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SEVERE WIND AND FIRE REGIMES IN NORTHERN FORESTS: HISTORICAL VARIABILITY AT THE REGIONAL SCALE

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Abstract. Within the northern Great Lakes region, mesoscale (10s to 100s of km²) forest patterning is driven by disturbance dynamics. Using original Public Land Survey (PLS) records in northern Wisconsin, USA, we study spatial patterns of wind and fire disturbances during the pre-Euroamerican settlement period (ca. 1850). Our goals were: (1) to determine how effectively wind and fire disturbance can be reconstructed from the PLS, (2) to assess the roles of wind and fire in shaping vegetation patterns, (3) to evaluate landscape to regional controls of wind and fire regimes, and (4) to assess the potential for interactions between these disturbances.

Our analyses indicate that only relatively intense fire and wind disturbance can be reliably detected from the PLS (62–68% canopy removal). Heavy windthrow was more prevalent than fire disturbance in presettlement forests, and wind-disturbed patches were comparatively smaller and more complex in shape. Disturbance rotation periods ranged between 450 and 10 500 years for heavy windthrow and between 700 and 93 000 years for stand-replacing fire. Occurrences of wind and fire disturbance were related to geographic province and to regional soil patterns; analysis further suggests a negative interaction between the two disturbance types.

Given that severe wind disturbance was infrequent, mature to old forests of late-successional species dominated much of pre-Euroamerican northern Wisconsin, but wind disturbances may have allowed regional persistence of less shade-tolerant species, such as *Betula alleghaniensis*. Pine-dominated vegetation was limited to regions with more frequent fire, but frequencies of stand-replacing fire derived from survey records were insufficient to maintain these successional vegetation types; we suggest that frequent surface fires, not recorded in the PLS, along with infrequent stand-replacing fire, maintained these vegetation types.

The extensive nature of the PLS provides a powerful baseline for addressing changes in forest conditions and disturbance regimes associated with climate and land use for both the present and more distant past. Such baselines are informative in discussions of historical variability and restoration silviculture.

Key words: Betula alleghaniensis; *disturbance; fire ecology; landscape ecology; pre-Euroamerican settlement;* Pinus; *Public Land Survey; restoration baselines; windthrow.*

INTRODUCTION

Forests of the northern United States Great Lakes region consist of a complex mosaic of conifer, hardwood, and conifer–hardwood types in a diverse range of successional states. In this region, where climatic and topographic gradients are weak, mesoscale (10s to 100s of km²) forest patterning is largely driven by disturbance dynamics (Loucks 1970, Heinselman 1973, Frelich and Lorimer 1991*a*, He and Mladenoff 1999). Humans have been the predominant landscape engineers for over a century, but before Euroamerican settlement (ca. 1850) wind, fire (lightning and Native American), ungulate herbivory, insect infestation, and beaver activity were the major agents of change. Of these, both windthrow and fire can cause rapid changes in composition and structure at broad spatial scales (Heinselman 1973, Canham and Loucks 1984).

Natural disturbances are a part of current northern forests as they were in the past, but present forests are so affected by human land uses (e.g., forestry, agriculture, settlement) that it is difficult to tease apart natural dynamics from human-influenced patterns (White and Mladenoff 1994, Cole et al. 1998). Baker (1992) showed that even the large Boundary Waters Canoe Area Wilderness (BWCAW; 438 746 ha) in northern Minnesota is currently too small to support the "natural" fire regime. Replacement of predominantly uneven-aged conifer–hardwood forests by even-aged young hardwoods in the region has likely altered the susceptibility of the landscape to windthrow (Foster and Boose 1992, Sinton et al. 2000, Canham et al.

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2001). Here we characterize severe wind and fire disturbance in northern Wisconsin for the period immediately prior to Euroamerican settlement (ca. 1850; hereafter, presettlement) using data extracted from the original U.S. Public Land Survey (PLS).

Collected between 1833 and 1866 in northern Wisconsin, the PLS data represent landscape patterns that developed largely through long-term interactions among vegetation, physical factors, and disturbance (Webb 1986, Frelich and Lorimer 1991*a*). Although humans were present and influencing these forests prior to and during this period, archeological and enthnobotanical evidence suggests that the magnitude and extent of their impact was relatively modest (Cleland 1983, Whitney 1994), especially in comparison to agriculturally more productive regions (Vale 1998), and in comparison to the Euroamericans that followed. Regional pollen analyses show that vegetation change during the past 150 years exceeded that of the previous 1000 years by several orders of magnitude (Cole et al. 1998).

Originally collected for legal and navigational purposes, the PLS records possess both advantages and limitations as a source of ecological information (Schulte and Mladenoff 2001). They are unparalleled by any other data source, historical or current, in respect to detail over broad spatial extents, providing quantitative data on both vegetation composition and structure at high spatial resolution (0.8 km) for the majority of the United States (Ohio to the Pacific Coast). Limitations include data ambiguity and potential sample bias (Bourdo 1956, Delcourt and Delcourt 1996, Manies et al. 2001), which affect their meaning and utility in ecological study (Schulte and Mladenoff 2001). Most ecological studies that use PLS records draw upon bearing tree information (Grimm 1984, Whitney 1987, Johnson 1994, Schwartz 1994, Schulte et al. 2002), but other quantitative data of ecological interest are contained within the surveyors' notebooks. Records on the incidence of wind and fire have been previously used to study disturbance in the Lake States (Stearns 1949, Canham and Loucks 1984, Whitney 1986, 1987, Zhang et al. 1999), and elsewhere (Lorimer 1977, Seischab and Orwig 1991).

Here, we use the PLS to define presettlement wind and fire regimes in northern Wisconsin, and to study their spatial variability. Aspects of disturbance regime that we consider include severity, patch characteristics, and rotation period. "Severity" refers to the amount of "damage" caused by the disturbing force, and differs from "intensity," which is a measure of the "strength" of the disturbing force. Patch characteristics include measures pertaining to the size and shape of disturbed areas. Rotation period is the expected number of years between disturbances of comparable area at a particular location. We develop objective, sensitivity-based approaches for effective reconstruction of wind and fire disturbance from survey data. Other goals are to assess the roles that wind and fire played in shaping vegetation patterns, to evaluate landscape to regional controls of wind and fire regimes, and to assess the potential for interactions between wind and fire disturbance. Although the landscapes and disturbance regimes that we characterize are ephemeral (Sprugel 1991), evaluating these ecological characteristics for the pre-Euroamerican period provides an important historical point of reference for addressing landscape change and understanding historical variability.

Study Area

The study area includes the northern Wisconsin portion of the Laurentian Mixed Forest Province (Fig. 1; Keys et al. 1995, WDNR 1999). Northern Wisconsin (78 000 km^2) has a humid continental climate, with extreme variations in temperature and moderate precipitation (76–87 cm annually). Mean January and July temperatures are -12°C and 20°C, respectively, and growing season varies from 80 days in the northeast to >160 days along Lake Michigan (Karl et al. 1990).

Pleistocene glaciations created a diverse regional geomorphology, including moraines, depressions, and outwash, till, and lake plains. Soils are deep (>0.6 m), predominantly glacial in origin, and have been largely influenced by forest vegetation since the retreat of the last ice sheet (Hole 1976). Prior to settlement, hemlock–northern hardwoods forests (Eastern hemlock, *Tsuga canadensis* (L.) Carr.; sugar maple, *Acer saccharum* Marsh; yellow birch, *Betula alleghaniensis* Britton; American basswood, *Tilia americana* L.; elm, *Ulmus* spp.; nomenclature according to Little 1979), which included American beech (*Fagus grandifolia* Ehrh.) near Lake Michigan, dominated on heavier soils (silt loams–sandy loams; Curtis 1959, Mladenoff et al. 2002, Schulte et al. 2002). White, red, and jack pine (*Pinus strobus* L.; *P. resinosa* Ait.; *P. banksiana* Lamb.), in variable proportions and densities, occupied sandy outwash and lacustrine plains. Lowland conifer (tamarack, *Larix laricina* (Du Roi) K. Koch; black spruce, *Picea mariana* (Mill.) B.S.P.; northern white-cedar, *Thuja occidentalis* L.) patches were scattered throughout the upland matrix, and large patches of aspen (quaking aspen, *Populus tremuloides* Michx.; bigtooth aspen, *P. grandidentata* Michx.) and oak-dominated communities occurred along the southern boundary of the study area (Schulte et al. 2002).

Extensive wind damage in Great Lakes forests can be due to straight-line thunderstorm winds, tornadoes, and cyclonic winds or gales. All three are highly variable in intensity and the damage they cause (Fig. 2a). Complete canopy windthrow is generally associated with straight-line thunderstorm winds and tornadoes. Cyclonic winds, or gales, can affect very large swaths of forest (millions of km^2), but generally cause low to moderate damage (Frelich 2002).

Fire severity varied throughout the Great Lakes region (Fig. 2b). Low intensity surface fires maintained

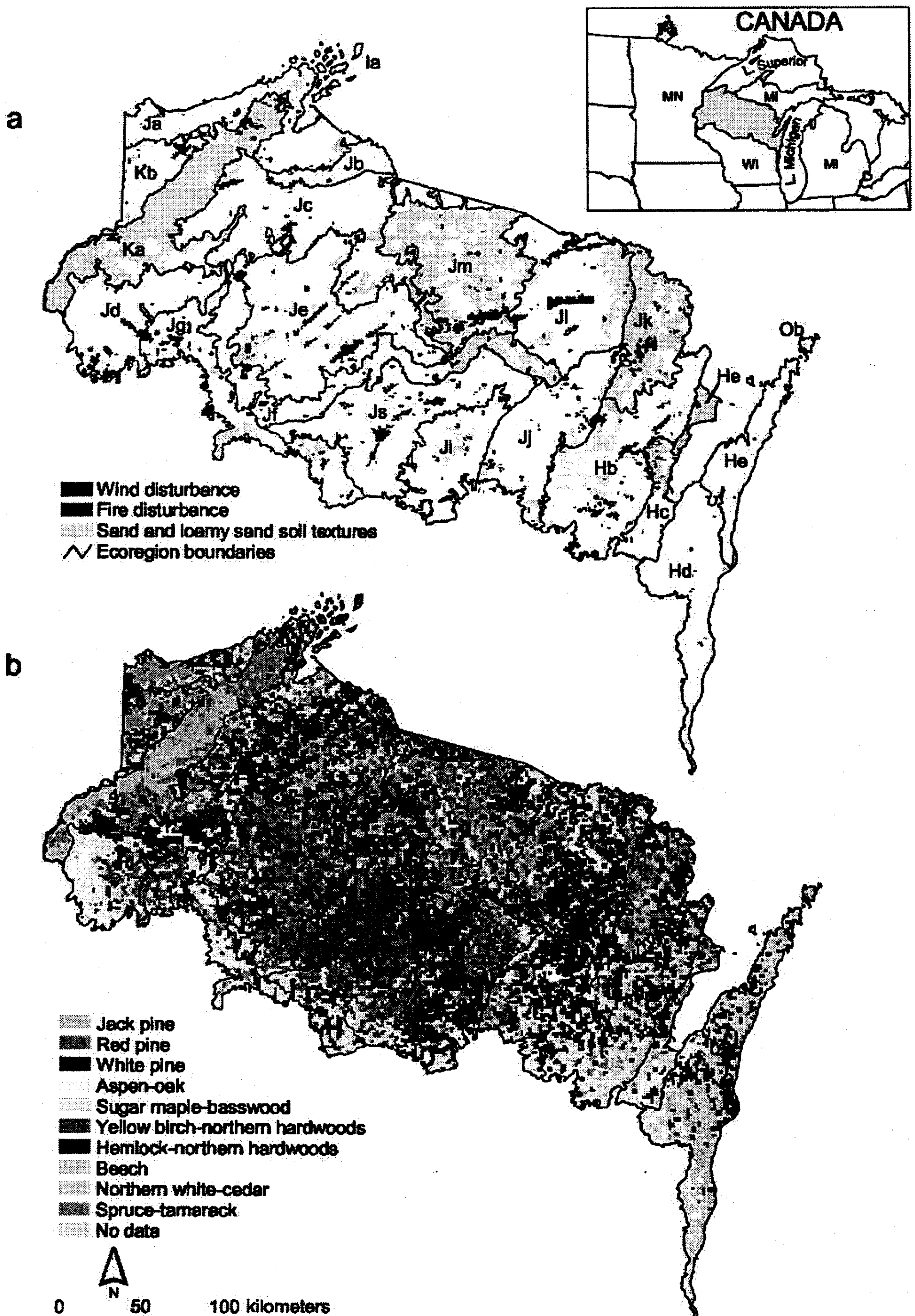

FIG. 1. The study area (see inset) with (a) the location of heavy windthrow and stand-replacing fire and (b) land cover from the original Public Land Survey records. Subsection-level ecoregion boundaries within the Laurentian Mixed Forest Province (Keys et al. 1995, WDNR 1999) and locations of coarse-textured soils (USDA NRCS 1994) are also shown in panel (a).

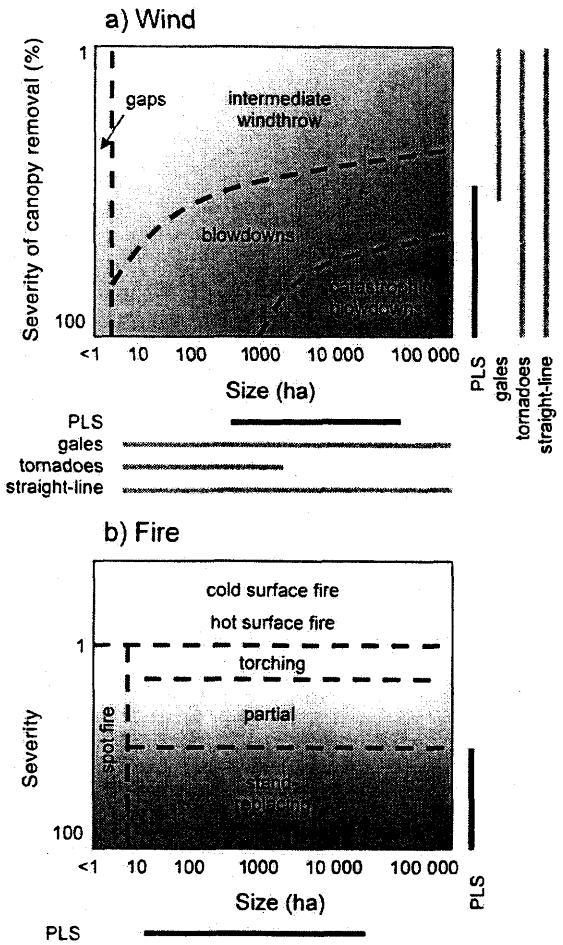

FIG. 2. Conceptual classification of different (a) wind disturbance and (b) fire disturbance types according to size and severity continua. Also shown are the ranges of these distributions that are likely to be represented by the original Public Land Survey (PLS) and the typical intensities and size of area affected by major wind weather phenomena in the northern Great Lakes Region. Straight-line refers to straight-line thunderstorm winds. Torching refers to fires that reach the canopy of a small percentage of trees (<10%), due to localized blowups of a surface fire. Partial fires consume a greater percentage of the canopy (10–50%), but are very patchy in character.

savannas, barrens, and pine forests (Curtis 1959), but most documented cases of severe canopy fire are attributable to the heavy fuel buildup of logging slash associated with Euroamerican settlement (Curtis 1959, Frelich 2002). The combination of conditions required to support a severe crown fire in northern Wisconsin, including extremely dry weather (occurring on a decadal basis; Lorimer and Gough 1988), fuel, ignition, and wind, coincide infrequently.

METHODS AND MATERIALS

The original Public Land Survey

The Public Land Survey (PLS) divided the landscape into a grid of "townships" and "sections." Townships measuring 9.7 × 9.7 km (6 × 6 miles) were surveyed first, and then later divided into 1.6 × 1.6 km (1 mile × 1 mile) sections. Surveyors marked and described the intersections of survey lines, or "section corners," and the midpoint between section corners, or "quarter corners." Corners were marked by blazing 2–4 nearby trees, termed "bearing trees." Surveyors recorded bearing tree species, diameter, azimuth, and distance to corner post within their notebooks (see Stewart 1935, Bourdo 1956, and Manies et al. 2001 for further description). U.S. General Land Office instructions called for reporting of uncommon natural phenomena and, beginning in 1850, survey instructions explicitly stated that incidents of wind disturbance be recorded (Stewart 1935). Data on wind or fire disturbance were recorded as points or transects. Point data are derived from surveyors' statements regarding the environment surrounding survey corners. Fire disturbance was recorded in phrases such as "timber mostly burned and dead," "timber mostly fire killed," or simply "burnt," and wind disturbance was recorded as "windfall," "badly fallen," or "nearly all blown down." Transect data are derived from locations along survey lines where surveyors noted they entered and left disturbed areas (e.g., "19.88 chains, entering windfall," and "44.91, leaving same"; 1 chain = 20.12 m).

Delineating disturbance regimes

Mapping disturbance patches.—To estimate disturbance patch number, size, and shape from the PLS notes, we developed a seven-step mapping technique using GIS (ArcView, Version 3.2; ESRI 1999). (1) Circles of a specified radius ("buffers") were centered on point locations noted by surveyors as disturbed (Fig. 3). Points (and lines) were buffered to expand their spatial influence to an area. (2) If the edge of a buffer polygon was located close (less than half of a buffer distance) to a point where a surveyor entered or left a disturbed area, the location of the edge was shifted to pass through that point. (3) We used disturbance transect data to form disturbance ellipses (Fig. 3). The length of an ellipse corresponded to the transect length and the width of an ellipse corresponded to twice the buffer radius. (4) All point buffers and ellipses were then overlaid and intersected to form disturbance polygons ("patches"). The distribution of data points (section corners and quarter corners) associated with the PLS undersamples the centers of sections, giving some disturbance polygons a "donut" effect. (5) We filled these holes using a simple rule: if at least three-quarters of the section and quarter corners surrounding the section were listed as disturbed, then the section center was also disturbed. (6) We intersected disturbance polygon data layers with a hydrographic data layer, and removed all areas overlapping permanent lakes and streams. (7) Lastly, we performed a sensitivity analysis to determine the effect of buffer distance on the calculation of patch statistics.

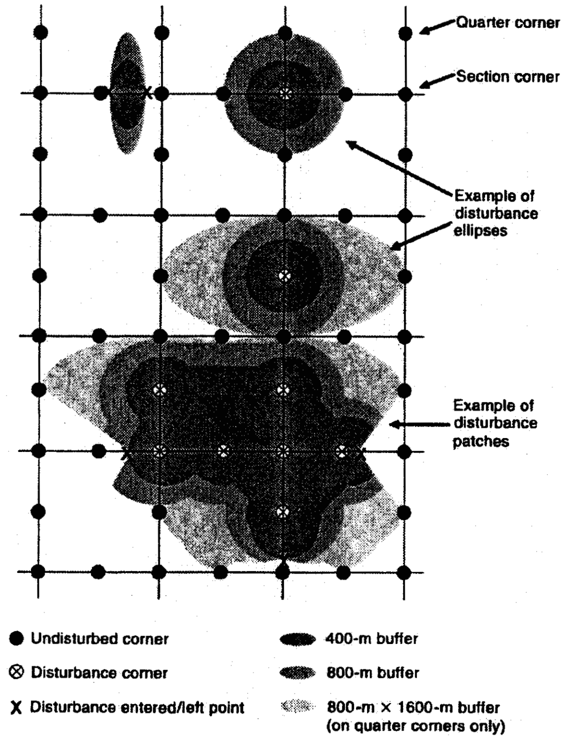

FIG. 3. Diagram of different buffer sizes used in mapping disturbance patches. Buffer sizes included two circular buffers with either a 400-m or an 800-m radius; the third buffer used was elliptical in shape at quarter corners, with an 800-m radius in one direction and a 1600-m radius in the other direction.

We chose distances of 400 m and 800 m for circular buffering in the sensitivity analysis. Four hundred meters (~1/4 mile) and 800 m (~1/2 mile) are equal to half the distance and the full distance between section corner and quarter corner points, respectively. Polygons created using a 400-m buffer represent the average area "potentially" disturbed given the distribution of the PLS data (Fig. 3), assuming a random distribution of disturbance exit points along the survey transect. A polygon created using an 800-m buffer represents a maximum area potentially disturbed (Fig. 3). Given the distribution of points on the square PLS grid system, the centers of the 1.6 km × 1.6 km sections are underrepresented. We implemented a third scenario to address this in which section corners were given a "standard" 800-m buffer (reaching adjacent quarter corner points), while quarter corners were given elliptical buffers, with dimensions of 800 m in the direction of the two closest section corner points and 1600 m in the direction of the two quarter corner points perpendicular to the survey line (Fig. 3). This third algorithm gives greater weight to quarter corners than section corners, but more closely approximates the maximum area potentially disturbed given the design of the survey system. Patch statistics calculated on the disturbance patch data included area, perimeter, and shape index (Baker and Cai 1992).

For 27 townships within northern Wisconsin, surveyors included sketch maps along with their notes. Sketch maps are 1:63 360 scale (2.43 cm = 1.64 km or 1 inch = 1 mile) representations of notable features within a township (e.g., streams, swamps, marshes, ledges, Native American trails and encampments) hand drawn by surveyors in the field. We made visual comparisons of the shape and extent of disturbance patches between available sketch maps and our GIS algorithm-generated maps.

Disturbance severity.—We estimated the severity of surveyor-recorded wind and fire disturbance by comparing estimated tree density within disturbance gaps to estimated tree density in adjacent undisturbed areas. Tree density was calculated from bearing tree (surveyors only used live trees as bearing trees) distances using the following equations, which assume a random distribution of trees and are based on surveyors' units (1 foot = 30.48 cm; 1 link = 20.12 cm):

$$\text{tree density} = (1/\text{MA})(107\,600\ \text{ft}^2/\text{ha}) \quad (1)$$

$$\text{MA} = \left[\left(\sum d_i/n\right)/c \times 0.66\ \text{ft/link}\right]^2 \quad (2)$$

where MA is the mean area per tree in ft^2, d_i is the distance of tree i from corner in links for $i = 1 \ldots n$, n is the total number of trees at corner, and c is a multiplier based on n: if $n = 1$, $c = 0.50$; if $n = 2$, $c = 0.66$; if $n = 3$, $c = 0.81$; if $n = 4$, $c = 1.00$ (Cottam and Curtis 1956, Anderson and Anderson 1975, Manies et al. 2001). Density was also calculated in areas surrounding disturbance patches (defined using the same algorithms used in defining disturbance patches, but with 1600-m, 3200-m, and 4800-m buffers), which served as undisturbed controls. Nonforested corners, including those in open ecosystems (e.g., "marsh," "meadow," "opening," "field," "barren"; Appendix A) or natural lakes and streams, within undisturbed "control" regions were removed from this analysis; surveyors generally only recorded disturbance within forested areas. Preliminary analysis suggested that more reliable density estimates were obtained when larger numbers of survey points were contained within a patch; thus, (1) we used the disturbance patch generation algorithm that contained the greatest number of points per patch (800-m × 1600-m buffer), (2) we eliminated patches that had fewer than three survey points (166 wind and 30 fire patches), and (3) we eliminated patches with densities greater than the maximum density value occurring in the surrounding undisturbed areas (two wind and one fire patch).

Density differences between disturbance patches and surrounding areas were tested using paired t tests. Wind and fire severity were estimated by subtracting absolute tree density within the disturbance patch from tree density within surrounding undisturbed areas. We also test-

TABLE 1. Disturbance severity estimates in northern Wisconsin, USA, derived by comparing tree density within (a) wind-disturbed and (b) fire-disturbed patches to density within three surrounding undisturbed areas (1600-m, 3200-m, and 4800-m buffer on disturbance patch).

		Disturbance patch density (trees/ha)		Undisturbed region density (trees/ha)	
Paired comparison	N	Mean	Median	Mean	Median
a) Wind-disturbed patches					
Wind patch–1600-m buffer	65	109.29	63.10	155.55	163.99
Wind patch–3200-m buffer	65	109.29	63.10	167.00	167.69
Wind patch–4800-m buffer	64	106.46	55.49	156.66	160.85
b) Fire-disturbed patches					
Fire patch–1600-m buffer	66	48.21	17.54	68.90	55.33
Fire patch–3200-m buffer	65	42.38	14.38	88.37	80.49
Fire patch–4800-m buffer	60	47.76	14.21	102.73	96.75

ed for a relationship between disturbance patch size and disturbance severity using linear regression.

Disturbance rotation periods.—Disturbance rotation periods for a given unit of area were calculated as

$$\text{Rotation period} = (f \times y)/d \quad (3)$$

where f is the total number of forested corners (nonforested corners excluded from analysis; Appendix A), y is the number of years over which a disturbance is recognizable and thus recordable (disturbance recognition window), and d is the number of corners noted as disturbed by the surveyors. This equation assumes that all surveyors recorded all wind and fire disturbances above a severity threshold (Fig. 2). Manies et al. (2001) tested whether some surveyors were more likely to record disturbances than others and found no statistical difference; however, recording was also likely to be variable depending on disturbance type (wind or fire), ecosystem type, and the age of the disturbance at the time of the survey. Appropriate values for this last factor, the disturbance recognition window, have been debated: Lapham (1872; cited in Canham and Loucks 1984) suggested a 10-yr window; Canham and Loucks (1984) suggested a 15-yr window for windthrow in hemlock–northern hardwoods; Lorimer (1977) suggested a 25-yr window for fire in Maine; and Whitney (1986) suggested a 30-yr window for fire in pine. By comparing date of survey for township and section lines, we found that individual wind and fire disturbances were recognizable by different surveyors 18 and 17 years apart, respectively, suggesting a minimum recognition window; however, recognition windows may vary by ecosystem type. As existing data do not allow resolution of this issue, we used the 15-yr window used by several other researchers in similar forests (Canham and Loucks 1984, Whitney 1986, Zhang et al. 1999). If the actual window was longer, rotation periods are underestimates.

We estimated rotation periods for the entire study area and by subsection ecoregions (Keys et al. 1995, WDNR 1999), soil texture (USDA NRCS 1994), and forest type (Schulte et al. 2002). Subsections are a level within the hierarchical USDA Forest Service vegetation classification corresponding to patterns in subregional climate, surficial geology, and soil (Appendix B; Cleland et al. 1997). All three factors contribute to the incidence of disturbance in the region (Schulte et al. 2005). Because estimates could not be generated for areas that lacked wind or fire disturbance, we arbitrarily assigned them to our >4000-yr category in maps.

RESULTS

Disturbance severity

Tree density distributions within both wind-disturbed and fire-disturbed patches were skewed (skewness wind patches = 3.01; skewness fire patches = 5.85), with medians consistently lower than mean values; similar values were recorded for both mean and median tree density among the adjacent undisturbed areas (Table 1). Tree densities within wind disturbance patches were generally <100 trees/ha, with 19 patches with <10 trees/ha remaining. In contrast, tree densities in adjacent areas were mostly >100 trees/ha. Using mean density, 46–58 trees/ha were removed by windthrow (Table 1a), which corresponds to 30–35% canopy removal (Fig. 2a). Using median density, we calculated removal of 101–105 trees/ha, or 62–66% canopy removal by windthrow. Tree densities within burned patches and adjacent areas were usually <100 trees/ha, though both mean and median values are higher for the undisturbed areas (Table 1b). Thirty fire disturbance patches had densities of <10 trees/ha. The mean proportion of stems removed by fire disturbance was variable (30–75% removal; Table 1b); median values were more stable (68–85% removal; Fig. 2b).

Disturbance patch characteristics

Patches mapped by our algorithm bracketed sizes of corresponding patches drawn in surveyors' township sketches. Sensitivity analysis showed patch size variables to be more sensitive to buffering technique than overall number of patches or patch shape (Table 2).

Burn patches were larger than wind patches regardless of buffering method (Table 2 and Fig. 4; 400-m

TABLE 1. Extended.

Density difference				Proportion of stems removed	
Mean	Median	t	P	Mean	Median
−46.26	−100.89	−2.30	0.02	0.30	0.62
−57.71	−104.59	−2.68	0.01	0.35	0.62
−50.20	−105.36	−2.27	0.03	0.32	0.66
−20.69	−37.79	−2.14	0.04	0.30	0.68
−45.99	−66.11	−4.57	<0.01	0.75	0.82
−54.97	−82.54	−4.39	<0.01	0.54	0.85

buffer, $t = 2.27$, $P < 0.02$; 800-m buffer, $t = 3.40$, $P < 0.01$; 800-m × 1600-m buffer, $t = 3.37$, $P < 0.01$), but windthrow patches were four times more numerous, displayed a broader range of sizes, and covered two and a half times more area overall. The effect of buffering rule (see *Methods and materials: Mapping disturbance patches*) on windthrow patch size distribution was minimal; large windthrow patches dominated in terms of area and small windthrow patches were more numerous (Fig. 4a, b). Mean windthrow area varied between 93 and 337 ha, depending on buffer size. We considered the lower value more representative, given that most incidents of surveyor-recorded wind disturbance existed as single section corner or quarter corner points surrounded by undisturbed points; little spatial contiguity existed for a larger buffer size to uncover (Fig. 4a). In contrast, the three buffering rules obtained different results for burn patch extent; the proportion of total fires peaks in successively larger size classes (Fig. 4c). Small buffers did not pick up the spatial proximity of fire disturbance points. Buffer size also affected the distribution of fires within patch size classes (Fig. 4d). The smallest disturbance patches recorded were 0.5 ha for wind and 4.5 ha for fire. For both disturbance types, mean shape index was close to 1, indicating prevalence of nearly circular shapes (Baker and Cai 1992). The simple shapes we used in buffer algorithms lacked the complex edges and in all likelihood influenced this measure (Fig. 3); results should only be interpreted in a comparative way. Wind disturbances generally had a more complex shape than fire disturbances, as both mean and maximum shape indices were significantly higher (Table 2; 400-m buffer, $t = 8.87$, $P < 0.01$; 800-m buffer, $t = 16.68$, $P < 0.01$; 800-m × 1600-m buffer, $t = 10.53$, $P < 0.01$).

Patch size and tree density were negatively correlated for both wind ($n = 101$, $F = 5.70$, $P = 0.02$) and fire disturbances ($n = 55$, $F = 4.58$, $P = 0.04$). The largest wind-disturbed patches occurred in a variety of forest types, including spruce–tamarack, northern white-cedar, hemlock–northern hardwoods, northern hardwoods dominated by yellow birch, aspen–oak, and white pine. In contrast, large fire-disturbed patches generally occurred in the more xeric jack, red, and white pine ecosystems.

Disturbance rotation periods

Rotation periods of heavy windthrow were generally shorter in the central portion of the study area (Fig.

Table 2. Patch statistics for (a) wind-disturbed and (b) fire-disturbed patches, as delineated from the original Public Land Survey records using a GIS algorithm with three different buffer sizes.

Buffering method	No. patches	Patch size (ha)			Total area of patches (ha)	Mean patch perimeter (km)	Mean shape index†	Maximum shape index†
		Mean	1 SD	Maximum				
a) Wind-disturbed patches								
400-m circular	829	92.9	297.5	4360.5	77 043.5	3.5	1.3	4.0
800-m circular	668	200.0	582.1	8336.5	133 573.7	6.0	1.7	5.7
800-m × 1600-m elliptical	591	336.9	884.3	11 566.6	199 106.0	8.1	1.7	5.7
Coefficient of variation (%)	17.5	58.3	49.9	44.6	44.7	38.9	13.7	18.7
b) Fire-disturbed patches								
400-m circular	158	143.8	174.8	994.0	22 712.8	4.7	1.2	2.2
800-m circular	138	372.1	456.7	3203.4	51 345.7	7.6	1.2	2.6
800-m × 1600-m elliptical	124	587.2	757.6	4690.8	72 812.9	10.1	1.3	2.7
Coefficient of variation (%)	12.2	60.3	62.9	62.8	51.3	36.2	5.7	10.6

† Shape index is the corrected perimeter-to-area index (Baker and Cai 1992), which varies from 1.0 for a circle to infinity for an infinitely complex shape.

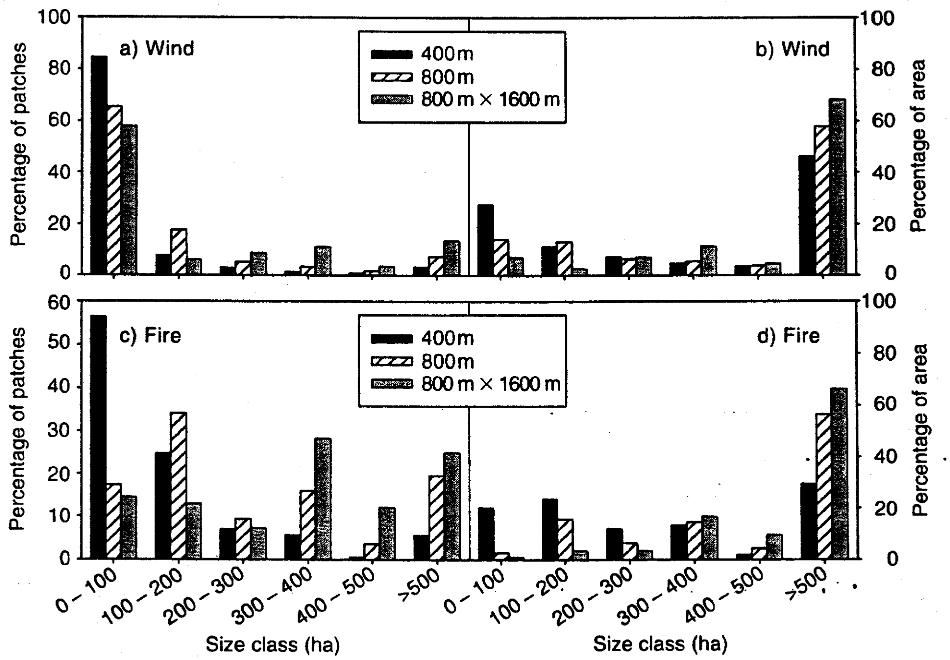

FIG. 4. Patch size and area distributions for (a, b) wind-disturbed and (c, d) fire-disturbed patches using three different buffer sizes.

5a), on organic soils, and in northern hardwoods dominated by yellow birch, red pine, and aspen–oak forests (Table 3). Jack pine, hemlock–northern hardwood, and American beech forests had especially long wind rotations. There is no clear relationship between windthrow and soil texture.

Stand-replacing fires were less frequent than windthrows, on average, and were never recorded by surveyors on some of the mesic glacial lake and till plains and moraines (Table 3). Fire disturbance was most prevalent on two of the three sandy glacial outwash plains (subsections Jk and Ka) and near the southern boundary of the study area (subsections Jd and Jg; Fig. 5b). Fire rotations were shortest on loamy sands (Table 3), but there is no clear relationship between rotation period and soil texture. Fire rotation periods were shorter than average in pine and aspen–oak forests and longer in mesic upland and lowland forests.

The overall rotation period for combined wind and fire disturbance was 900 years (Table 3). The shortest overall rotation periods generally occurred in the central portion of the study area. Jack pine forests were dominated solely by frequent fire, whereas both frequent wind and fire affected red pine, white pine, and aspen–oak forests. American beech forests experienced disturbance least frequently.

DISCUSSION

Disturbance regime reconstruction

This research speaks to reconstruction of the regional ecology of 19th century northern Wisconsin. Because the Public Land Survey (PLS) records are the primary data source used to address presettlement vegetation, wind disturbance, and fire disturbance patterns, their strengths and limitations were carefully considered in methodology developed and employed. These strengths and limitations have been previously assessed (Bourdo 1956, Canham and Loucks 1984, Delcourt and Delcourt 1996, Manies et al. 2001, Schulte and Mladenoff 2001); we focus on developing objective, sensitivity-based approaches for estimating disturbance severity, patch characteristics, and rotation periods.

The PLS records are assumed to represent catastrophic disturbances (Canham and Loucks 1984, Whitney 1986), but we know of no previous attempt to quantitatively assess the range of disturbance severity that they represent. Our method compares estimated tree density within disturbance patches to tree density in adjacent undisturbed areas. This measure of severity was used in lieu of an estimate using basal area because the PLS data do not represent absolute basal area well (Schulte and Mladenoff 2001). As windstorms tend to remove larger diameter trees first (Everham and Brokaw 1996), severity estimates calculated here may be lower than if a basal area estimate were used (Canham et al. 2001). Surface fires tend to remove smaller diameter trees first (Frelich 2002) and may have an opposite bias in comparison to wind disturbance; however, surveyors were instructed to choose sound trees that would have a lasting presence (Stewart 1935) and mid-sized trees (25.5–40.6 cm diameter at breast height) were recorded preferentially (Manies et al. 2001). The potential opposing biases may cancel.

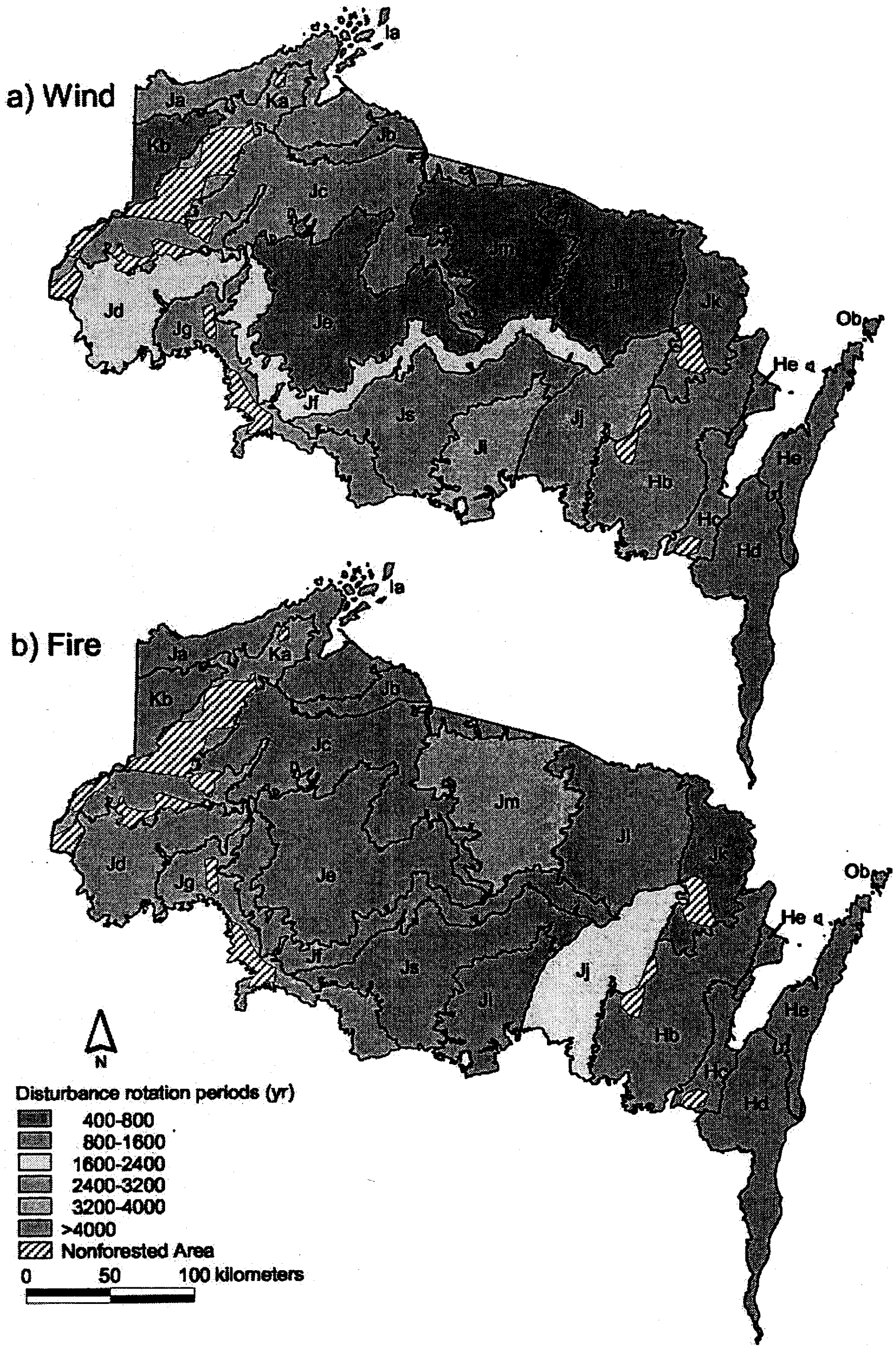

FIG. 5. Disturbance rotation periods (in years) for (a) heavy windthrow and (b) stand-replacing fire by subsection-level ecoregions (Keys et al. 1995, WDNR 1999). Estimates do not apply to nonforested ecosystem types, as delineated by surveyors.

TABLE 3. Number of survey corners and disturbance rotation periods.

Summary units	No. corners					Rotation period (yr)		
	Total	Forest†	Wind	Fire	Combined wind and fire	Heavy windthrow	Stand-replacing fire	Combined wind and fire
Subsection-level ecoregions‡								
Lacustrine								
Green Bay lake plain (Hc)	1260	1092	16	0	16	1024		1024
Door/Escanaba peninsulas (He)	2555	2496	7	0	7	5349		5349
Lake Superior islands (Ia)	219	213	1	0	1	3195		3195
Lake Superior clay plain (Ja)	4020	3933	21	11	32	2809	5363	1844
Green Bay islands (Ob)	78	78	0	0	0	0		
Morainal								
Winegar moraines (Jc)	7948	7660	75	2	77	1532	57 450	1492
St. Croix moraine (Jd)	3908	3559	24	63	87	2224	847	614
Perkinstown end moraine (Jf)	4432	4357	37	0	37	1766		1766
Mille Lacs upland (Kb)	1758	1658	44	0	44	565		565
Green Bay stagnation moraine (Jj)	4615	4468	22	29	51	3046	2311	1314
Till plain								
Green Bay till plain (Hb)	6532	6165	86	6	92	1075	15 413	1005
Manitowoc till plain (Hd)	4291	4197	6	0	6	10 493		10 493
West Lincoln till plain (Jg)	4003	3576	53	51	104	1012	1052	516
Rib Mountain rolling ridges (Ji)	3177	3130	14	4	18	3354	11 738	2608
East Lincoln till plain (Js)	6350	6222	106	1	107	880	93 330	872
Outwash plain								
Spread Eagle/Dunbar (Jk)	3334	2992	7	63	70	6411	712	641
Northern Highland (Jm)	5696	5302	125	24	149	636	3314	534
Bayfield sand plain (Ka)	5710	3115	15	58	73	3115	806	640
Other								
Gogebic-Penokee Iron Range (Jb)	1104	1098	2	0	2	8235		8235
Northwest loess plain (Je)	8219	8017	152	2	154	791	60 128	781
Brule/Paint River drumlins (Jl)	5815	5578	180	9	189	465	9297	443
Soil texture§								
Sand	5763	4964	61	11	72	1221	6769	1034
Loamy sand	11 003	8782	88	134	222	1497	983	593
Sandy loam	26 460	24 855	313	86	399	1191	4335	934
Loam	9058	8785	51	5	56	2584	26 355	2353
Silty loam	26 927	25 949	395	73	468	985	5332	832
Silty clay	2456	2402	14	9	23	2574	4003	1567
Organic	2626	2470	56	3	59	662	12 350	628
Other	525	515	7	0	7	1104		1104
Forest type‖								
Jack pine	3368	1530	1	47	48	22 950	488	478
Red pine	6241	4969	77	92	169	968	810	441
White pine	17 336	16 153	223	80	303	1087	3029	800
Aspen–oak	4970	4408	68	50	118	972	1322	560
Maple–basswood	11 707	11 296	104	26	130	1629	6517	1303
Yellow birch–northern hardwoods	9732	9525	162	10	172	882	14 288	831
Hemlock–northern hardwoods	18 512	18 222	201	8	209	1360	34 166	1308
Beech	3096	3034	17	2	19	2677	22 755	2395
Northern white-cedar	3418	3345	48	3	51	1045	16 725	984
Spruce–tamarack	6645	6425	92	4	96	1048	24 094	1004
Overall	85 025	78 907	993	322	1315	1192	3676	900

† The number of corners in a forest was obtained by subtracting the number of corners in open vegetation types, as defined by the surveyors, and in permanent lakes or streams.

‡ For subsection-level ecoregions, see Keys et al. (1995) and WDNR (1999). Subsections are grouped by dominant surficial geology.

§ Soil texture is defined by USDA NRCS (1994).

‖ Forest types are described in Schulte et al. (2002).

As surveyors recorded information at discrete points, the actual spatial characteristics of recorded windthrows and burns are uncertain. We chose not to use the U.S. General Land Office plat maps (1:63 360 scale representations of PLS notes drawn by draftsmen who never visited actual survey locations) to recreate disturbance patches (as in Canham and Loucks 1984); the criteria used in drawing these maps are unclear and it is unknown whether they were consistently applied. Further, preliminary analysis showed that some disturbances recorded within the PLS notes were not drawn on plat maps. Other studies have used additional data layers (i.e., surface geology, soils, topography) to subjectively interpolate between disturbance points to derive patches (Comer et al. 1995), but statistical modeling has shown that relationships between disturbance and physical factors in the region are complex and often nonlinear (Schulte et al. 2005). Rather, we mapped disturbance patches using an objective, sensitivity-based GIS algorithm, with the goal of capturing the upper and lower bounds of disturbance extent suggested by the PLS data. Comparison of mapped disturbance patches with surveyor-drawn sketch maps showed we accomplished this goal; however, resulting patch statistics should not be interpreted rigidly, but in a general, comparative way.

In estimating disturbance rotation periods, line transect theory has been applied previously to estimate the number of small patches missed by the PLS sampling grid (Canham and Loucks 1984, Zhang et al. 1999). This theory is based upon the relationship between section area and section perimeter (Van Wagner 1968, Canham 1978), and was originally developed for objects with spatial extents much smaller than the resolution of the actual sampling network (DeVries 1974). The methodology assumes that probability of sampling the same object twice is low and the number of objects in the sample is much smaller than the number in the actual population. It was clear in our study area that many disturbance patches crossed multiple transect lines, especially at the intersection of north-south and east-west survey lines (Fig. 3), and disturbance patches tended to be large in area in comparison to the resolution of the sampling grid. Because the line transect method may be misapplied in this situation, we opted for a simpler, point-based measure for estimating proportion of the region disturbed (disturbance rotation periods were calculated by comparing the number of wind-disturbed or fire-disturbed corners to the overall number of forested corners within the study region).

Presettlement wind regimes

Wind disturbance recorded by the PLS.—We found that surveyors recorded windthrow with a median of 62% canopy removal, not solely the catastrophic disturbances that the survey records are generally assumed to represent (Canham and Loucks 1984). Surveyors likely recorded a variety of windthrow severity levels within the general category of heavy windthrow (40–100% canopy removal; Frelich and Lorimer 1991*a*). Our median of 62% windthrow may result from the averaging of forests severely damaged with areas less severely affected by straight-line winds and tornadoes, and possibly the high end of effects that gales can have on forests (Fig. 2a).

Most patches of heavy windthrow were small in extent (Fig. 4a; Canham and Loucks 1984, mean = 93 ha; Zhang et al. 1999, mean = 169 ha; Whitney 1986, range = 0.12–336 ha); however, very large patches of blowdown did occur and represented the majority of area in windthrow (Fig. 4a, b; Canham and Loucks 1984, Zhang et al. 1999). Although we focus on patches rather than events (an event is attributable to a single wind weather system or initial fire ignition and can be composed of several patches; a patch could be the result of several events occurring within a decade or two), it is possible to compute the extent of damage associated with the largest event recorded. By using proximity and directionality to qualitatively group patches of windthrow together, we calculate that the largest blowdown event recorded by the surveyors damaged 34 000 ha of forest (median 62% canopy removal; see large blowdown in Fig. 1 extending between subsections Jm and Jl). Comparing this event to two other well-known blowdowns within the Great Lakes region, the 4 July 1977 Flambeau Forest blowdown in northern Wisconsin (24 000 ha of 344 000 ha in "catastrophic" damage; Fujita 1978, Dunn et al. 1983) and the 4 July 1999 Boundary Waters blowdown in northern Minnesota (57 000 ha of 190 000 ha in >66% forest damage; MN DNR 1999), shows that large historical and modern wind disturbances in the region have impacts over similar spatial scales (Fig. 2a).

Our calculation of rotation period for heavy windthrow in historical hemlock–northern hardwoods (1360 years), though conservative, is comparable to other studies from within the Great Lakes region and beyond (Canham and Loucks 1984, 1210 years; Whitney 1986, 1220 years; Lorimer 1977, 1150 years); Zhang et al. (1999) found a much longer wind rotation period (2500 years) in conifer–hardwoods in the eastern Upper Peninsula of Michigan. Whitney (1986) reports similar overall wind rotation periods in conifer forests, although rotation periods in red and white pine tended to be shorter in northern Wisconsin. Reasons may be related to differences in the magnitude and return interval of wind events across the region, or due to differences in the forest environments.

Wind disturbance and vegetation.—Because rotation periods for heavy wind disturbance were longer than the maximum age of shade tolerant tree species, Frelich and Lorimer (1991*b*) suggest that wind-prone landscapes were dominated by multicohort to multiaged and mature to old forests. Eastern hemlock, sugar maple, and American beech forests covered 29% of presettlement northern Wisconsin (Schulte et al. 2002), and an even larger percentage of landscapes that were not prone to fire (36%). Large windthrows added complexity to this late-successional matrix by maintaining successional hardwoods on the landscape (Peterson 2000, Woods 2000*a*, *b*) and altering future disturbance susceptibility (He and Mladenoff 1999). Eastern hemlock is the slowest growing and most shade tolerant tree species in this region (Woods 2000*a*, Webster and Lorimer 2002), especially when American beech is absent (Woods 2000*b*), as in most of the study area. Light to moderate levels of windthrow likely facilitated or maintained dominance of hemlock (Abrams and Orwig 1996, Webster and Lorimer 2002), but heavy windthrow may have shifted the balance in favor of hardwoods (Abrams and Orwig 1996, Canham et al. 2001). Heavy windthrow was likely essential in maintaining less tolerant yellow birch on the presettlement landscape (Peterson 2000). In contrast to previous work in old-growth northern hardwoods forests of Wisconsin (Curtis 1959), we interpret survey records to indicate substantial areas dominated by this species in presettlement forests (Mladenoff et al. 2002, Schulte et al. 2002; 11% overall and 17% in wind-prone landscapes). Structural changes due to settlement and current forest management may have eliminated the light environments that maintained this species (Webster and Lorimer 2002). Historically heavy deer browse over recent decades has had further negative effects on yellow birch, as well as eastern hemlock (Mladenoff and Stearns 1993, Rooney and Waller 2003). Woods (2000*a*) has also documented a decline of yellow birch in the Upper Peninsula of Michigan.

Landscape to regional controls.—Our results suggest that wind was the prevalent disturbance throughout much of northern Wisconsin, except in areas adjacent to Lakes Michigan and Superior and where fire is nearly absent (Fig. 5 and Table 3). The pattern of longer wind rotation periods (>2400 years) near the Great Lakes is likely due to lake influences on climate, including increased humidity and amelioration of the more severe thunderstorms (Changnon 1966, Changnon and Jones 1972; though these areas are prone to gales; Fig. 2a). The long rotation periods found by Zhang et al. (1999) for the eastern Upper Peninsula of Michigan may also relate to proximity to the Great Lakes. At the regional scale, the Great Lakes may provide refugia from both severe wind and fire disturbance.

Presettlement fire regime

Fire disturbance recorded by the PLS.—Fire removed a higher proportion of stems than wind, and fire events were effectively stand replacing (68–85%; Table 1b, Fig. 2b). This result is qualitatively consistent with the near lack of fire records in the southern portion of the Bayfield Sand Plain (subsection Ka; Fig. 1), an area of open pine barrens maintained by frequent surface fires (Curtis 1959, Radeloff et al. 1999). The visible legacy of surface fire was likely too short lived for the surveyors to consider recording them (Whitney 1986).

Because of rapid alteration of the fire regime with Euroamerican settlement, it is difficult to find an adequate "natural" baseline to compare with fire sizes derived from the PLS records. The largest fire event we map (21 047 ha; see cluster of fire patches in subsection Jd in Fig. 1) is small in comparison to the largest presettlement burn in Minnesota's Boundary Waters Canoe Area Wilderness (BWCAW; 112 000 ha; Heinselman 1996) and the postsettlement 1872 Peshtigo Fire, the largest conflagration known to have occurred within northern Wisconsin (518 000 ha; Lorimer and Gough 1988). The Boundary Waters fire regime is different from that of northern Wisconsin, however, and the Peshtigo Fire is considered anomalous, due to a profusion of logging slash across the landscape and the injudicious use of fire during this period (Pernin 1999). The PLS provides the best estimate of the size distribution of severe fires within presettlement northern Wisconsin ecosystems.

Our rotation periods were longer than dendrochronological estimates of recurrence interval (Heinselman 1973) and PLS-based estimates of rotation period (Whitney 1986, Zhang et al. 1999) for comparable vegetation types in the northern Lake States (Table 3). Several reasons may account for this difference. Other studies were conducted in regions where fire-prone conifer vegetation forms a matrix in which more mesic conifer–hardwood types are imbedded. In such systems, the likelihood of fire spread is greater than in northern Wisconsin, which was dominated by more mesic conditions not conducive to burning (Stearns 1949, Mladenoff and Pastor 1993, Schulte et al. 2002). The more flammable vegetation types existed as pockets embedded within or on the fringe of mesic systems (Curtis 1959, Radeloff et al. 1999). Charcoal preserved in lake sediments supports long fire-free intervals within mesic conifer–hardwoods (>2000 years) and more frequent fires in pine forests and barrens (140 years; Swain 1978, Clark and Royall 1996). Still, the 488-yr, 810-yr, and 3029-yr fire rotation periods that we found are too long to support jack, red, and white pine, respectively (Frelich 2002). We suggest that a fire regime of combined fire types provides explanation.

Severe canopy-killing fire, as recorded by the surveyors, was likely only one type of fire that affected northern Wisconsin forests; surface fires were also likely to be important. This hypothesis is supported by forest composition within and tree densities surrounding the presettlement burns in northern Wisconsin (Table 1b). Tree densities computed from the PLS bearing tree data suggest that many areas were in open forest (65–98 trees/ha; Anderson and Anderson 1975) and even savanna-like conditions (0.5–65 trees/ha), which generally do not carry continuous crown fires (Johnson 1992). Furthermore, many of these areas were dominated by pine and oak species, which can survive surface fires. Frequent surface fire can maintain pines and oaks in the region (Curtis 1959, Clark 1990, Heinselman 1996), and elsewhere (Agee 1993, Swetnam and Baisan 1996). Under this scenario, the fire regime in many of the fire-prone areas of northern Wisconsin was one of frequent surface fires that were not recorded by the surveyors, and infrequent, canopy-killing fires that were recorded.

Fire disturbance and vegetation.—Both wind and fire were important in generating the complex pattern of vegetation on the presettlement landscape, but their importance was separated in space (Fig. 5). Fire added complexity to the presettlement landscape by maintaining forests in an earlier successional state and a different stand structure than windthrow (Mladenoff and Pastor 1993). Frequent fires maintained pines, oaks, and aspens in lieu of the many more shade tolerant hardwoods in the region (Curtis 1959, Mladenoff and Pastor 1993, Bolliger et al. 2004). Stand structures were probably even-aged or multicohort systems, in comparison to the all-aged systems found within the more wind-prone regions.

Potential disturbance interactions

As postsettlement mesic forest types are generally not conducive to burning in the northern Great Lakes region (Lorimer and Gough 1988), a link with windfall preceding and encouraging fire has been hypothesized (Stearns 1949). Qualitative evidence for this potential interaction is found within surveyors' written descriptions, where they noted two disturbance types in combination: "dead timber and windfall, old burning," "timber on ridges mostly destroyed by wind and fire," and "timber fire killed and blown down by winds." We suggest that such interactions were rare rather than inevitable, and likely dependent on historically important events, such as drought years. We base this hypothesis on the overall low proportion of early-successional forest on the mesic portions of the presettlement landscape. Aspen and white birch (*Betula papyrifera* Marsh.) types require fire or clear-cut logging disturbance to establish and, respectively, comprised 1.4% and 2.6% of northern Wisconsin's presettlement forests (Schulte et al. 2002), and an even smaller proportion of Wisconsin's mesic hemlock–northern hardwood landscapes (aspen = 0.5% and white birch = 2.1%).

The spatial separation of heavy windthrow and stand-replacing fire across presettlement northern Wisconsin suggests another interaction, in which more frequent fire reduces the incidence of windthrow. Presettlement wind disturbance was distinctly less frequent near the Great Lakes, where all disturbances were rare, and on sandy outwash plains, where fire was more frequent (Fig. 5; Curtis 1959, Radeloff et al. 1999). Although a negative feedback between wind and fire has been documented at a local level (Baker et al. 2002, Platt et al. 2002), where short fire rotation periods keep forests in an open and/or young condition less susceptible to windthrow, our results suggest this feedback may extend to regional scales. This conclusion is supported by simulation modeling of wind and fire disturbance within the study area (He and Mladenoff 1999).

Summary

Due to their extensive nature, the original PLS records are a unique data source for detailing regional-scale spatial variation in presettlement (ca. 1850) wind and fire regimes: disturbance severity, patch characteristics, and rotation periods can all be assessed. These records, however, provide data on only a portion of disturbance severity and size spectra (i.e., large patches of heavy windthrow and stand-replacing fire; Fig. 2). These disturbance types were infrequent, but our research shows that windthrow defined landscape structure across most of northern Wisconsin. Heavy windthrow was important in maintaining a diversity of cover types on the mesic glacial moraines and till plains, especially yellow birch. As low to moderate severity windthrow were more frequent, forests were dominated by late-successional species and were multicohort to multiaged in structure (Frelich and Lorimer 1991*b*). In contrast, fire disturbance was of strong subregional importance. Fire-prone landscapes were located on sandy glacial outwash plains and along the southern boundary of the study area, and were highly variable in tree densities (Radeloff et al. 1999, Bolliger et al. 2004). Our estimates of stand-replacing fire rotation periods, however, were not short enough to maintain the pine and oak forests observed on these landscapes (Schulte et al. 2002). Although prevalence of stand-replacing fires on sandy outwash has generally been assumed for pre-Euroamerican northern Wisconsin forests, we suggest instead a combined fire regime of common surface fire and less frequent stand-replacing fire. Ecoregions bordering the Great Lakes show lower incidence of both severe disturbances, suggesting influence of lake-effect climate. Our work detailing spatial variation in disturbance regimes provides an important baseline for discussions of historical variability and restoration silviculture within the limits of the data set and procedures. Future work can address how climate change and humans may have altered these disturbance regimes during both the more distant past and the present.

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APPENDIX A

A table of ecosystem types included and excluded from the calculation of disturbance rotation period is available in ESA's Electronic Data Archive: *Ecological Archives* E086-021-A1.

APPENDIX B

A table of climate, landform, and soil characteristics of landscapes within northern Wisconsin is available in ESA's Electronic Data Archive: *Ecological Archives* E086-021-A2.