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A SIMULATION OF LANDSCAPE-LEVEL STAND DYNAMICS IN THE NORTHERN HARDWOOD REGION

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SUMMARY

(1) The STORM simulation was developed to predict the response of regional stand age structure to a given disturbance regime. The outcome of STORM depends upon rotation periods of canopy disturbance, diameter growth rates of trees, and the relative susceptibility of pole, mature and large trees to windthrow.

(2) The simulation was run using data on disturbance frequencies from remnants of primary forest in western Upper Michigan. Rotation periods ranged from 69 years for >10% canopy removal to 3734 years for >70% canopy removal. Stands were classified into eight structural types, ranging from even-aged sapling stands to steady-state stands, which reflect the state of recovery from recent disturbances.

(3) The model suggests that most (87.4%) stands in the primeval hardwood forest were multi-aged, with several major and many minor age classes. Quasi-even-aged stands resulting from catastrophic disturbance occupied 9.2% of the landscape, and steady-state stands about 3.6%. The low frequency of steady-state stands on the landscape appears to be determined primarily by the high frequency of disturbances removing part of the canopy, rather than the interval between catastrophes.

(4) Sensitivity analyses indicate that changes in disturbance rates result in disproportionately large changes in the proportion of even-aged stands on the landscape, while mean canopy residence time for trees shows a damped effect.

INTRODUCTION

Most hardwood stands in North America are relatively young and even-aged as a result of heavy past cutting. Several studies have been made of the characteristics of individual old-growth stands (e.g. Hough & Forbes 1943, Leak 1975). Little is known however, about the stages of stand development beyond an age of 80–100 years, or the relative abundance of stands of different ages on the landscape under conditions largely free of human influence. Bormann & Likens (1979) proposed several functional stages of stand development for northern hardwoods in which an even-aged (aggrading) phase undergoes a transitional stage culminating in a steady-state or equilibrium phase. They recognized that it would be difficult to distinguish transitional and steady-state stands using field data, and that existing data are insufficient to establish whether or not the steady-state phase is commonly attained.

Recent studies based on both historical records and field data have indicated that

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the frequency of intense natural disturbances is inherently low in much of the northern hardwood region (Canham & Loucks 1984, Whitney 1986, Frelich & Lorimer 1991) A study of large remnants of primary forest in Upper Michigan indicated that 70% of the stands are in the old-growth stage, and nearly all of these are broadly uneven-aged (Frelich & Lorimer 1991) It was not possible to determine directly what proportion of these stands might be in the transition and steady-state phases

Some of these questions that are difficult to answer from field data can potentially be resolved by computer simulation With historical information on the frequency and intensity of natural disturbances, and the rate of forest recovery, it is possible to investigate the nature of the landscape mosaic including the proportion of stands in transition and steady-state phases The STORM simulation was devised for this purpose The objective of this paper is to characterize the primeval landscape of the northern-hardwood region as a mosaic of stands in various stages of response to natural disturbance, and to look at sensitivity of landscape structure to changes in disturbance frequency

METHODS

Simulation development

STORM is a rule-enhanced model (Starfield & Bleloch 1986) in which episodic disturbances of varying intensity cause mortality of canopy trees within individual simulated plots After each disturbance, a new cohort of trees enters the plot and follows a deterministic growth model over time, until eliminated by further disturbance or senescence Four size categories of trees are recognized, slightly modified from Unites States Forest Service definitions sapling (0–10 9cm dbh), pole (11 0–25 9cm dbh), mature (26 0–45 9cm dbh) and large (≥46 0cm dbh) The model keeps track of the disturbance history and current size structure of each plot The characteristics of the landscape as a whole are determined by combining a large number of plots at the end of the simulation

Disturbance intensity is defined as percent canopy area of a plot removed by disturbance in one time step (10 years) Canopy area is the sum, for all canopy trees, of exposed crown area, or the cross-sectional area of an individual tree crown at its widest point, excluding areas of overlap with adjacent trees Disturbance intensity is referred to as light (0–19 9% canopy removal) medium (20 0–39 9% canopy removal) or heavy (>40% canopy removal) Any disturbance or combination of disturbances removing at least two-thirds of the canopy is referred to as a catastrophe The term partial disturbance is used for any disturbance less intense than a catastrophe Stands developing after catastrophic disturbance are here called even-aged stands for convenience however, it is actually the canopy accession dates rather than germination dates that are nearly synchronous in these stands (Lorimer 1985)

For each plot, the following procedures are completed at 10-year intervals

(a) The plot is subjected to disturbance Occurrence of disturbances is determined stochastically For example if the rotation period for a certain category of disturbance is 100 years, then there is a 10% chance of such a disturbance in a given decade Rotation periods are entered into the simulation by 10% categories of intensity If a plot escapes disturbance in a given decade, then 'background mortality' caused by senescence of individual trees is simulated by removing 5% of the large trees A disturbance is assumed to remove trees that would otherwise have died from senescence The model was developed for areas where wind is the dominant type of disturbance, thus, susceptibility of trees to disturbance is assumed proportional to tree size (large > mature > pole > sapling)

(b) A new cohort is added and tree growth projected 10 years Trees removed by disturbance are replaced by a new cohort, which is divided into six size classes that approximate a normal distribution (Fig 1) A regression of tree dbh on age is used to predict the size class boundaries for the six cohort classes over time The simulation follows the six cohort classes through the sapling, pole, mature, or large categories each decade The largest size class of each cohort (5% of the individuals) is transferred from the sapling to the pole category during the decade in which the upper 90% confidence limit of the age–diameter curve intersects the lower diameter threshold of the pole category (11 0 cm) The second (15%) and third (30%) size classes are transferred from sapling to pole when the upper 60% confidence limit and mean (regression line), respectively, intersect the 11 0-cm threshold (Fig 1) The last three classes of each cohort are handled as a mirror image of the first three classes As shown in Fig 1 and Table 1, class 1 of a new cohort will transfer to the pole category in the first decade after disturbance but class 6 will not cross the lower threshold of the pole category until the fifth decade Similar procedures are used to determine the times of transfer to mature and large size classes

(c) Plot structural type is classified Eight types of forest were recognized, based on physiognomy and disturbance history The simulation takes into account the proportion of plots in each structural type, and the time individual plots spend as a given type, and transfers from type to type Six of the structural types represent stages in the development from an even-aged sapling stand to an all-aged, steady-state forest There are three even-aged types (sapling, pole and mature), two transitional types (multi-aged break-up and old multi-aged), and the steady-state type

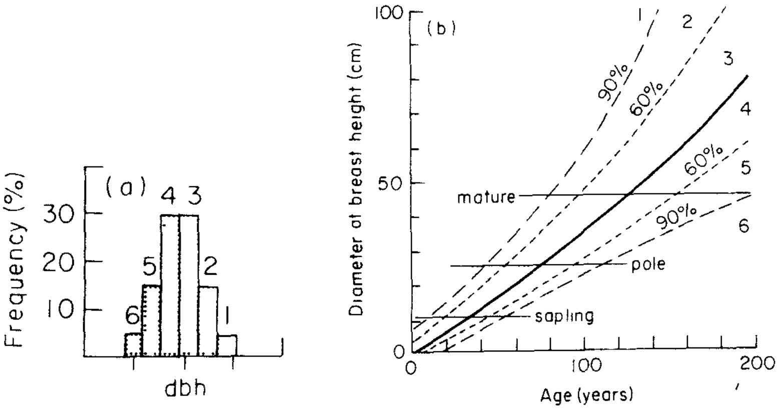

FIG 1 Scheme for growth of a cohort of trees in northern-hardwood forests in the STORM simulation (a) Approximately normal size distribution of a newly formed cohort Shape of the distribution will change as the six size classes of the cohort undergo different rates of growth and disturbance events (b) Diameter–age from release relationship Ninety per cent and 60% contours for individual observations are shown about the regression (solid curve) Solid horizontal lines show the upper diameter limit for sapling (10 9 cm dbh) pole (25 9 cm dbh) and mature (45 9 cm dbh) size classes

TABLE 1 Growth schedule for a cohort The letters in each column represent the stage of development for each size class of a cohort from the first decade after formation of the cohort to the twenty-first decade S=sapling (0–10 9 cm dbh), P = pole (11 0–25 9 cm dbh), M = mature (26 0–45 9 cm dbh), and L = Large ($\geq$46 0 cm dbh)

Decade	Size class of a cohort					
	6(5%)	5(15%)	4(30%)	3(30%)	2(15%)	1(5%)
1	S	S	S	S	P	P
2	S	S	S	P	P	P
3	S	S	S	P	M	M
4	S	S	P	P	M	M
5	P	P	P	M	M	M
6	P	P	P	M	M	L
7	P	P	P	M	M	L
8	P	P	M	M	L	L
9	P	M	M	M	L	L
10	P	M	M	M	L	L
11	M	M	M	L	L	L
12	M	M	M	L	L	L
13	M	M	M	L	L	L
14	M	M	M	L	L	L
15	M	M	M	L	L	L
16	M	M	L	L	L	L
17	M	M	L	L	L	L
18	M	L	L	L	L	L
19	M	L	L	L	L	L
20	M	L	L	L	L	L
21	L	L	L	L	L	L

In addition, there are two structural types (multi-aged pole and multi-aged mature) that result when moderate windstorms remove many of the large trees from old growth stands, causing temporary retrogression in the stand development process The even-aged structural types are distinguished by a predominance of trees (>2/3 of canopy area) in two adjacent size categories up to the mature stage Specific definitions are as follows

Sapling stand at least two-thirds of the canopy occupied by saplings and poles, with aggregate exposed crown area of saplings greater than that of poles May result from a catastrophe or from two heavy partial disturbances occurring during consecutive decades

Pole stand at least two-thirds of the canopy occupied by saplings and poles, with area of poles greater than that of saplings, or at least two-thirds poles and mature, with area of poles greater than that of mature

Mature stand at least two-thirds of the canopy occupied by poles and mature trees, with area of mature trees greater than that of poles, or at least two-thirds mature plus large trees, with mature greater than large

Multi-aged break-up stand a stand that has suffered a catastrophe during the last 250 years, but no longer meets the definitions of any of the previous three stand types Typically an old-growth first-generation stand after catastrophic disturbance that has more mature and large trees than a mature forest, but does not yet have a broadly uneven-aged structure

Multi-aged pole stand a stand with size structure similar to that of a pole stand, but not originating from a sapling stand Unlike a pole stand, widely scattered age classes are present Results from any other type of multi-aged or all-aged stand that has undergone partial disturbance

Multi-aged mature stand a stand with structure similar to that of a mature stand, but not originating from a pole stand Unlike a mature stand, widely scattered age classes are present Results from continued growth in a multi-aged pole stand or from partial disturbance in any other type of old-growth stand

Old multi-aged stand a stand that has gone at least 250 years since the last catastrophic disturbance and has more mature and large trees than a multi-aged mature stand At least 20% mature and 30% large, or at least 50% large trees are present Usually composed of at least several widely scattered age classes that may be unequally represented

Steady-state or balanced all-aged stand a stand that has gone more than 250 years since the last disturbance greater than 20% in intensity The stand has experienced four or fewer light disturbances, and at least forty years apart, during the last 250 years

Analysis of input data

Data on frequency of disturbances, tree growth rate, and relative susceptibility of different-sized trees to disturbance are necessary to run STORM These data were collected from three study areas in western Upper Michigan – the Porcupine Mountains Wilderness State Park, the Huron Mountains, and Sylvania Wilderness Area The study areas contain 23 000 ha of primary forest remnants set aside between 1890 and 1944, when extensive areas of virgin forest were still present in Upper Michigan (Cunningham & White 1941, Braun 1950, United States Department of Agriculture 1964) The study was restricted to closed-canopy mesic forest heavily dominated by *Acer saccharum* Marsh (sugar maple), but with substantial amounts of *Tsuga canadensis* (L)Carr (hemlock) and *Betula alleghaniensis* Britt (yellow birch) The climate is cold temperate, with ample precipitation in all months of the year Soils are deep and loamy, with slopes of 0–15%

A disturbance chronology was prepared for each of seventy 0 5-ha plots randomly located within the three study areas An increment core was obtained from the nearest tree at between ten and thirty randomly located points on a plot Increment cores were sanded, and the annual rings measured with an optical micrometer The radial increment patterns were examined to determine the most likely year of gap formation that allowed each tree to enter the canopy (Lorimer, Frelich & Nordheim 1988, Lorimer & Frelich 1989) Gap formation dates for nearly all trees were indicated by either rapid early growth (suggesting that the tree colonized a new gap), or by a sudden increase in radial growth of 100% or more (suggesting that an existing understorey tree responded to a gap) Disturbance intensity is estimated by the percentage of all sample trees with canopy accession in each decade The resulting chronology is an estimate of the proportion of the canopy converted to gaps each decade

All disturbances detected among the seventy plots were tallied by intensity classes (0–10% canopy removal etc) Rotation periods were then estimated by dividing the sum of the chronology lengths for all seventy plots (7420 years) by the number of events in each intensity class Mean canopy residence time for trees was estimated by the reciprocal of the mean disturbance rate for all seventy plots Details are given in Frelich & Lorimer (1991)

Data on the relationship between dbh and time since gap formation were obtained from 304 *Acer saccharum* selected randomly from among the seventy plots The natural logarithm of dbh was regressed on age from release by the method of least squares After calculation of 90% and 60% confidence bands for individual observations, the relationship was transformed back to the arithmetic scale (Fig 1) The growth schedule for a cohort of *Acer saccharum* trees in Upper Michigan (Table 1) shows the size distribution from the first decade to the twenty-first decade, when all of the trees have attained large stature

Data on relative susceptibility of trees to windfalls were obtained from a tally of recently fallen trees in the Porcupine Mountains, which was adjusted to take into account relative abundance Large trees were approximately 1 5 times as susceptible to windthrow as mature trees There were insufficient data from the tally to estimate the relative susceptibility of pole trees to windthrow However, King (1986) surveyed two *Acer saccharum* stands in the vicinity of a 1977 thunderstorm downburst in northern Wisconsin, and found that mature trees suffered approximately 1 5 times as much damage as pole trees

RESULTS AND DISCUSSION

Characteristics of the simulated natural landscape

A box model (Fig 2) was developed to represent the dynamics on a quasiequilibrium landscape subjected to the historic disturbance regime for western Upper Michigan (Table 2) The numbers in Fig 2 are averages from 800 simulated plots after 1000 years of simulated disturbance Data were stored during the last 250 years of the 1000-year runs, so that 750 years were allowed for the effects of initial conditions to disappear

The model predicts that the even-aged path of stand development is relatively unimportant (Fig 2) Under the historic disturbance regime, sapling, pole and mature stands collectively occupy 9 2% of the landscape, and even-aged stands in transition to the multi-aged path of development (multi-aged break-up stands) occupy 9 5% of the landscape After a stand transfers to the multi-aged path of development there is no structural evidence left of any catastrophic disturbance Thus, first-generation stands after catastrophic disturbance occupy about 18 7% of the landscape, similar to that inferred by Canham & Loucks (1984) from land-survey data in adjacent northern Wisconsin Overall, the model shows that partial disturbances dominate the disturbance regime The majority of stands are composed of several major and many minor age classes Multi-aged stands of all types occupy 87 4% of the landscape

The hub of the box model (Fig 2) is the old multi-aged stand category with 50 4% of the landscape and the longest average residence time (84 years) A large majority of the transfers among stand types that take place in the model are among old multi-aged stands and the other types of multi-aged stands An area equivalent to 142% of the entire landscape is transferred among multi-aged pole, multi-aged mature and old multi-aged stands each century as these old-growth stands respond to repeated disturbances of light and medium intensity The short average residence time of multi-aged pole stands (24 years) and multi-aged mature stands (30 years) indicate that these stands recover quickly to old multi-aged stands after a partial disturbance

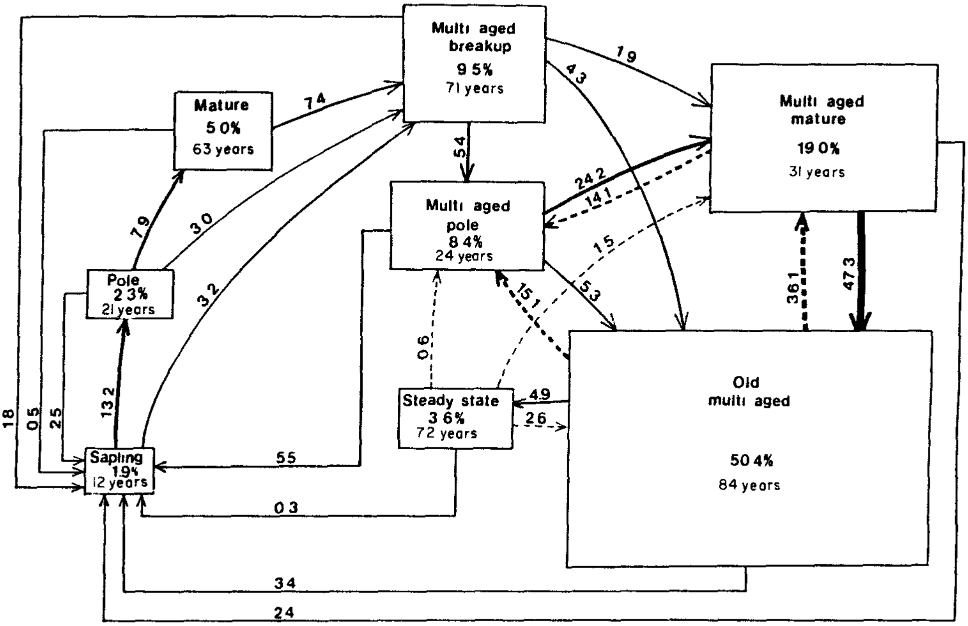

FIG 2 Box model of landscape dynamics in Upper Michigan based on historic natural disturbance frequency from 1850 to 1969 The boxes represent eight stand types as defined in text Percentage of the landscape occupied by each stand type and average residence time derived from the STORM simulation are shown in each box Straight arrows represent transfer to sapling stands as a result of catastrophic disturbance Solid curved arrows represent transfers to stands of greater stature dashed arrows show transfers to stands of lesser stature Arrow labels represent the percentage of the landscape transferred per century

Occasionally, an old multi-aged stand escapes significant disturbance long enough to be classified as a balanced all-aged stand for several decades The low frequency of these steady-state stands (3 6%, Fig 2) reflects the high probability of a stand being hit by several substantial partial disturbances between catastrophes

TABLE 2 Disturbance rotation periods used as input for runs of the STORM simulation The 'historic' disturbance regime refers to data from the last 130 years in Upper Michigan The remaining three columns were used for sensitivity analysis, to simulate landscapes with 1/2× or 2× historic frequencies, and a hypothetical landscape with a high frequency of catastrophic disturbance

Disturbance intensity(%)	Rotation period (years)			
	Historic	1/2×	2×	Frequent catastrophe
>10	69	138	35	138
>20	134	268	67	200
>30	261	522	130	210
>40	508	1016	254	220
>50	987	1974	493	230
>60	1920	3840	960	240
>70	3734	7468	1760	250

The frequency and importance of partial disturbances means that the dynamic pathway in any one stand is largely unpredictable For example, a stand in the multi-aged break-up category may proceed directly to an old multi-aged stand, or be struck by a partial disturbance and proceed to a multi-aged pole or multi-aged mature stand In fact, the only part of the model where stand development is fairly predictable is the sapling–pole–mature–break-up sequence which occurs after a catastrophe

Comparison with field data

If the historic disturbance regime has been fairly constant for the last 300 years, and the procedure for handling cohorts in the model is realistic, the predicted and observed proportions of the eight stand types on the landscape should be similar The seventy field plots were classified by stand type, using the same criteria listed for the simulation, but because various kinds of old growth stands cannot be distinguished from field evidence, a single old growth category was recognized that includes the multi-aged break-up, old multi-aged, and steady-state categories

The difference between the field plots and simulated historic data set in proportion among stand types (Table 3) is not significant at the 95% level (χ^2_5=10 09) There are minor differences, however The formation of sapling, pole, mature, multi-aged pole and multi-aged mature stands depends on recent disturbance history There have been variations in disturbance frequency from decade to decade in the field plots (Frelich & Lorimer 1991), which are smoothed out in the simulation

The percentage of the landscape actually occupied by saplings is also less than in the simulation (Table 4) This reflects a relatively quiescent period during the 1960s (Frelich & Lorimer 1991) A reconstruction of long-term average percentage of saplings and poles from the field data agrees closely with predictions of the simulation (Table 4) Thus, the simulation gives a reasonable prediction of landscape characteristics

TABLE 3 Comparison of frequency (%) of stand types on the landscape in the field with several simulated disturbance regimes

	Stand type								
	Even-aged types			Multi-aged types				Steady	Total
	Sapling	Pole	Mature	Break-up	Pole	Mature	Old	state	old growth*
Field plots	1 4	5 7	0 0	*	2 9	17 1	*	*	72 9
Simulation									
Historic	1 9	2 3	5 0	9 5	8 4	19 0	50 4	3 6	63 5
1/2×	1 3	1 3	1 3	6 7	5 0	10 7	47 3	27 3	81 3
2×	9 7	16 3	14 0	20 3	12 3	15 3	11 3	0 7	32 3
Frequent catastrophe	11 0	9 0	13 3	33 3	0 3	2 0	8 0	22 7	64 0

* Multi-aged break-up Old multi-aged and Steady state cannot be distinguished using field data so the sum of all three old-growth types is given for comparison

TABLE 4. Comparison of percentage size distribution and average residence time of canopy trees in the field with several simulated disturbance regimes. Values in the first four columns are the average percentage among all plots of canopy area occupied by sapling, pole, mature or large trees

	Size category				Average canopy residence time (years)
	Sapling	Pole	Mature	Large	
Field plots					
Current average	5.3	16.4	34.1	44.3	155
120-year average*	14.2	18.7	–	–	175
Simulation					
Historic	12.9	17.7	28.2	41.2	175
1/2×	10.4	15.1	25.7	48.8	213
2×	21.9	27.7	32.6	17.8	111
Frequent catastrophe	15.7	19.5	29.0	35.8	161

* Reconstruction of average percent saplings and pole trees over the last 120 years on the field plots (Frelich & Lorimer 1991).

Sensitivity of the landscape to changes in disturbance regime

Three simulations were done using disturbance frequencies other than the historic ones for western Upper Michigan. The first two simulations have disturbance frequencies reduced by half and doubled (referred to as 1/2× and 2×, respectively; Table 2). A third simulated disturbance regime has a relatively short (250-year) rotation period for catastrophes, and a frequency of light disturbances identical to the 1/2× simulation. Medium intensity disturbances were kept to very low frequencies to provide contrast with the historic Upper Michigan data set (Table 2).

The relationships between rate of disturbance and landscape characteristics, such as proportion of even-aged stands and average canopy residence time for trees, are not proportional. Even-aged stands are predicted to occupy nearly 40% of the landscape under the 2× disturbance regime, compared with 9.2% and 3.9% with 1× and 1/2×, respectively (Table 3). The average canopy residence time for trees is reduced from 175 years to 111 years and raised to 213 years when disturbance rates are doubled or cut in half, respectively (Table 4).

Thus, changes in the lifespan of the trees are considerably damped, while changes in proportion of even-aged stands on the landscape are large relative to the changing disturbance rates. The probable explanation for damped changes in tree lifespan is the relative lack of susceptibility of young cohorts to windthrow. Each catastrophe or heavy partial disturbance removes a crop of susceptible old trees from a given stand. It takes several decades for a new crop of susceptible trees to develop, both in the simulation, and in observed field data (Runkle 1982, Foster 1988).

The proportion of even-aged stands increases fourfold with a doubling of disturbance rates for two reasons. Single-event catastrophes are doubled in frequency. More importantly, the probability that two partial disturbances (e.g. 40% and 40%) occur in two successive decades is increased fourfold for all possible combinations. The probability that a given partial disturbance will occur in two successive decades is equal to the square of that probability. If the probability is first doubled, and then squared, the result is four times the square of the original probability

Similar synergistic effects account for the dramatic changes in the predicted proportion of steady-state stands on the landscape among the historic, 1/2× and 2× simulations The frequent-catastrophe landscape is predicted to have nearly as high a proportion of steady-state stands (22 7%) as the 1/2× simulation (27 3%) If stands are hit by random catastrophes with a rotation period of 250 years the age distribution of stands on the landscape follows a negative exponential curve, and about 37% of the stands are expected to survive one rotation period (Van Wagner 1978) Since 250 years is the minimum time required for development of a steady-state stand in the northern hardwoods, 37% of the 2× landscape could potentially be occupied by steady-state stands Higher proportions of steady-state stands could potentially occur in Upper Michigan, where catastrophes are much more rare (Canham & Loucks 1984, Whitney 1986, Frelich & Lorimer 1991), but the frequent occurrence of partial disturbance prevents the development of many steady-state stands

Implications for management of natural areas

Existing meteorological evidence on the frequency of extreme winds suggests a moderate amount of variation across the northern-hardwood region For example, tornado frequency in eastern Upper Michigan is only about one-half that of western Upper Michigan (Thom 1963) Extreme winds of all types with a 100-year recurrence interval range from 130 km h^{-1} in eastern New York State to 167 km h^{-1} in northern Upper Michigan (Changery 1982) Thus, it is likely that the 1/2×, 1×, and 2× simulations cover most of the range in disturbance frequencies that would be expected in the region

Data such as those in Tables 3 and 4 could serve as a general guide for restoration of nature reserves in various parts of the northern hardwood forest region For example, in a region like central Wisconsin with a relatively high frequency of extreme winds (Simiu & Filliben 1979), a natural landscape might be expected to have as much as 40% even-aged stands, similar to the 2× simulation With knowledge of the disturbance regime in the vicinity of a given nature reserve in second growth forest, a manager could use simulation to assess how far the recovery process toward a natural landscape has progressed Conversely, the simulation can be used to gain insight into the disturbance regime by analysing stand structure in large remnants of primary forest A detailed examination of the data in Tables 3 and 4 suggests some guidelines for inferring disturbance regime from landscape characteristics The combined proportion of stands with sapling, pole and mature size structure serves as an overall indicator of severity of the disturbance regime This proportion ranges from about 19% for the 1/2× simulation, a very mild disturbance regime, to about 68% for the 2× simulation, an extremely harsh disturbance regime for the northern hardwood region In addition, the size-class structure for individual trees is markedly different for the 2× simulation than for the other three, with the proportion of large trees only half that in the frequent catastrophe landscape (Table 4) Therefore, a combination of high proportion of stands with sapling, pole and mature size structure and few large trees indicates a landscape with high disturbance rates at all intensities

The frequent-catastrophe landscape differs considerably from the historic landscape in Upper Michigan with respect to the proportion of multi-aged and steady-state stands, but the overall proportion of old growth is similar in both cases (Table

3) Since the various types of old-growth stands cannot be distinguished by field evidence, some other measure is needed to separate these disturbance regimes in the field In addition to the higher proportion of sapling stands in the frequent-catastrophe landscape, most of the pole and mature stands are even aged in the frequent-catastrophe landscape (i e canopy accession dates are synchronous), but multi-aged in the historic landscape Thus, the age structure of pole and mature stands is of considerable value for interpreting disturbance regimes

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