

Tanaka, H. and T. Nakashizuka. 1997. Fifteen years of canopy dynamics analyzed by aerial photographs in a temperate decidous forest, Japan. Ecology 78:612-620.

Tesch, D. 1982. Presettlement vegetation of Portage County, Wisconsin, 1839-1852. M.S. thesis, University of Wiscsonsin, Stevens Point.

Tyrrell, L.E. and T.R. Crow. 1994. Structural characteristics of old-growth hemlock-hardwood forests in relation to age. Ecology 75:370-386.

Walters, R.S. and H.W. Yawney. 1990. Red maple. Pp. 60-69 *in* R.M. Burns and B.H. Honkala, eds., Silvics of North America, Vol. 1. Agricultural Bulletin 654, U.S. Department of Agriculture, Washington, D.C.

Webb, S.L. 1989. Contrasting windstorm con-sequences in two forests, Itasca State Park, Minnesota. Ecology 70:1167-1180.

West, R.G. 1961. Late and postglacial vegetational history in Wisconsin, particularly changes associated with the Valders re-advance. American Journal of Science 259:766-783.

White, P.S. 1979. Pattern, process, and natural disturbance in vegetation. Botanical Review 45:229-299.

Whitney, G.G. 1986. Relation of Michigan's presettlement pine forests to substrate and disturbance history. Ecology 67:1548-1559.

Appendix. Five-year diameter growth rates for two overstory trees at New Hope Pines Natural Area, Wisconsin. Tree number 21 exhibited three release events beginning in years 1906, 1921, and 1941. Tree number 15 showed one release event beginning in year 1956. See Methods for criterion used to define release.