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NATURAL DISTURBANCE REGIMES IN HEMLOCK–HARDWOOD FORESTS OF THE UPPER GREAT LAKES REGION[1]

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Abstract. The frequency of natural disturbances and their influence on the forest landscape mosaic were investigated on three large tracts of primary forest in Upper Michigan. Seventy 0.5-ha plots were randomly distributed in a total forest area of 23 000 ha dominated by sugar maple (*Acer saccharum*) and eastern hemlock (*Tsuga canadensis*). Radial increment patterns were used to estimate canopy accession dates for each of a number of randomly selected overstory trees on each plot. From these data a disturbance chronology, representing the percentage of stand area occupied by cohorts originating during each decade over the last 130 yr, was compiled for each plot.

Average rates of disturbance or canopy mortality are estimated at 5.7 to 6.9% per decade. The corresponding average canopy residence time of a tree is 145–175 yr. No significant differences were detected in average disturbance rates among the three study areas, between plots near the coast of Lake Superior and inland plots, among several different aspects, and among several different slope positions.

Natural rotation periods increase exponentially with increasing disturbance intensity, which is defined as the approximate percentage of the plot area converted to gaps during a disturbance episode. Estimates of rotation periods range from 69 yr for ≥10% canopy removal to 1920 yr for ≥60% canopy removal. Spatial autocorrelation analysis indicated that plots with light and medium disturbances (<40%) are randomly distributed over the landscape. Plots with heavy disturbances (≥40%) are clustered with a patch radius of ≈2 km, consistent with the sizes of thunderstorm downbursts.

The data indicate that light and medium disturbances dominate the disturbance regime. The majority of stands on the landscape are composed of several major and many minor age classes. Even-aged stands with one predominant age class are uncommon. The age distribution of individual patches or cohorts in the two larger study areas (14 500 and 6073 ha) follows a nearly uniform distribution. None of the three study areas had more than 15% of the forest area converted to gaps in a single decade. The two larger areas meet most of the criteria that have been proposed for equilibrium landscapes.

Key words: eastern hemlock; equilibrium landscapes; fire; landscape ecology; natural disturbance; presettlement forests; steady-state forests; sugar maple; Upper Michigan; windthrow.

INTRODUCTION

Over the last few centuries human activity has replaced natural disturbance as the primary force in the dynamics of many forest landscapes. Recently, ecologists have increased efforts to characterize the natural disturbance regimes in forests before the opportunity to do so is lost. One important effect of the disturbance regime on forests is to create a mosaic of different successional and structural types on the landscape (Horn 1974, Connell and Slatyer 1977, Whittaker and Levin 1977). Disturbances in forests may be so frequent that late-successional stages of vegetation that would otherwise develop are rarely seen (Graham 1941, Loucks 1970, Heinselman 1973, Romme 1982). Shugart (1984) has proposed the concept of a quasi-equilibrium forest landscape in which the proportion of the landscape in each age class or successional stage remains fairly constant over time. In other words, there are enough disturbance-created patches so that no one patch dominates, and the properties of the landscape are statistically predictable. Many natural areas may be too small to attain a quasi-equilibrium condition, leading to periodic loss of certain types of habitat (Pickett and Thompson 1978, Shugart 1984). Knowledge of patch dynamics can help a natural-area manager decide whether adequate habitat is likely to continue to exist for rare species dependent upon certain post-disturbance forest types for survival.

A number of landscape-level studies of forest disturbances have been carried out in North America. Heinselman (1973) was one of the first to examine the age structure of an entire landscape and its relationship to the disturbance regime and topography of a region. Heinselman estimated a natural rotation period of ≈100

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yr for stand-initiation fires on the 215 000-ha remnant of pine and aspen forest in the Boundary Waters Canoe Area in Minnesota. Fire rotation periods for various parts of the boreal forest are generally estimated to be ≤130 yr (Van Wagner 1978, Yarie 1981, Cogbill 1985). Much longer rotation periods of ≈465 yr have been estimated for stand-replacement fires in Douglas-fir (*Pseudotsuga menziesii* Mirb. Franco)-dominated forests of the west slope of the Cascade Mountains (Hemstrom and Franklin 1982).

In contrast to these landscape-level studies, studies in the temperate hardwoods of eastern North America, eastern Asia, and western Europe have mostly not progressed beyond case studies of individual stands for two major reasons. First, large landscape units of virgin forest are rare. In North America, sizable remnants appear to exist only in the Great Smoky Mountains of North Carolina and Tennessee, the Adirondacks of New York, and Upper Michigan. Second, the age structure of hardwood stands is often complex, and it has not been clear how disturbance chronologies could be prepared for uneven-aged stands. Old trees may be found in several of the stages of forest development described by Bormann and Likens (1979), and the age of the oldest trees in a stand does not necessarily correspond to the date of the last major disturbance. Recent methodological studies, however, have suggested a framework for analyzing disturbance frequency and intensity in uneven-aged stands (Frelich and Martin 1988, Lorimer et al. 1988, Lorimer and Frelich 1989).

It is widely acknowledged that northern hardwoods can be subjected to catastrophic disturbance by fire and wind (Stearns 1949, Haines and Sando 1969, Dunn et al. 1983, Foster 1988*a*). However, there are differences of opinion as to frequency and type of large-scale disturbance. Several investigators have hypothesized that intense natural disturbances are so frequent that even-aged stands would predominate in wilderness landscapes (Graham 1941, Maissurow 1941, Raup 1957, 1981, Henry and Swan 1974, Heinselman 1981). Yet, there is also evidence in the literature that old-growth hardwood forests are often broadly uneven aged (Gates and Nichols 1930, Hough and Forbes 1943, Leak 1975, Hett and Loucks 1976, Lorimer 1980).

Techniques for reconstructing forest disturbance history (fire scar analysis, field disturbance chronologies, historical land-survey records, contemporary records, simulations, etc.) are all subject to different kinds of data constraints or interpretive difficulties, and so it is likely that a comprehensive analysis of disturbance regimes in northern hardwoods will require integration of evidence from several independent approaches. Existing evidence on natural disturbance regimes in northern hardwoods at the landscape level comes largely from data on the amount of "recently" disturbed forest recorded in 19th century government land surveys. Based on such records, Canham and Loucks (1984) and Whitney (1986) estimated rotation periods of ≈1200 yr for catastrophic disturbance in mesic hardwood forests of northern Wisconsin and Lower Michigan, respectively. Under such a disturbance regime, several generations of trees would generally pass between each episode of severe disturbance. This evidence suggests that most stands would be uneven aged, although no detailed information on stand conditions is directly available from land survey records.

The purpose of the present study is to describe the natural disturbance regime of three large preserves of hardwood forest in western Upper Michigan based on field techniques of stand history reconstruction. Specific objectives are: (1) to use the disturbance history data of 70 stands to calculate rotation periods for natural disturbance of different intensities; (2) to characterize spatial patterns on the landscape caused by natural disturbance; and (3) to evaluate the degree to which each preserve incorporates an equilibrium landscape. The field techniques provide an independent means of evaluating the prediction from land survey studies that most hardwood stands in tracts free of major human disturbance would be uneven aged. Although the study areas do not cover as much area as the 19th century land surveys, the spatial and temporal resolution is much higher. With the field approach it is possible to recognize a continuum of disturbance intensity rather than a binary classification of heavily disturbed vs. relatively undisturbed. The chronology length of 110–130 yr for most stands is also higher than the 15–25 yr record from land surveys. While fire-caused mortality can generally be distinguished from various types of treefall disturbance in both methods, it is often difficult to determine if treefalls were caused by wind, drought, insects, disease, ice storms, lightning strikes, or senescence. Drought and insect-caused mortality can sometimes be distinguished from other causes of treefalls from the ring patterns of surviving trees (Blais 1962, Stuart et al. 1989). However, determination of the exact cause of death requires a pathological investigation (e.g., Worrall and Harrington 1988), and the invasion of secondary pathogens makes an accurate diagnosis difficult after a tree has been dead more than a few years. The emphasis of this study is therefore on the overall impact of various kinds of natural disturbance on stand age structure and properties of the landscape mosaic.

STUDY AREAS

History and location

In western Upper Michigan there are three relatively large areas of forest that escaped major logging (Fig. 1). Although logging of white pine (*Pinus strobus* L.) started in Upper Michigan in the 1880s (Graham 1941), on loamy soils in this region pines occurred only in small isolated groves or as scattered individual trees among the hardwoods (Stearns 1949, Bourdo 1956, Mladenoff and Howell 1980). The three study areas

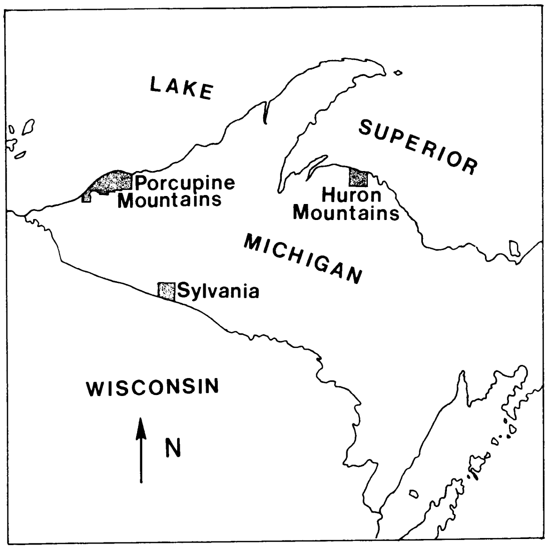

FIG. 1. Location of the study areas (shaded) in Upper Michigan.

appear to have been culled only lightly for pine by the early loggers. Logging of hardwoods and hemlock began much later. As late as 1940, one-third of the original 1 800 000 ha of hardwood forest in Upper Michigan had still not been logged (Cunningham and White 1941). All three study areas, however, had some logging around the periphery prior to their establishment as natural areas, and so logged sections were excluded from sampling in the current study.

The largest of the three study areas, the Porcupine Mountains Wilderness State Park (Townships 50–51 north, Ranges 42–45 west), contains ≈14 500 ha of primary or virgin forest, mostly in one large contiguous block (Fig. 2). Records at the park headquarters indicate that most of the shoreline of Lake Superior was logged between 1890 and 1917, and that a large slash fire in 1919 burned much of this tract (see also Darlington 1930). Much of the eastern and southern portion of the park was clearcut between 1910 and 1944. Formation of the park in the mid-1940s prevented logging from progressing farther toward the interior. Exclusion of second-growth stands in the present study was based on a map of the logged areas at park headquarters. A blowdown of 1800 ha in 1953, partly salvaged for fallen timber, was considered a natural disturbance and was therefore included in the study area (Fig. 2).

The second largest study area is the Sylvania Wilderness Area (Township 44 north, Range 40 west) in the Ottawa National Forest. Sylvania was established as a private preserve in 1901, and was sold to the United States Forest Service in 1966. Logging during the time of private ownership affected only a limited area, primarily a 97-ha clearcut made during World War II (USDA 1964). Sylvania includes ≈6000 ha of primary forest, also essentially in one large block.

The third study area is a tract of 2500 ha of primary

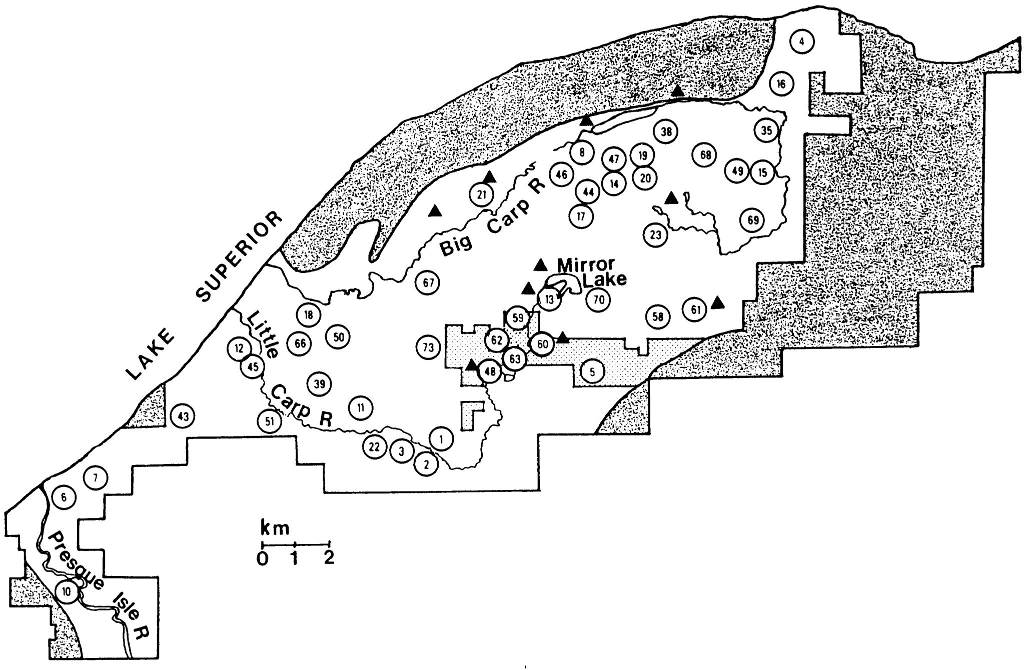

FIG. 2. Map of the Porcupine Mountains study area. Circled numbers indicate plot locations. Dark stippled areas around the periphery of the park indicate areas logged prior to park formation, based on a map at park headquarters, and not included in the study. Light stippled area south of Mirror Lake indicates the principal area of the 1953 blowdown, most of which was salvaged for fallen timber. Black triangles indicate locations of hills >450 m in elevation.

forest (Townships 52–53 north, Ranges 28–29 west) on the shore of Lake Superior west of Marquette, Michigan, owned by the Huron Mountain Club. The club initially purchased 186 ha of old-growth forest in the late 19th century, gradually acquiring a total of 6880 ha. Since the 1930s the Huron Mountain Club has recognized two zones: a central "reserved area" where no cutting has been permitted, and a peripheral "managed area" where some cutting is allowed. Only the reserved area was sampled in the present study.

Since our objective was to characterize the natural disturbance regime as accurately as possible, we conducted detailed studies only on these three sizable landscape units. These large units are more likely to preserve the natural age-class mosaic than small natural areas, which may have been preserved specifically for their old-growth characteristics. The history and location of the three study areas suggest that the mountain and lake scenery, and the opportunities for establishing game preserves, were stronger motives in the preservation of these tracts than the specific character of the forests (cf. Westover 1971).

Environmental characteristics

Vegetation.—Sampling was restricted to habitats capable of supporting closed-canopy northern mesic forest (Curtis 1959), which is the principal vegetation type in all three study areas. Sugar maple (*Acer saccharum* Marsh.) dominates most of the forest inland from Lake Superior, and mixes extensively with hemlock (*Tsuga canadensis* (L.) Carr.) near the lake. Stands of hemlock are also found inland, especially in Sylvania. Lesser amounts of yellow birch (*Betula alleghaniensis* Britt.), red maple (*Acer rubrum* L.) and basswood (*Tilia americana* L.) occur throughout the area. All other tree species are of local or sporadic occurrence.

Topography and soils.—Elevations range from 182 m on the surface of Lake Superior to ≈600 m at 5 km inland in the Porcupine Mountains and 450 m in the inland sections of the Huron Mountains. Glacial Lake Duluth covered parts of both study areas until ≈8000 yr BP (Hough 1958). These lake-plain areas have very deep deposits of silty lake-bottom sediments at elevations up to 120 m above Lake Superior, with deep Haplorthods and Fragiorthods (Michigan State University Cooperative Extension Service 1981) on predominantly gentle north slopes (0–10%). Farther inland, bedrock comes nearer the surface and topography is more rugged, with slopes up to 30% in steepness on the predominantly north slopes. Bedrock types in the Porcupine Mountains are shale and sandstone near Lake Superior, and amygdaloidal basalt, granite, or Copper Harbor Conglomerate at higher elevations (Dorr and Eschman 1970). Bedrock in the Huron Mountains consists of granite and gneiss (Dorr and Eschman 1970).

Sylvania has lower topographic relief than the other two study areas. A glacial end moraine known as the Watersmeet Moraine covers the area (Dorr and Eschman 1970, Jordan 1973). The pitted ice-contact topography varies from 500 to 550 m in elevation and contains many small lakes and bogs. The drift is deep (>30 m) and of sandy loam texture (Jordan 1973). The upland soils at Sylvania are spodosols and a large majority are classified as Fragiorthods. A moderately developed clay fragipan is found at a depth of 50 to 110 cm. The remaining soils are Haplorthods (Jordan 1973, Spies and Barnes 1985).

Climate.—The climate of Upper Michigan is humid continental. Summers are short and cool; average July temperatures are 19.1°C at Marquette near Lake Superior and 19.8° at Rhinelander near Sylvania. Winters are long and cold; average January temperatures are −7.5° at Marquette and −10.9° at Rhinelander (NOAA 1980*a*, *b*). Mean annual frost-free period ranges from ≈90 d at Sylvania to ≈120 d near Lake Superior (Phillips and McCulloch 1972). Annual precipitation averages 80–90 cm over Upper Michigan and is fairly evenly distributed throughout the year.

The Lake Superior region is one of the most active weather zones in the northern hemisphere, with the polar jet stream positioned overhead much of the year (Bryson 1966, Eichenlaub 1979). More cyclones pass over the area than any other part of the continental United States (Visher 1954, Whittaker and Horn 1982). Major cyclone tracks cross the region every month of the year (Klein 1957, Whittaker and Horn 1982). Outbreaks of severe weather are known to occur in the region when the polar jet stream lies just to the north and the subtropical jet stream lies just to the south during the summer months (Eagleman et al. 1975, Whitney 1977, Doswell 1980). Some of the most severe thunderstorms ever observed by meteorologists have occurred in northern Wisconsin, not far from the study areas (Fujita 1978).

FIELD AND LABORATORY METHODS

Seventy plots were located by random coordinates within the zones of primary forest. The two larger study areas (Porcupine Mountains and Sylvania) were stratified into blocks of ≈2000 ha to prevent excessive clustering of plots. The number of plots in each study area is proportional to its size. Forty-six plots were allocated to the Porcupine Mountains, 18 plots were allocated to Sylvania, and 6 to the Huron Mountains. During the summers of 1981–1984, each plot was located in the field by pacing the appropriate distance and azimuth, as measured on the map, from a known landmark.

A plot size of 0.5 ha (70.7 × 70.7 m) was selected after preliminary field work indicated that this was the minimum size necessary to include at least 50 canopy trees of each major dominant. Because the objectives of this study include detection of large-scale disturbance, we did not want the plots to be so small that individual treefall gaps due to normal senescence of older trees would have a large influence. Each main plot was divided into 21 numbered 10.1 × 23.6 m subplots, so that the dispersion of species, size classes, and fire scars could be studied.

At each plot the following physiographic data were recorded: Percentage of slope, slope position (lower, lower middle, middle, upper middle or upper), aspect, and elevation. The species and diameter at breast height (dbh; diameter at 1.4 m) as well as presence of fire scars or stilt roots were recorded for all trees >1.4 m tall. Crown class was recorded as either canopy or understory for each tree. All trees receiving direct sunlight from above were considered canopy trees, including saplings in gaps. The nearest canopy tree to each of 10–30 randomly located points was cored in each plot. Generally, trees >60 cm dbh were hollow or otherwise uncorable. If inspection of a core from a hollow tree revealed a lengthy tree-ring sequence, it was included in the study. Otherwise another tree was selected. In plots with evidence of past fire, cores of early successional species were used to help date the fire events. On plots with numerous fire scars, cores were supplemented by wedges cut from fire-scarred trees. In the laboratory all cores and wedges were prepared with a razor blade or sanding, and annual radial increments were measured to the nearest 0.01 mm under a binocular microscope with an optical micrometer.

Estimates of crown area, defined as the area intersected by a horizontal plane at the widest part of the crown, were obtained from a random subsample of 212 trees from a number of plots. The distance from the stem to the edge of the crown was measured in the four cardinal compass directions. The exposed portion of the crown was defined as that portion not overtopped by branches of adjacent trees, and the radii of the exposed portion of the crown were also measured in the four cardinal directions. Crown area was then calculated as the sum of the areas of four quarter-ellipses. Regressions of exposed crown area vs. dbh were developed for each species (Lorimer and Frelich 1989), and used to estimate the fraction of plot area occupied by each size class.

DATA ANALYSIS

Stand history reconstruction

In this study, a disturbance chronology was prepared for each plot based on the estimated "canopy accession date" of each sampled canopy tree. Canopy accession dates were based on analysis of both radial growth rates and growth patterns. These criteria provide a better indication of the timing of disturbances in complex uneven-aged stands than simple age distributions (Henry and Swan 1974, Lorimer 1980, 1985, Glitzenstein et al. 1986). The rationale and procedures for estimating canopy accession dates and constructing disturbance chronologies are described more thoroughly in Frelich and Martin (1988), Lorimer et al. (1988), and Lorimer and Frelich (1989). The procedures are briefly summarized below along with some specific comments about the Michigan data sets.

Canopy accession dates for most trees in the present study were indicated by either release from suppression (55%) or rapid growth in the sapling stage with no indication of early release (35%). Growth-pattern criteria described by Lorimer and Frelich (1989) were applied to the remaining 10% of the trees to determine the most likely date of canopy accession. Sensitivity to the assumptions made in these procedures was evaluated by varying the analytical criteria for canopy accession over a reasonable range. The "conservative analysis" included the following criteria: (1) to qualify for release, radial growth in the subsequent 15-yr period had to be at least double that in the previous 15 yr, (2) growth increases on trees >25 cm dbh were not counted as releases, because data indicated that most trees >25 cm dbh are already part of the canopy layer, (3) to qualify for rapid early growth, the sapling growth rate at 4 cm dbh had to exceed the threshold required for 95% confidence of gap origin, based on Eq. 1 in Lorimer and Frelich (1989).

The criteria for canopy accession in the "moderate analysis" were less strict. Growth increases of $>50\%$ of the previous 15-yr period and sustained for more than 10 yr, on trees up to 46 cm dbh, were counted as releases. Trees were considered to be already in gaps as saplings if the growth rates at 4 cm dbh exceeded the threshold for 90% confidence of gap origin.

The minimum average radial growth rate required for 90% confidence of gap origin ranged from 1.0 to 1.2 mm/yr for sugar maple and 0.8 to 1.2 mm/yr for hemlock. Corresponding minimum rates for 95% confidence were 1.2–1.5 mm/yr for sugar maple and 1.0–1.3 mm/yr for hemlock. The value for a particular stand is dependent on the cumulative amount of gap formation during the stand chronology (i.e., the variable Qg' in Eq. 1 of Lorimer et al. 1988).

Past occurrence of surface or ground fires was indicated primarily by fire scars on living trees. The number, spatial distribution, and percentage of canopy trees with fire scars were used to distinguish fires that spread over part or all of the plot from local spot fires and to estimate the plot area covered by spreading fires. Isolated spot fires are common in both western and eastern forests (Kilgore and Briggs 1972, Miller 1978, Michigan Department of Natural Resources, *unpublished data*), and are generally omitted from fire chronologies (Arno and Sneck 1977).

Estimates of plot area burned by fires severe enough to kill canopy trees (not necessarily crown fire) were based on canopy accession data as well as the fraction of plot area dominated by the pioneer species paper birch (*Betula papyrifera* Marsh.), quaking aspen (*Populus tremuloides* Michx.), bigtooth aspen (*Populus grandidentata* Michx.), white pine (*Pinus strobus* L.), or red pine (*Pinus resinosa* Ait.). Scattered trees of these species may become established on blowdowns, but prolific establishment usually requires a burned or scarified seedbed (Dana 1909, Maissurow 1935, Hough and Forbes 1943, Ahlgren and Ahlgren 1960, Horton and Brown 1960, Frissell 1973, Henry and Swan 1974, Foster 1988*a*). All five of these pioneer species are nearly absent on the 1800-ha blowdown of 1953 in the Porcupine Mountains and a smaller blowdown of 1971 in Sylvania. They are also nearly absent on former clearcuts in the study areas that never burned; yet paper birch and aspen are dominant on the cutover areas that subsequently caught fire (e.g., 1919 fire in the Porcupine Mountains).

Evaluations of this overall method for constructing disturbance chronologies have indicated that the estimated rate of gap formation and average residence time of canopy trees are similar to estimates for northern hardwoods in the literature based on direct studies of recent gaps (Runkle 1982, 1985, Lorimer and Frelich 1989). The equation for estimating probability of gap origin has also yielded predictions of the percentage of trees in the data set exceeding a threshold growth value x that are very similar to observed percentages (Lorimer and Frelich 1989). Differences in results obtained by the conservative and moderate analyses were small, also indicating that the results are not substantially affected by moderate variations in the criteria used to determine the canopy accession date (Lorimer and Frelich 1989; see also Fig. 3A in the present paper).

Calculation of disturbance intensity

The method of estimating disturbance frequency and intensity used in this study is based on the concept that each incident of release from suppression or rapid early growth of a tree in a gap can be considered a point estimate of disturbance in the corresponding decade. Disturbance intensity is therefore defined operationally as the percentage of all sample trees with canopy accession in each decade. The resulting chronology is an approximation of the proportion of the stand converted to gaps in each decade. The method is primarily intended for detecting disturbances of moderate and high intensity, and because of the type of evidence used the frequency of small gaps may be underestimated. However, the method does provide a good indication of the proportion of canopy trees that successfully reached the canopy during episodes of small gap disturbance as compared with heavier disturbances.

Since some of the larger and older trees became established prior to the start of the chronology, and other trees may have been released more than once, disturbance intensities do not necessarily add to 100% for a given plot (cf. Table 1). Because of the heartrot problem the larger size classes were often undersampled in relation to their actual abundance on a plot. Therefore, the initial calculations of disturbance intensity were weighted by a factor consisting of the actual fraction of plot area occupied by a size class divided by its fractional representation in the sample data. Exposed crown area was used as the measure of area occupied by a size class (Lorimer and Frelich 1989).

In cases where disturbance episodes of ≥10% intensity overlapped the usual decade boundaries shown in Table 1, decade boundaries were adjusted to give the maximum amount of gap formation that would fall within a 10-yr period. Estimates of rotation periods were therefore based on data from the adjusted decades rather than the format shown in Table 1.

Calculation of disturbance rotation periods

Disturbance rotation periods (or turnover time) are generally calculated as the inverse of the average annual disturbance rate, especially in cases of stand-replacement fires or severe blowdowns (Heinselman 1973, Canham and Loucks 1984). In this study three different types of rotation periods were calculated. Rotation periods for fire were calculated in the usual fashion based on the cumulative fraction of aggregate plot area disturbed during the chronology. Alternative maximum chronology lengths of 70 and 90 yr were assumed for the purpose of calculating average rotation periods for surface fires. A large surface fire in the Porcupine Mountains in the late 1920s indicated that fire scars on both sugar maple and hemlock can persist for at least 60 yr. These scars appear unlikely to heal, and given that scarred trees (ranging from 25–50 cm dbh) are vigorous with no signs of imminent physiological decline, 70 yr appears to be an appropriate minimum time period for evidence on surface fires. The alternative time period of 90 yr is based on estimates of total canopy residence time of 155 yr for northern hardwood trees (Runkle 1982, Lorimer and Frelich 1989). Thus, a pole-sized tree scarred at age 55–65 would be expected to survive on average for an additional 90–100 yr.

An appropriate chronology length for stand-replacement fires was based on the estimated "common maximum" life span of paper birch, since it seems to be the most reliable indicator of intense fire. Although paper birch is a comparatively short-lived species, numerous individual trees are usually still present with ages 110–160 yr (Dana 1909, Weigle and Frothingham 1911, Heinselman 1973). In the present study areas, 60–70 yr old stands of paper birch are still vigorous and fully stocked, and scattered trees >150 yr old are common in post-fire stands. Alternative time periods of 110 and 130 yr were adopted for evidence of stand-replacement fires.

Rotation periods for all types of disturbance combined are based on the evidence from canopy accession dates (e.g., Table 1). Because many of these disturbances caused only diffuse mortality, we calculated rotation periods for various disturbance-intensity classes (e.g., 20–29% canopy removal or ≥20% canopy removal). With this approach, the rotation period corresponds to the "equivalent" time required for all 70

TABLE 1. Disturbance chronologies for a representative subset of plots from the Porcupine Mountains, based on the conservative criteria for canopy accession (see *Data analysis: Stand history reconstruction*). Each entry in the table indicates the percentage of existing canopy trees with canopy accession dates in the decade beginning in the year shown, and is also an estimate of the current % aggregate exposed crown area occupied by trees with canopy accession dates in that decade.

Plot	1850	1860	1870	1880	1890	1900	1910	1920	1930	1940	1950	1960	Mean
					Percentage of trees reaching canopy								
1	5.3	0.0	5.2	0.0	12.7	5.3	7.4	0.0	5.3	12.4	4.1	11.5	5.8
3	0.0	0.0	0.0	8.2	7.2	2.9	4.1	3.1	3.1	6.1	22.2	4.1	5.1
4	12.0	0.0	5.6	7.6	12.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.1
5	...	...	...	3.7	3.7	3.7	3.7	13.7	0.0	10.3	48.3	0.0	9.7
7	0.0	4.7	8.2	4.7	11.6	8.9	8.2	8.9	13.6	3.5	11.7	3.9	7.3
8	0.0	5.3	5.0	27.2	18.7	8.7	0.0	5.0	3.7	3.7	0.0	0.0	6.4
11	...	8.4	6.9	3.3	6.9	7.4	3.3	3.3	0.0	0.0	0.0	6.6	4.2
13	...	0.0	0.0	4.5	21.5	8.7	5.2	2.6	0.0	2.6	2.6	0.0	4.3
16	5.8	0.0	12.4	0.0	17.8	0.0	0.0	4.9	0.0	0.0	0.0	0.0	3.4
20	...	...	...	15.3	35.9	3.3	3.3	0.0	21.7	0.0	0.0	0.0	8.8
21	2.8	11.9	5.1	0.0	13.3	1.4	4.2	8.3	4.2	0.0	0.0	0.0	4.3
23	0.0	0.0	0.0	8.7	37.6	1.8	0.0	0.0	0.0	0.0	0.0	3.7	4.3
38	...	...	...	...	...	...	...	0.0	84.0	0.0	0.0	0.0	16.8
43	7.4	0.0	0.0	0.0	5.1	12.5	6.2	7.4	10.2	29.3	5.6	0.0	7.0
45	...	7.9	7.2	0.0	0.0	0.0	0.0	0.0	15.1	24.9	7.2	0.0	5.7
46	0.0	0.0	8.5	15.0	18.7	5.1	0.0	8.5	5.1	1.6	0.0	0.0	5.2
47	...	0.0	13.8	0.0	13.8	3.6	6.2	16.0	3.6	3.6	0.0	0.0	5.5
48	0.0	12.0	0.0	6.2	8.8	17.6	0.0	0.0	4.2	0.0	17.2	4.2	5.8
49	...	0.0	10.3	0.0	46.3	1.3	9.0	0.0	0.0	0.0	1.3	0.0	6.2
50	0.0	9.4	6.0	29.0	14.0	8.2	0.0	0.0	3.0	3.0	2.2	0.0	6.2
51	...	15.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0	24.8	0.0	0.0	3.7
58	4.3	17.1	36.7	7.8	0.0	3.6	8.4	3.6	4.2	0.0	0.0	0.0	7.1
60	...	...	...	0.0	0.0	0.0	3.7	10.1	0.0	18.4	54.0	0.0	9.6
62	...	...	...	...	...	...	...	0.0	0.0	12.0	76.3	6.2	18.9
66	...	0.0	0.0	19.4	15.8	0.0	4.2	4.2	0.0	0.0	0.0	0.0	4.0

plots to be subjected to a disturbance of intensity class *i*, based on the total number of disturbances of that intensity level detected during the period of the chronology. To accommodate plots with variable chronology lengths, the following formula was used:

$$R_i = \frac{\sum L_j}{n_i}, \tag{1}$$

where

R_i = disturbance rotation period for disturbance-intensity class *i*,
L_j = length of chronology (in years) for plot *j*,
n_i = total number of events at disturbance-intensity class *i* observed on all *N* plots.

The chronology length for all types of disturbance combined was set at a maximum of 130 yr. This was selected to be slightly lower than the average canopy residence time of northern hardwood species, based on evidence reported by Runkle (1982) and Lorimer and Frelich (1989), in order to avoid underestimates of earlier disturbances from the loss of evidence from older trees. The actual disturbance chronologies give no indication of a consistent decrease in disturbance intensity of the earlier decades as far back as 1850 (cf. Fig. 5). The most recent decade (1970–1979) was omitted from the chronology because age data were not taken from saplings shorter than 1.4 m in gaps. Some plots had disturbance chronologies starting later than 1850 because of subsequent heavy disturbance or because of excessive heartrot among the larger trees. In such cases the chronology was limited to a period equal to the minimum time required for trees to reach the largest diameter class sampled with complete increment cores. This minimum time was based on the upper 90% confidence limit of the diameter–age regression. The average chronology length of the 70 plots was 116 yr.

In addition to estimates of disturbance intensity based on rates of gap formation, a third analysis of the disturbance regime was based on structural aspects of canopy turnover. This approach is based on the recognition that a series of low-intensity disturbances, removing, for example, 70% of the canopy over a period of several decades, can have structural effects similar to those of a disturbance removing 70% of the canopy in a single year. In both cases the stands will be heavily dominated by saplings and poles in the first few decades after disturbance. In the present study we found stands of these two types difficult to distinguish by structural criteria such as diameter distributions and stand profile diagrams. Since both people and wildlife often perceive differences in stands on the basis of structural attributes, we analyzed the frequency at which stands are occupied by various proportions of sapling and pole trees as a response to the cumulative impact of various types of disturbances. To calculate the percentage of exposed crown area occupied by saplings or poles on a plot for each decade, the size of each sample tree at the time of canopy accession was noted. Based on the record of annual ring widths, the year in which each tree reached the upper size limit for saplings (10.9 cm dbh) and pole trees (25.9 cm dbh) was recorded. A running tally of the total percentages of sample trees that had already acceded to the canopy but were still in the sapling and pole stages were then summarized for each decade. Note that because each sample point represents a fraction of the total stand area (e.g., each of 25 sample points represents 4% of the plot area), the final tally of the percentage of saplings and pole trees represents the aggregate proportion of stand area occupied by these trees, not a percentage of the total number of trees. In this analysis it is assumed that saplings and pole trees are taking the place of mature or large trees that have fallen over.

Confidence intervals for rotation period estimates

To calculate confidence intervals for estimates of disturbance rotation periods, numbers of independent sample plots disturbed during a given time period was calculated. The formula for binomial confidence (Snedecor and Cochran 1980) was then applied to the proportion of disturbed plots. These upper and lower bounds for the proportion of disturbed plots were then converted back to numbers of plots and used in Eq. 1 to get estimates of rotation periods.

There is no significant clustering on the landscape for light- and medium-intensity disturbances (10–39.9% canopy removal; see *Results: Spatial distribution of disturbances*), and as a result there is little covariance among the plots. However, most plots were hit more than once by light- and medium-intensity disturbances over the last 130 yr. Because the binomial classification requires a single yes or no for each plot, data for light- and medium-intensity disturbances were compiled separately for five relatively short 20-yr time periods (1860–1879, 1880–1899, 1900–1919, 1920–1939 and 1940–1959). Variances were calculated for each of these five time periods and then pooled, resulting in a single confidence limit for each disturbance-intensity class.

There are some difficulties with the use of the standard binomial confidence limits for heavy disturbances ($\geq$40% canopy removal) which may cover an area large enough to affect several plots. The presence or absence of one heavy disturbance strongly affects the proportion of plots that is classified as disturbed, thereby contributing a large part of the variability of the estimates of rotation periods. The formula for binomial confidence requires the addition of a covariance term for use in this context. The covariance term used in this study (Frelich 1986) is based on the likelihood that >1 plot will be hit by a single heavy disturbance, given the distances between plots and the size distribution of blowdowns from Canham and Loucks (1984).

Analysis of spatial patterns of disturbance

The Porcupine Mountains study area was selected for detailed statistical analysis of spatial patterns of disturbances because a relatively large number of plots (46) are contained within a contiguous block of forest. Statistical significance of spatial clustering among plots that experienced similar types of disturbances was judged using formulas given in Sokal and Oden (1978*a*, *b*). Small sample corrections given by Sokal and Oden (1978*a*) for data sets with 10 to 50 observations were employed here for all analyses.

The spatial autocorrelation program for categorical data requires classification of plots into at least two categories—in this case disturbed and undisturbed during a certain time period. The program calculates the expected number and variance of linkages between disturbed plots, given random spatial distribution and distances linked. The program also tallies the actual number of linkages between disturbed plots, given the configuration of the data and distances linked. If the actual number of linkages exceeds the upper 95% threshold calculated from the expected number and variance of linkages, there is statistically significant positive spatial autocorrelation at the 95% confidence level.

Possible differences in clustering among light (10–19.9%), medium (20–39.9%), heavy (>40%), and all (>10%) disturbances were evaluated using the spatial autocorrelation program for categorical data. Disturbance intensity figures are based on the conservative analysis. Each of the four disturbance categories was analyzed separately as described below. The 46 plots from the Porcupine Mountains were divided into two categories—disturbed or not disturbed—based on whether or not each plot had a disturbance during the 110-yr period from 1860 to 1969. Because light disturbances were so numerous (many plots having more than one hit during the 110 yr), two short time periods (1880–1919, 1920–1959) were used and analyzed separately. Five runs of the spatial autocorrelation program were done for each analysis. All plots within the following distances (km) of each other were linked: 1.0–1.9, 2.0–2.9, 3.0–3.9, 4.0–4.9, and 5.0–5.9.

The spatial autocorrelation program for continuous data calculates Moran's I, which is a two-dimensional analog of the standard correlation coefficient. Moran's I ranges from $+1.0$ if there is a perfect (spatial) gradient from low numbers (in this case low disturbance levels on a given plot) to high numbers, to 0.0 if the data are randomly arranged, to -1.0 if high numbers are always adjacent to low numbers. Each value of Moran's I was tested for positive significance at the 95% confidence level, using procedures given in Sokal and Oden (1978*a*).

Classification of stand structural types

To facilitate a study of the effects of disturbance on stand structure at the landscape level, a simple struc-

TABLE 2. Number of disturbance events observed by categories of intensity for the analyses using conservative and moderate criteria for assigning canopy accession dates. Each disturbance event represents the cumulative amount of gap formation over a 10-yr period, with decade boundaries adjusted in some cases as explained in *Data analysis: Calculation of disturbance intensity.*

	Disturbance intensity class (%)						
	10–19.9	20–29.9	30–39.9	40–49.9	50–59.9	60–69.9	>70
	Conservative analysis						
Number of events	97	22	9	9	1	3	2
Rotation period (yr)	77	337	842	842	7420	2473	3710
	Moderate analysis						
Number of events	103	38	13	10	2	3	2
Rotation period (yr)	72	195	571	742	3710	2473	3710

tural classification for individual stands was developed based on the proportion of aggregate exposed crown area (ECA) occupied by saplings (0–10.9 cm dbh), poles (11.0–25.9 cm dbh), mature trees (26.0–45.9 cm dbh) and large trees (≥46.0 cm dbh).

The following categories were recognized:

Sapling stand: ≥67% of ECA in saplings plus poles, with more crown area in saplings than in poles.

Pole stand: ≥67% of ECA in saplings plus poles, with more crown area in poles than in saplings; or ≥67% of ECA in poles plus mature trees, with more crown area in poles than in mature trees.

Mature stand: ≥67% of ECA in poles plus mature trees, with more crown area in mature trees than in poles; or ≥67% of ECA in mature plus large trees, with more crown area in mature than in large trees.

Old-growth stand: ≥67% of ECA in mature plus large trees, with more crown area in large than in mature trees.

Mature–sapling mosaic: Any stand not meeting the above criteria.

The distribution of crown area among size classes in a hypothetical steady-state forest is not known. However, if a simplifying assumption is made that a steady-state forest would have an approximately equal amount of ECA in each 4.0 cm dbh size class up to 76 cm as a result of a constant gap-formation rate (Lorimer 1985), a steady-state northern hardwood canopy would be occupied roughly by 12% gap saplings, 18% poles, 24% mature trees and 46% large trees. Steady-state forests, as well as old even-aged stands, would therefore be classified as old growth by this system. Stands in the mature–sapling mosaic category generally represent either mature or old-growth forests with episodes of moderate disturbance that have reduced the proportion of large trees, or stands in a transitional phase between sapling, pole, or mature stands.

RESULTS

Age structure of stands

Disturbance chronologies indicate that the age structure and disturbance history of most hemlock–hardwood stands are complex (cf. Table 1). If decades prior to 1850 are included, the mean number of effective age classes (decades with canopy accession events) detected per 0.5-ha plot was 10.5 and ranged from 1 to 19. Only one of the 70 plots, a young stand of paper birch that developed after a fire in the late 1920s, was even-aged.

Most stands have evidence of >1 episode of light or moderate disturbance during the period of the plot chronology (1850–1969, Table 1). If 6–10% mortality of canopy trees per decade is considered a common background level for old-growth forests as a result of the deaths of scattered old trees (Lorimer 1980, Romme and Martin 1982, Runkle 1982), then 80% of the plots had at least one decade with light exogenous disturbance removing 10–19% of the canopy. The mean number of decades per plot with light exogenous disturbance was 1.4, with a range from 0 to 4. Twenty-nine of the plots (41.4%) had at least one episode of moderate disturbance (20–39% canopy removal), 12.9% of the plots had at least one episode of moderately heavy disturbance (40–59% canopy removal) and 7.1% of the plots had one episode of very heavy disturbance (≥60% canopy removal, Table 2).

The 1953 blowdown (≈1800 ha) in the Porcupine Mountains was the single largest high-intensity disturbance detected in this study (Fig. 2). It removed at least 45% of the canopy on 3 of the 46 plots in the Porcupine Mountains, and removed at least 20% of the canopy on 2 others. Nearly complete destruction of the canopy appears to have been uncommon; only on two plots was >60% of the canopy removed (Table 1: Plots 60, 62). However, the surviving canopy trees in many of the 1953 blowdown plots were often comparatively small, with canopy accession dates between 1920 and 1950 (Table 1: Plots 5, 60, 62). Thus little of the original, high forest canopy on several of the blowdown plots appears to have survived the storm.

Evidence for disturbances of similar magnitude was not found in other decades or on other study areas. Two other plots had a decade with ≥60% canopy removal, and two other plots had episodes of 40–59% disturbance, but these events occurred in several different decades and in isolated locations.

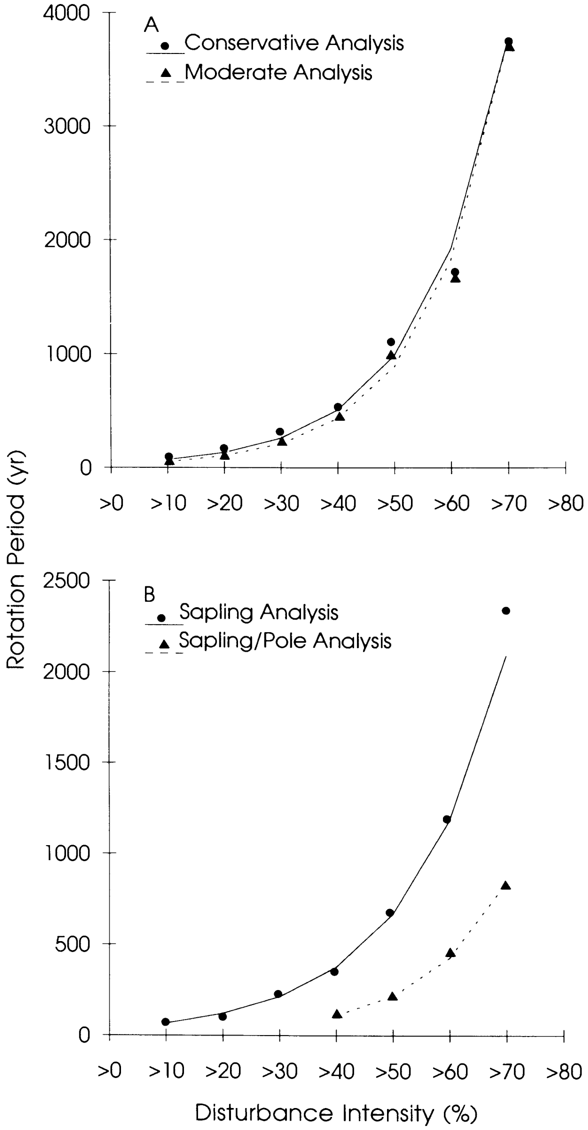

FIG. 3. (A) Rotation periods for various levels of disturbance intensity (canopy removal) using the conservative criteria (——) and moderate criteria (– – –) for assigning canopy accession dates. (B) Rotation periods for events leading to various proportions of a plot covered by sapling trees (——) and saplings plus pole trees (– – –).

Because of the small percentage of stands with heavy disturbance in the past 130 yr, old-growth forest dominates the landscape in all three study areas. Using structural criteria described above (see *Data analysis: Classification of stand structural types*) 0.0% of the plots are classified as sapling stands, 8.6% as pole stands, 17.1% as mature stands, 4.3% as mature–sapling mosaics, and 70.0% as old growth.

Average rates of disturbance

Average rates of gap formation for all plots and all decades are 5.7% and 6.9% per decade for the conservative and moderate analyses, respectively. Corresponding average residence time for trees in an overstory position (inverse of gap formation rates) are 175 yr for the conservative analysis and 145 yr for the moderate analysis, which is similar to previous estimates in northern hardwoods from independent data (Runkle 1982, Lorimer and Frelich 1989).

The average disturbance rate during the 1850 to 1969 time period is fairly uniform among the three study areas. A Kruskal-Wallis test indicates no significant difference ($H = 3.372$ and 4.187, 2 df, for the conservative and moderate analyses, respectively) among medians for study areas. However, there is a gently decreasing trend from the Porcupine Mountains (6.1%) to Sylvania (4.9%) to the Huron Mountains (4.6%). This apparent trend may be the result of a slightly decreasing trend in the frequency of thunderstorms and tornados from west to east across Upper Michigan (Thom 1963, 1968, Court 1974, Eagleman et al. 1975, Fujita 1978).

Rotation period and its relationship to disturbance intensity

Rotation periods increase exponentially with increasing disturbance intensity. Both the conservative and moderate cumulative tabulations are described well by exponential functions (Fig. 3A). The functions were fit by linear regression, using the logarithmic transformation of rotation period interval. Both functions have good residual patterns that reveal no bias in the parameters. Rotation periods from the conservative analysis range from 69 yr for >10% canopy removal to 1920 yr for >60%. Similar values for the moderate analysis are 51 yr and 1819 yr, respectively. These rotation periods are strictly applicable only to the scale of a 0.5-ha stand, although work by Canham and Loucks (1984) on blowdowns of >1.0 ha and our own data on the spatial extent of diffuse low-intensity disturbance both suggest that rotation periods in this forest type are probably not greatly affected by the scale of the stand, at least up to a limit of 100 ha.

The 95% confidence limits for light- and medium-intensity disturbances are 52–119 yr, 251–516 yr, and 512–2113 yr for disturbance in the 10–19.9%, 20–29.9%, and 30–39.9% intensity categories, respectively. The 95% confidence limits are 40–76 yr and 98–412 yr for all disturbances >10% and >20% intensity, respectively.

The 95% confidence interval for disturbance with ≥60% canopy removal was calculated using the formulas in Frelich (1986). The covariance was found to be 3.4 times as large as the variance, and the confidence interval runs from 535 yr to infinity. Assuming no covariance, the same interval ranges from 805 to 9553 yr. Substantially smaller confidence intervals would probably not be feasible for heavy disturbances. Assuming no covariance, it would require 300 plots to reduce the confidence interval to a span of 1050 to 2500 yr. The covariance among the plots, however, would be negligible only if one plot were allocated to each 3700 ha, which is the largest size disturbance found in the northern Wisconsin land survey data (Canham and Loucks 1984). These area requirements exceed the 23 000 ha of primary forest remaining in western Upper Michigan.

The rotation periods for moderately heavy disturbance (40–59% canopy removal) are rather long—742 and 618 yr for the conservative and moderate estimates, respectively. However, the rotation periods drop to 412 and 323 yr, respectively, for disturbances removing 30–49% of the canopy. It is clear, then, that there is a high probability of partial stand destruction at least once during the 300 yr lifespan of an individual cohort of trees.

An assessment of the relative impact of moderate and heavy disturbance vs. light disturbance and the formation of small gaps can be obtained by comparing the sums of the percentage of stand areas affected by each type of disturbance, based on the plot chronologies such as those in Table 1. Trees recruited during decades with ≥20% disturbance intensity currently occupy 40.1% of the aggregate area of the 70 plots affected by disturbance during the period of the chronology. Trees recruited during episodes of ≥30% disturbance intensity occupy 27.7% of the plot area. Thus while moderate and severe disturbances have an important effect on the recruitment of canopy trees, 60% of the aggregate plot area is occupied by trees recruited during episodes of small-gap formation and from light disturbances removing ≤19% of the canopy area.

Disturbance rotation periods based on structural criteria are substantially shorter than those based on the actual rate of gap formation. For example, disturbances resulting in ≥60% of a stand being occupied by saplings have a rotation period of 1183 yr, compared with 1920 yr for disturbances removing ≥60% of the canopy in a single decade (Fig. 3B). For all plots and decades, the average proportion of time spent in a structural condition of ≥60% saplings and ≥40% saplings was 1.4% and 4.6%, respectively.

The analysis of disturbances leading to various combined proportions of saplings and pole trees yields insights into the frequency with which stands are dominated by relatively small and young trees. A hypothetical steady-state forest would probably have slightly less than 30% of the area occupied by crowns of saplings and pole trees (Lorimer 1985). Rotation periods for various intensities of disturbances leading to ≥50% saplings and poles is 203 yr, and the corresponding period for ≥60% saplings and poles is 456 yr (Fig. 3B). Twelve of the 70 plots (17.1%) had at least one decade during the chronology in which ≥60% of the exposed crown area was occupied by saplings and pole trees. The average duration of such episodes was 31 yr.

Relative frequency of fire and treefall disturbance

Nineteen plots (27%) had at least one fire-scarred tree (Table 3). Ten of these plots appeared to have been affected by spreading surface fires over ≥10% of the plot. On these plots, the percentages of canopy trees with scars ranged from 5 to 29%. The percentage of trees with scars on burned subplots was more consistent, averaging 35% and ranging from 21 to 44%. On five of the remaining plots there were only one or two scarred trees. On four other plots there were ≤5 scarred trees, and these were either so tightly clustered or so widely scattered that they appeared to be local spot fires.

Five of the 10 plots with spreading surface fires were located in a small area of ≈500 ha in the upper Big Carp River Valley, in the Porcupine Mountains, near Scott Creek and Lake of the Clouds. Wedges from fire-scarred trees and cores from young yellow birch and paper birch in fire-created gaps suggest that there were two separate fires, one in ≈1928 and a second fire in ≈1942. Ages of the paper birch are the same as on nearby cutover lands near the Carp Lake smelter; thus it is not certain if these were natural fires. Both fires spread primarily as surface fires in the old-growth forests, although isolated pockets of canopy trees were killed on both the south- and north-facing slopes. The areas covered by the fires overlapped, and some trees had more than one scar, but more detailed sampling and mapping would be needed to determine the amount of overlap. For this reason, fire rotation periods were calculated solely on the presence or absence of fire on each plot.

Evidence of more intense canopy-killing fires was examined by compiling the total living plus standing dead basal area of the five pioneer species (paper birch, quaking aspen, bigtooth aspen, white pine, red pine) on each plot. Fifty-seven plots (81.4%) had no trees at all of any of the five pioneer species. Nine plots (12.9%) had small amounts, with the aggregate basal area of the five species averaging 3.1% of the total (range: 0.3–7.4%). On the four remaining plots (5.7%) pioneer species made up a substantial portion of the canopy, averaging 51% and ranging from 35 to 75%. Charcoal fragments were found on two of the sites, and in all four cases, trees of pioneer species were spatially well distributed across the plot. Two of these stands were dominated by a nearly even-aged cohort of pioneer species over most of the plot, apparently from fires in 1840 and 1928. The other two stands had a more complex age structure, including two distinct cohorts of paper birch and other pioneer species, dating from 1820–1845 and 1890–1895. The fires of 1890–1895 removed 40–50% of the canopy in these two stands.

A human origin for two of these six intense fires is likely. The fire in ≈1895 near Mountain Lake in the Huron Mountains is probably the same as a historically

TABLE 3. Data on surface or ground fires in the three study areas. The final column shows the estimated proportion of plot area burned, which is used in calculations of fire rotation periods for Table 4.

Plot no.	Location*	Slope position†/ Aspect	No. of fire-scarred trees per 0.5 ha	% Subplots with scars	% Trees scarred on plot‡	% Trees scarred on burned subplots§	Estimated % of plot burned
		Plots with spreading fires					
8	Lake of Clouds, PM	LM/North	16	43	21.9	39.0	60
19	South of Scott Cr., PM	M/North	24	67	26.7	36.3	100
20	South of Scott Cr., PM	UM/North	10	29	9.2	37.0	30
27	Pine Lake, HM	UM/North	4	14	6.7	33.3	10
46	Scott Cr., PM	UM/Northwest	38	81	29.2	36.9	100
47	Scott Cr., PM	LM/Northwest	23	62	26.7	36.5	100
58	North of White Pine Camp, PM	UM/Northeast	4	14	6.7	28.6	15
69	Northwest of Lost Lake, PM	U/East	4	14	8.3	44.4	15
70	Southeast of Mirror Lake, PM	U/Southwest	7	29	18.4	33.3	50
72	East of Crooked Lake, SWA	U/Southwest	4	14	4.9	21.0	15
		Plots with spot fires‖					
13	Southwest of Mirror Lake, PM	M/Northeast	1	5	1.6	...	<5
17	North of Mirror Lake, PM	U/North	3	14	4.6	17.6	<5
21	Big Carp River, PM	LM/Southeast	1	5	1.1	...	<5
24	Rush Lake, HM	LM/Southeast	1	5	1.2	...	<5
26	Trout Mt., HM	L/Northwest	2	10	1.1	11.1	<5
40	Southeast of Katherine Lake, SWA	UM/Northwest	5	10	11.9	...	<5
52	Devils Head Lake, SWA	M/Northwest	1	5	1.8	...	<5
61	Northeast of W. Pine Camp, PM	UM/Southwest	5	24	4.7	14.7	<5
63	Northwest of Lily Pond, PM	UM/Southeast	3	14	7.5	...	<5

* Location: PM = Porcupine Mountains, HM = Huron Mountains, SWA = Sylvania Wilderness Area.

† Slope position: LM = lower middle, M = middle, UM = upper middle, U = upper.

‡ The number of fire-scarred trees as a % of the total number of trees ≥30 cm in pole or mature stands and ≥40 cm in old-growth stands.

§ Only calculated in cases where at least 8 trees ≥30 cm were present on burned subplots.

‖ Cases where the number and spatial pattern of scars suggested that fire burned <5% of the 0.5-ha plot area.

documented case of arson in the fall of 1894 by a lumberjack who "set fire to the woods at the two ends of Mountain Lake. The fire at the northern end swept across Trout Mountain and burned the Trout Lake boathouse . . ." (Mayor 1988). The 1928 burn in the Porcupine Mountains may have started on cutover land as noted above.

Disturbance chronologies for individual plots were also analyzed for other possible evidence of canopy-killing fires based on radial increment patterns. We assumed that trees developing after stand-killing fire would show a predominance of rapid early growth pattern rather than release from suppression, and that a higher proportion of releases would be more indicative of treefall disturbance. Plots within the historically documented 1953 blowdown had an average of 57% trees with release from suppression, ranging from 22 to 100% on different plots.

All other plot chronologies were therefore examined for episodes of disturbance after 1870 in which ≥30% of the canopy trees were recruited over a period of ≤20 yr. A total of 18 plots met these criteria. The average percentage of trees showing release from suppression during these episodes was high (68.3%). Only two plots had <30% of the trees with releases, and only one had <20% with releases. Thus the evidence on these plots appears to be more consistent with the hypothesis of treefall disturbance as the primary mechanism of canopy recruitment. A possible exception is Plot 20, in which 43% of the canopy trees were recruited between 1880 and 1899 (Table 1), all with rapid early growth. However, the total lack of pioneer species (living or dead), and the fact that a nearby plot with 54% recruitment in the same two decades had 100% releases, suggests that the evidence for a stand-replacement fire on this plot is not strong.

In summary, the evidence suggests that between 1870 and 1980, 14.3% of the plots had spreading surface fires on at least part of the plot, 4.3% of the plots had an intense canopy-killing fire, and 31.4% of the plots had ≥30% of the canopy trees recruited over a period of ≤20 yr as a result of treefall disturbance. The remaining plots (49.9%) had only evidence of minor episodes of gap formation, also evidenced primarily by releases from suppression.

Estimates of natural fire rotations from these data vary according to the length of the chronology, the study area or site type within a study area, and whether or not possible anthropogenic influences are included. Table 4 shows 21 different estimates for surface fire rotations and 12 estimates for canopy-killing fires based on various combinations of these factors. In general,

TABLE 4. Fire rotation periods (yr) for the study areas. Estimates for surface/ground fires are based on data in Table 3. "S slopes" includes plots facing south, southwest, and southeast. Canopy-killing fires include those which killed canopy trees over an area of at least 500 m^2 but not necessarily the entire 0.5-ha plot.

Study area	Surface/ground fires			Canopy-killing fires			All fires	
	1890–1980	1910–1980	1890–1930	1850–1980	1870–1980	1850–1930	1870–1980	1870–1930
All study areas (n = 70)								
All sites	1273	990	566	4545	3846	2797	956	522
S slopes only	1385	1077	615	···	···	···	1692	923
Porcupine Mountains (n = 46)								
All sites	882	686	392	6912	5069	3687	887	484
S slopes only	1080	840	480	···	···	···	1320	720
Sylvania (n = 18)								
All sites	10 843	8434	4819	5856	4955	3604	1721	939
S slopes only	1800	1400	800	···	···	···	2200	1200
Huron Mountains (n = 6)								
All sites	5389	4191	2395	1300	1100	800	550	300

however, fire rotation periods are quite long regardless of the particular assumptions. Rotation periods for all study areas combined are 566 yr for surface fires and 2797 yr for canopy-killing fires even if the chronology is restricted to the pre-fire-suppression era and the fires of possible human origin are included. If the entire fire chronology is used, rotation periods are 1273 yr for surface fires and 4545 yr for canopy-killing fires.

Disturbance and the landscape mosaic

The results presented above imply only that a proportion of the landscape equal to the reciprocal of the rotation period is hit by a given type of disturbance in an average year. Whether the average annual proportion of the landscape hit by disturbance results from many disturbances small in extent and uniformly distributed in time, or from a few relatively widespread and infrequent disturbances can only be assessed by detailed analysis of spatial and temporal distribution of disturbances.

Spatial distribution of disturbances.—Results of the spatial autocorrelation analysis show that plots having had relatively heavy disturbances (≥40% canopy removal) during the 1850–1969 period are significantly clustered, while plots having had medium disturbances (20–39.9% canopy removal) and light disturbances (10–19.9% canopy removal) are not (Fig. 4). When considered together, all disturbances ≥10% are not significantly clustered either, since there are enough light disturbances to mask the clusters of heavy disturbances. The heavier disturbances occur in two main clusters, both of which are in the hilly upland part of the Porcupine Mountains (Fig. 4). The cluster in the northeast part of the park does not correspond to events from a single disturbance, but rather from events in three decades (1890s, 1930s, and 1960s). The cluster in the southcentral part of the park corresponds to events in three other decades (1860s, 1940s, and 1950s). This pattern might initially suggest that the upland region in the eastern and southern parts of the Por-

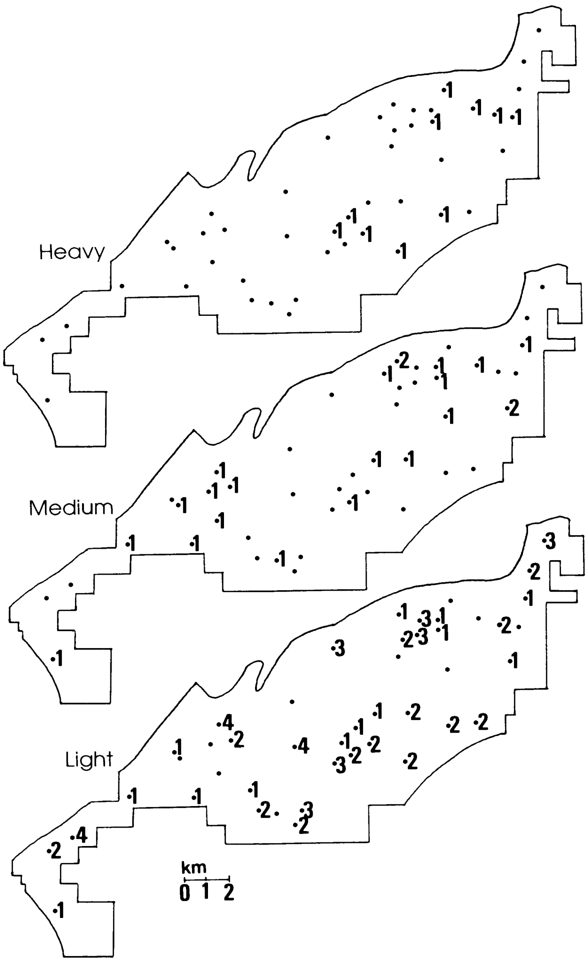

FIG. 4. Estimated number of disturbances during the 1850–1969 time period on each of the 46 0.5-ha plots (●) in the Porcupine Mountains study area. Light disturbances represent 10–19% canopy removal; medium disturbances, 20–39% canopy removal; and heavy disturbances, ≥40% canopy removal.

cupine Mountains is subject to a different disturbance regime than the lowland region, with repeated moderately heavy disturbances. On the other hand, the lack of clustering in light and medium disturbances implies that their frequency is similar throughout the park.

A Mann-Whitney test was used to test the hypothesis that the mean rate of disturbance on those plots in the uplands was higher than in the lowlands. An elevation of 300 m was chosen as the dividing point between lowland and upland. This corresponds to the maximum elevation once occupied by Lake Superior (current elevation 182 m). Lands on the former lakebed have very deep soil and gentle slopes; lands above the former lakebed have relatively shallow soil and steep slopes on numerous hills. No significant difference in mean disturbance rates was found between the lowland and upland groups of plots ($P = .185$). A Chi-square test was also done as an alternative to the Mann-Whitney test. The number of light, medium, and heavy disturbances that occurred during the 1880 to 1969 period was tallied for the upland and lowland group of plots, resulting in a 3 × 2 contingency table. Because of autocorrelation among heavy disturbances, each cluster of heavy disturbances was counted as only one observation (rather than one for each plot affected). The hypothesis that disturbances are uniformly distributed between upland and lowland areas cannot be rejected at $\alpha = .05$ ($\chi^2 = 2.19$, 2 df), thus supporting the result of the Mann-Whitney test. Spearman rank correlation between elevation and mean disturbance rate was also not significant ($P > .05$).

Similar pairs of Mann-Whitney and Chi-square tests were used to test for differences between the 3 km wide hemlock forest zone along Lake Superior and the predominantly sugar maple interior zone. No significant difference was found (Mann-Whitney $P = .59$, $\chi^2 = 1.99$, 2 df). Because it is possible that the effect of Lake Superior extends farther than 3 km, the same tests were made to compare the Porcupine Mountains as a whole to Sylvania. Again, no significant difference in the disturbance regime was found (Mann-Whitney $P = .62$, $\chi^2 = 0.24$, 2 df).

Two comparisons were made to test for differences in the disturbance regime on different aspects (using all three study areas). Plots on level sites were left out of these analyses. First, north, northwest, and northeast aspects were compared to all other aspects. No significant differences were found (Mann-Whitney $P = .98$, $\chi^2 = 0.44$, 2 df). Second, northwest, west, southwest, and south aspects were compared with southeast, east, northeast, and north aspects. Again no significant differences were found (Mann-Whitney $P = .68$, $\chi^2 = 2.35$, 2 df).

Finally, disturbance regimes were compared among the five slope positions; lower, lower middle, middle, upper middle, and upper. A Kruskal-Wallis test revealed no significant difference in mean disturbance rates among the five slope positions ($H = 7.59$, 4 df). A Chi-square test indicated no significant difference in the distribution of disturbance among light, medium, and heavy categories ($\chi^2 = 5.14$, 8 df). A Spearman rank correlation between slope steepness (%) and disturbance rate was also not significant ($P > .05$).

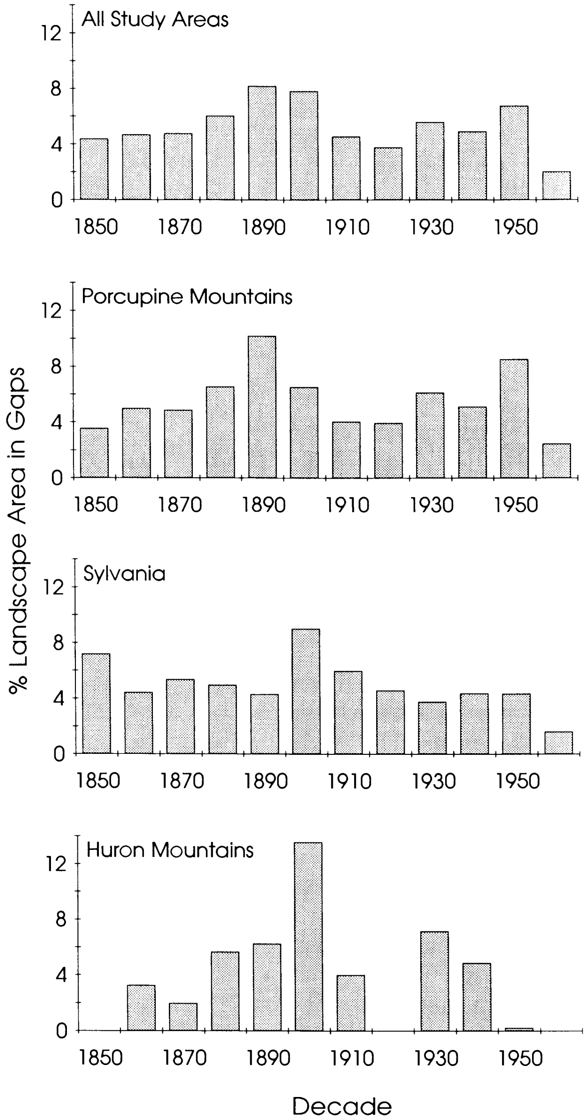

FIG. 5. Estimated percentage of each study area converted to gaps in each of the decades beginning with the years shown, based on the conservative criteria for assigning dates of canopy accession (see *Data analysis: Calculation of disturbance intensity*).

The overall lack of topographical influence on the disturbance regime of the hardwood forests of the Upper Great Lakes region may simply be a reflection of the fact that windstorms which cause major disturbances in the region have strong downward components, as opposed to the horizontal winds of cyclonic storms. Both thunderstorm downbursts and tornados can hit valley bottoms as well as any aspect (Fujita 1978).

TABLE 5. Analysis of spatial autocorrelation of disturbance among plots in the Porcupine Mountains for one decade with low disturbance levels (1920s) and two decades with high disturbance levels (1890s and 1950s). A "+" indicates significant positive spatial autocorrelation at the indicated range of interplot distances at the 95% significance level.

Distance class (km)	Decade		
	1890	1920	1950
0.0–1.9	+	–	+
2.0–3.9	+	–	+
4.0–5.9	–	–	–
6.0–8.9	–	–	–

Temporal variation in disturbance frequency.—There are at least two peaks in the landscape age distribution; 1890–1900, and 1950 (Fig. 5). However, Kolmogorov-Smirnov tests fail to reject the hypothesis that mean disturbance rate in any or all of the three study areas is uniformly distributed over a period of 12 decades (Fig. 5, $P > .2$ in all four cases).

The gently fluctuating disturbance rates for all study areas could be caused either by slight changes in the overall disturbance regime, or by the chance presence/absence of rare medium and heavy disturbances in each decade. When data from the three study areas are compared it is evident that the 1890 and 1950 peaks are due almost entirely to the large influence of the Porcupine Mountains on the data. There are few disturbances in either the Huron Mountains or Sylvania during the 1950 decade and fewer than average in Sylvania during 1890 (Fig. 5). The timing of peak disturbance among the three study areas does not coincide. It therefore seems unlikely that a common underlying factor, such as a shift in the location of major storm tracks, has caused the observed fluctuations in disturbance frequency. The observed fluctuations appear to be due to the chance presence or absence of medium and/or heavy disturbances in each decade.

Analyses of spatial patterns of two high-disturbance decades (1890s and 1950s) and one decade with low disturbance (1920s) in the Porcupine Mountains were carried out, using the spatial autocorrelation program for continuous data. Each of the three decades was analyzed separately as follows. The total percentage of disturbance (conservative analysis) was used for each plot. Four runs were done in which plots the following distances apart (km) were linked: 0–1.0, 2.0–3.9, 4.0–5.9, 6.0–8.9. It was necessary to use larger distance classes than with the previous analysis because of the smaller number of disturbances present in one decade as compared to the entire chronology.

No significant spatial autocorrelation was found in the low-disturbance 1920 decade (Table 5). A map for the 1920 decade (Fig. 6) reveals widely scattered light disturbances and one medium disturbance. The situation is much different for the high-disturbance decades (1890s and 1950s, Table 5). There are clear centers of heavy disturbance with significant spatial autocorrelation in the 0–1.9 km and 2.0–3.9 km distance classes (Fig. 6). In addition, several light and medium disturbances are widely scattered around the remainder of the park, similar to the pattern observed during the 1920 decade (Fig. 5). Thus, it is apparent that the two major high-disturbance decades (1890s and 1950s) are due to the occurrence of heavy disturbances in the Porcupine Mountains. The significant autocorrelation up to 3.9 km implies a patch radius of 2 km for the major disturbances in 1890 and 1950. This is well within the limits of downburst sizes given by Fujita (1978) and Canham and Loucks (1984).

DISCUSSION

Disturbance regimes in northern hardwoods

Results from the analysis of the overall disturbance regime in the Michigan northern hardwood forests differ considerably from the results of similar landscape-

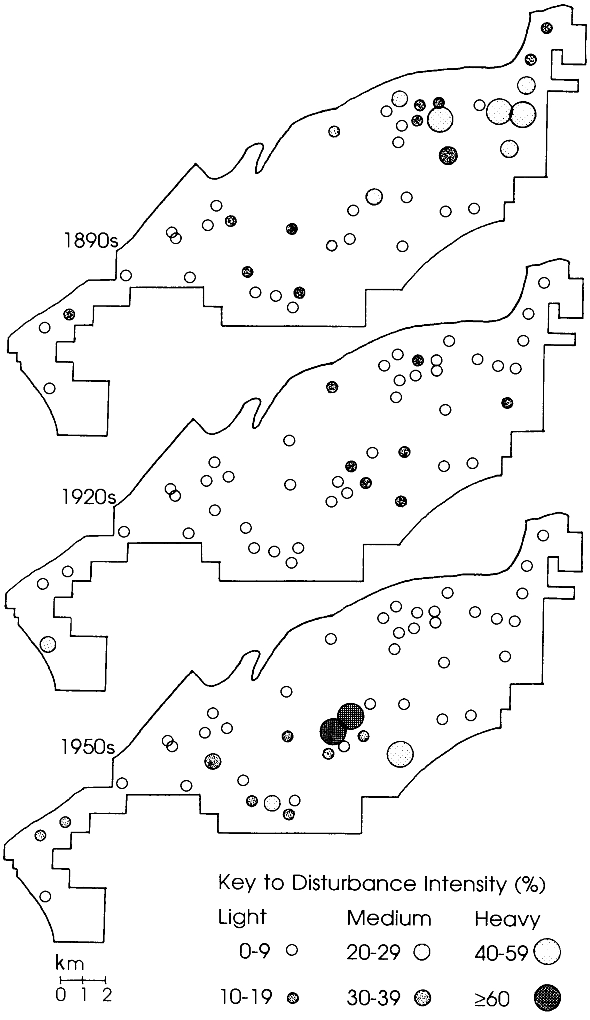

FIG. 6. Disturbance intensity (% canopy removal) maps of the Porcupine Mountains study area (46 0.5-ha plots) for a light-disturbance decade (1920–1929), and two heavy-disturbance decades (1890–1899 and 1950–1959).

level studies in boreal and montane coniferous forests. While boreal and montane conifer stands are frequently even aged and of fire origin (Heinselman 1973, Alexander 1980, Hemstrom and Franklin 1982, Johnson and Fryer 1989), the northern hardwood stands are mostly uneven aged, with an average of at least 10 age classes. About 60% of the trees enter the canopy as a result of periodic small-gap formation and from episodes of light disturbances removing <20% of the canopy. Very heavy disturbances removing ≥60% of the canopy do occur (e.g., the 1953 blowdown in this study), but they are infrequent on a given site, with an estimated rotation period of >1500 yr. Evidence of treefall disturbance is very common, and evidence of past fire is also present in some stands, but few stands appear to be of fire origin.

Although most trees enter the hardwood canopy as a result of relatively small disturbances, episodes of partial stand destruction have a major influence on the size structure of individual stands. Most stands are affected by disturbance removing 30–50% of the canopy at least once during the expected life span of a cohort. As a result, most stands, at least at a scale of 0.5 ha, depart markedly from an equilibrium age structure in spite of the large number of age classes (Table 1).

The field evidence on disturbance regimes obtained in this study is consistent with evidence from 19th-century land-survey records. Only general comparisons are possible because of differences in methodology and geographic location. The minimum intensity of disturbance classified as a blowdown by surveyors is not known. Nevertheless, both lines of evidence suggest long intervals (>1000 yr) between episodes of severe disturbance on a given site. The more appropriate figures for comparison from the present study are probably the rotation periods for high coverage of saplings, since the surveyors could only perceive the present condition of a disturbed area and had no knowledge of the exact sequence of events. The rotation period of 1183 yr for episodes leading to ≥60% coverage by saplings, which is toward the high end of disturbance intensity observed in this study, is similar to land survey estimates of 1210 yr obtained by Canham and Loucks (1984) for northern Wisconsin, and 1220 yr obtained by Whitney (1986) for northern Lower Michigan. The field data also support the inference from land survey records that most stands would be uneven aged.

Frequency of severe windstorms.—Treefall disturbance detected in this study may include several causes of tree mortality, but a limited amount of specific meteorological evidence on the frequency of severe storms is available for comparison with the current study. A tally of the path area of all tornados (excluding F0 tornados, in which winds do not exceed 120 km/h) during the 1950 to 1984 period in several northern Wisconsin counties adjacent to Upper Michigan indicates a rotation period of 6031 years (D. Clark, Wisconsin State Climatologist, *personal communication*). This is close to the estimate for western Upper Michigan of 5600 yr, calculated using data in Thom (1963). No data are yet available on the frequency of thunderstorm downbursts, which were not recognized as a distinctive phenomenon until the 1970s (Fujita 1978).

A more comprehensive analysis of extreme winds of all types was made by Simiu et al. (1979) and Changery (1982), based on annual, observed maximum recorded wind speeds for a number of weather stations. Their data for 11 stations in the northern hardwoods section of the Great Lakes Region (Minneapolis, Minnesota, to Syracuse, New York) indicate five events with winds ≥140 km/h and two events ≥160 km/h for 472 station-years of observations. This suggests a rotation period of 94 yr and 236 yr, respectively. There were no observations of winds ≥200 km/h, comparable to those of severe thunderstorm downbursts and severe hurricanes (cf. Dunn et al. 1983, Foster 1988*b*). While detailed information is not yet available on the effects of wind speed on forest disturbance intensity, wind speeds of 100–120 km/h are fairly common, often recurring at intervals of only a few years at individual stations (Simiu et al. 1979). It is likely that such winds usually cause only scattered treefalls. It is known that winds >200 km/hr usually cause heavy destruction, removing 60–70% or more of the canopy basal area (Dunn et al. 1983, Foster 1988*b*, Glitzenstein and Harcombe 1988). If winds causing partial stand destruction are those in the range of 140–180 km/h, the climatological data would be in general agreement with the results of the stand history work that episodes of moderate to moderately heavy disturbance (20–50% canopy removal) can be expected once or twice during the life span of a cohort of trees.

Natural fire rotations.—Rotation periods for the entire chronology (1850–1980) are generally about double those based on the pre-suppression era (Table 4). The policy of fire suppression after ≈1930 has probably reduced the natural fire frequency; there have been no canopy-killing fires since the advent of organized fire suppression, and no significant surface fires in the 70 stands since 1945. Estimates of natural fire rotations are customarily based on data solely from the pre-fire suppression era (e.g., Arno 1976, Arno and Sneck 1977). However, the occurrence of logging fires on the periphery of all three study areas from 1880 to 1930 probably indicates that fire frequency estimates for the pre-suppression era are higher than would have been the case in the absence of humans. Thus the best estimates of natural fire frequency probably lie between those obtained from the two time periods.

The overall finding of long fire-rotation periods is consistent with the fire rotation of 1400 yr in hemlock–hardwood forests of northern Lower Michigan estimated by Whitney (1986) from 19th-century land-survey evidence. These long rotation periods are also consistent with the land survey evidence indicating that trees of all pioneer species typically made up ≤5% of the presettlement northern hardwood forest (Stearns 1949, Bourdo 1956, Mladenoff and Howell 1980).

Formal studies of fire behavior in northern hardwoods are lacking, but evidence from fire suppression reports suggests that a major reason for the low fire frequency is that most fires, even in very dry weather, smolder in the duff layer and move very slowly. For example, although the year 1976 had the most severe and prolonged drought over a period of 116 yr (Lorimer and Gough 1988), fire records of the Porcupine Mountains State Park indicated no examples of severe fire activity in that year. A total of 11 fires occurred between 26 June and 17 September, 6 of which were caused by lightning. Four of these fires had been burning for 10–21 d before they were discovered and attacked. Although relative humidity occasionally dropped to <30%, coupled with winds as high as 26 km/h, no fire achieved a size of >0.1 ha. A lightning fire that had been burning for 21 d before it was attacked on 18 September was reported by the forest fire officer as having "a few hot spots inside the burn [but] there was no danger of the fire spreading at this time," even though the relative humidity was only 24%. On Isle Royale in Lake Superior, a lightning fire in August 1976 was allowed to burn unhindered for 2.5 mo but reached a final size of only 2 ha (Miller 1978). Clearly the behavior of certain fires (such as those of 1919 and 1928 in the Porcupine Mountains) indicates that fire does have the potential to spread through sizable areas of old-growth forest, but the conditions under which such spread can occur are not well known. In general, however, the available evidence on fire behavior for these study areas seems consistent with the assessment of fire behavior in the similar spruce–northern hardwood fuels in the forests of New England made by Hawley and Hawes (1912): "In ordinary years the forest fires all arise on cut-over lands, stands of uncut timber being practically immune, since they are too moist to allow a fire to start. A crown fire, however, may run through a virgin forest if it secures a good start on cut-over land and there is a strong wind." In presettlement times, some fires could have gained similar momentum by burning through areas of recent windfall (Stearns 1949).

Landscape-level age distribution

Because of the complex age structure of most northern hardwood stands, the concept of "stand age" has little meaning in this case. The concept of landscape age distribution is still useful, however, if the "stands" are defined to be the individual patches or cohorts resulting from treefall gaps or other disturbances. Because of the large numbers of small gaps of different ages, and the great variability in the size and configuration of blowdowns (Stearns 1949, Canham and Loucks 1984), the most feasible approach for assessing landscape age distribution is probably to determine the canopy accession date for the nearest tree for a large number of random or systematic sample points. Thus the graphs of gap formation rates noted in Fig. 5 can be interpreted as landscape age distributions in which each bar in the histogram shows the aggregate area on the landscape occupied by each 10-yr cohort. The ages of these cohorts are the "effective ages" or canopy accession dates, not necessarily the total age.

The uniform age distribution of patches on the landscape (Fig. 5) differs markedly from age distributions in fire-dominated ecosystems, which typically approach a negative exponential curve (Van Wagner 1978, Baker 1989). As Van Wagner (1978) has pointed out, the steeply descending age distributions are probably the result of a random spatial pattern of ignitions, which causes some stands to be burned more than once at short intervals and allows others to escape burning for a long period of time. The rotation period in such cases is equal to the mean stand age and not the maximum age. With a uniform age distribution the rotation period would ordinarily be equal to the maximum stand age, as would be the case for even-aged forest management. The most appropriate measure of small-scale rotation period in the present case, however, is probably the mean canopy residence time for individual trees.

Two factors may contribute to the relatively uniform distribution of patch ages in Upper Michigan. One is that most of the light and moderate disturbances are probably caused by thunderstorms, the number of which varies little from decade to decade (Visher 1954, Eichenlaub 1979, Lorimer and Gough 1988). This is opposed to the erratic distribution of disturbances in areas subject to rare large disturbances, such as conflagrations, hurricanes, earthquakes, and volcanic eruptions. A second factor is the low susceptibility of recently disturbed areas to further disturbance for several decades. After a medium or heavy disturbance it takes many years for young canopy trees to grow to sizes susceptible to windthrow (Foster 1988*b*). A period of quiescence within a patch following cohort establishment would help damp out extremes over time and prevent a predominance of young patches caused by repeat disturbances on the same spot.

Disturbance and the equilibrium landscape

The Upper Michigan study areas seem to meet the criterion for landscape equilibrium of a constant rate of disturbance over time. Not only does the Kolmogorov-Smirnov test on data in Fig. 5 indicate no significant departure from a uniform distribution, but the maximum proportion of the smallest study area (Huron Mountains, 2500 ha) disturbed in any one decade since 1850 is estimated to be <15%. The other two study areas, 14 500 ha and 6073 ha in size, have maximum disturbances of ≈10% in one decade (Fig. 5).

Two of the three Upper Michigan study areas also seem to meet the second criterion for equilibrium status—a relatively large number of patches. Shugart (1984) has suggested that a quasi-equilibrium landscape should be at least 50 times the size of an average disturbance-caused patch. Johnson and Van Wagner (1985) suggest that a landscape should be at least twice the size of the largest disturbance. If 97 ha and 3785 ha are used as average and maximum patches by severe wind disturbance in the Upper Great Lakes region (from Canham and Loucks 1984), the Porcupine Mountains Study Area would be about three times the size necessary to meet both of these criteria. Sylvania would be just large enough to meet the 50-patch criterion but is not twice the size of the largest disturbance patch. The Huron Mountain "reserved area" is only large enough to contain about 26 average-sized 97 ha patches.

Although 3785 ha is probably a good estimate of the maximum size of an individual downburst, some storms, such as the 1977 thunderstorm in northern Wisconsin, can produce more than one downburst in close proximity, leading to a mosaic of blowdown and forest covering a larger area (Fujita 1978, Dunn et al. 1983). No data are available on the frequency of such storms. If an aggregation of blowdowns covering 50 000 ha occurred once or twice each century in the 4 757 000 ha mesic forest area of northern Wisconsin, the implied rotation period would be 4000–8000 yr. Thus, regardless of the size of a landscape unit, there will occasionally be disturbances large enough to disrupt a quasi-equilibrium state.

Quasi-equilibria in areas as small as these contrast greatly with results from landscapes in boreal–transition forests and Rocky Mountain forests. Using the data of Heinselman (1973) from the Boundary Waters Canoe Area, Minnesota, Baker (1989) found that the 404 000-ha patch mosaic caused by fires was not stable. Data from Yellowstone National Park, Wyoming, indicate that even the 800 000-ha park is not large enough to achieve quasi-equilibrium status (Romme 1982, Romme and Despain 1989), due to periodic conflagrations. The Michigan study areas appear to be the first documented case of equilibrium landscapes within the normal size range of a wilderness preserve.

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