

Forest Dynamics and Disturbance Regimes

Studies from Temperate Evergreen–Deciduous Forests

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1 · *The forest setting*

Introduction: disturbance in temperate conifer–hardwood forests

More than one-fourth of the world's forest land lies within the cool-to-cold temperate zones of the northern and southern hemispheres. Their distinctive mosaics of evergreen conifers and deciduous hardwood species have been shaped by fire, wind and herbivory over thousands of years. In the last few centuries human activities have increasingly changed the dynamics of these mosaics. Over much of the conifer–hardwood forest zone fire frequencies have been reduced by fire suppression and exclusion, harvesting has replaced fire as the main disturbance, global warming may be causing an increase in the frequency of high winds, and the intensity of grazing has increased.

Scientists and forest managers would like to understand how changing disturbance regimes and interactions among disturbances will influence forest successional trajectories. Managers of nature reserves would like to know what types of manipulations would restore the forest to a natural condition. The main purpose of this book is to illuminate the role of disturbances in temperate conifer–hardwood forests for these scientists and managers. Therefore, I have chosen three major themes for the book:

1. To show how three major disturbance types – fire, wind and herbivory – work in combination to influence the successional trajectories and structural characteristics of forests.
2. To show how deciduous and evergreen tree species interact to form various mixtures by differentially influencing their environment and the disturbance regime. For this book, the deciduous and evergreen groups will be referred to as 'hardwoods', principally a mixture of maple (*Acer*), oak (*Quercus*), ash (*Fraxinus*), basswood (*Tilia*) and birch (*Betula*) species, and 'conifers', principally a mixture of pines (*Pinus*),

spruces (*Picea*), cedar (*Thuja*), fir (*Abies*) and hemlock (*Tsuga*) species. The common and scientific names of species referred to frequently in the book are listed in Appendix I.

3. To show how disturbance effects play themselves out over time at different spatial scales, which for purposes of discussion will be referred to as neighborhood (a small grove of trees 10–20 m across), stand (1–100 ha) and landscape (a collection of stands, >1000 ha) scales.

Forests of the Lake States region

These three themes are explored via case studies from forests in the Lake States (Minnesota, Wisconsin and Michigan, USA), which are described in the remainder of this chapter. The reader may ask why the relatively unknown Great Lakes region of the world warrants a book on forest dynamics. There are three major reasons. First is the exceptional diversity of forest types and their comparability to other forests around the world's cool-to-cold temperate zones. Second, the Great Lakes Region was settled by Europeans relatively late so that the first round of land-clearing did not occur until 1880–1940. Some large areas (14000 to 150000 ha), representing all of the important forest types, were protected from logging. These were influenced, but not cleared, by native Americans. Natural forces of wind and fire have been the main influences over the past several thousand years. Now that ecosystem management of forests is high priority and mimicking of natural disturbance is often incorporated in ecosystem management, the natural patterns found in the remnant areas are very relevant, and in fact desired by many forest managers. The final reason for writing a book on the Great Lakes Region is the availability of a vast scientific literature. The long-standing presence of several major universities with forest ecologists and the United States Forest Service's North Central Forest Experiment Station, along with its branches in Michigan, Wisconsin and Minnesota, means that much information is available on forest dynamics. This information has been widely scattered in many journals and research reports but it has never been presented to the scientific community in a synthesized fashion, as I attempt to do here.

The forest at the time of European settlement and today

Europeans first explored the Lake States during the 1600s. However, major settlement by large numbers of Europeans accompanied by widespread land-clearing did not occur until the mid-1800s in the southern

Table 1.1. *Forest area (thousands of hectares) in the Lake States just before European settlement (1850) and as of 1995 (Frelich 1995)*

Forest type	Forest area in 1850	Forest area in 1995	Area of primary remnants as of 1995
Jack pine	1352.9	803.9	40.7
Red and white pine	3953.9	831.0	23.1
Spruce–fir–birch	3155.4	6955.5	83.4
Swamp conifer	4272.4	1961.7	188.6
Oak–hickory	2786.7	2426.3	0.9
Riverbottom	1846.2	1605.9	3.1
Hardwood	15250.1	4670.8	29.3
Total	32617.6	19255.1	369.1

part of the region and the late 1880s to the early 1900s in the northern part. Therefore, the main questions to be answered here are: (1) How much forest existed prior to European settlement (say the mid-to-late 1800s)? (2) How much forest exists as of the 1990s? and (3) How has settlement changed the composition of the forest?

Extent and composition of forests

The distribution of major vegetation types corresponds to mean boundary positions of major air masses. The boreal forest exists north of the mean position of the arctic front during winter and during the month of June (Bryson 1966). The mixed deciduous–conifer forest exists between the boreal forest and prairie–forest border, where the arctic front sits during March and April. Thus, the prairie has long summers, the mixed forest short summers, and the boreal forest very short summers.

The Lake States included nearly 32.6 million ha of closed-canopy forests at the time of the United States General Land Office Survey just prior to European settlement, during the late nineteenth century (Frelich 1995, Table 1.1). Hardwoods, including oak–maple and maple–hemlock forests, were by far the largest component of presettlement forest landscapes, with over 15.3 million ha (47.1%), while red and white pine forest lands only occupied about 3.9 million ha, or 12% of the forest landscape (Figure 1.1). There were major differences in forest-type distribution among the three states. Nearly all of the jack pine and spruce–fir–birch forests occurred in northern Minnesota, on the Canadian Shield that has markedly colder winters and drier summers than the northern parts of Wisconsin and Michigan. The physiographic setting of northern Minnesota also allowed the development of large

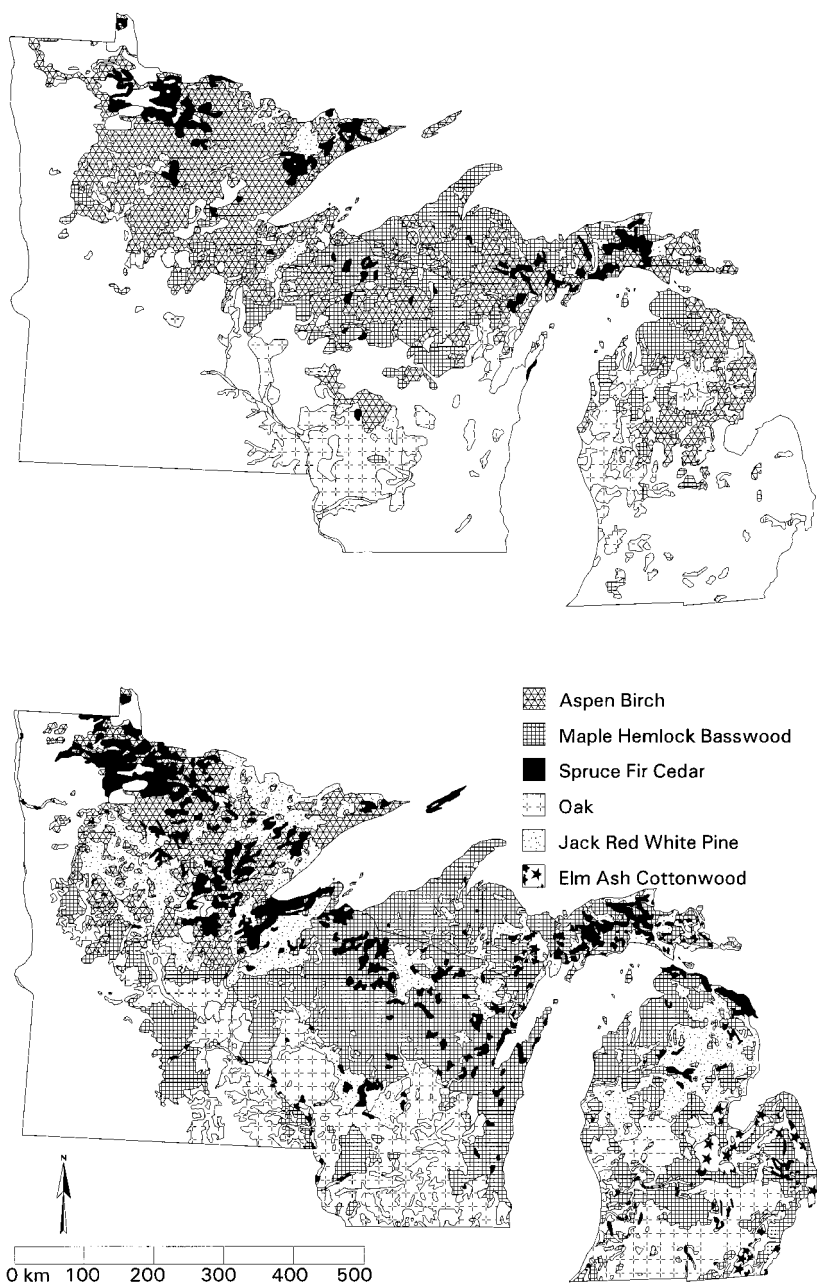


Figure 1.1 Lower panel, presettlement (c. 1850) and upper panel, post-settlement (c. 1980) forest vegetation of the Lake States. After Stearns and Gutenspergen (1987a,b).

areas of peatlands, with their associated swamp conifer forests. Michigan had the largest area of oak–hickory forest (1.5 million ha), but if oak savannas were included, both Minnesota and Wisconsin would have had twice the area of oak as Michigan (Curtis 1959, Marschner 1975). Both Wisconsin and Michigan had large areas of hardwoods, whereas Minnesota had a relatively small area of hardwoods that occurred as islands scattered within the northeastern two-thirds of the state (Marschner 1975).

The presettlement forest data can be interpreted as a stable baseline for comparison of changes in the landscape caused by humans. This is based on the knowledge that the ranges of major trees, such as maples, pines and oaks, only changed by 4–10 km/century over the last 10 000 years, and have changed little in the last few thousand years (Davis 1981). In addition, the overall rate of change in the spectrum of pollen types, on a per century basis during the 8000-year period ending prior to European settlement, was less than half that of the most recent century (Jacobson and Grimm 1986). Both of these statistics indicate great stability in area and species composition of forest in the Lake States prior to European settlement. According to United States Forest Service inventory data, there are currently 19.3 million ha forested lands – about 60% of the original 32.6 million ha (Table 1.1, Figure 1.1).

Frelich (1995) found evidence that approximately 369 000 ha of primary forest (or forest that was never logged) currently exist in the Lake States (Table 1.1). About 40% of the primary forest is in northern Minnesota's large wilderness reserve, the Boundary Waters Canoe Area Wilderness (BWCAN), and 50% is in northern Minnesota's swamp conifers. The remaining 36 000 ha is distributed among other smaller remnants, mostly hemlock–hardwood forest in Upper Michigan, including the Porcupine Mountains Wilderness State Park and Sylvania Wilderness Area, but also including substantial red and white pine at Itasca State Park, Minnesota (see Figure 1.2 for locations). The total current primary forest is about 1.1% of the presettlement primary forest of the Lake States. Percentages of original forest range from 0.02% for oak–hickory to 4.4% for swamp conifers. In addition to oak–hickory, other forest types with notably low percentages are areas of primary red and white pine (0.6%), riverbottom (0.2%) and hemlock–hardwood (0.2%) forest lands (Table 1.1).

Currently, aspen and mixed conifer–aspen stands (Figures 1.3, 1.4) occupy a much larger proportion of the forest landscape than they did prior to settlement (Figure 1.1, Table 1.1). This is due to extensive forest

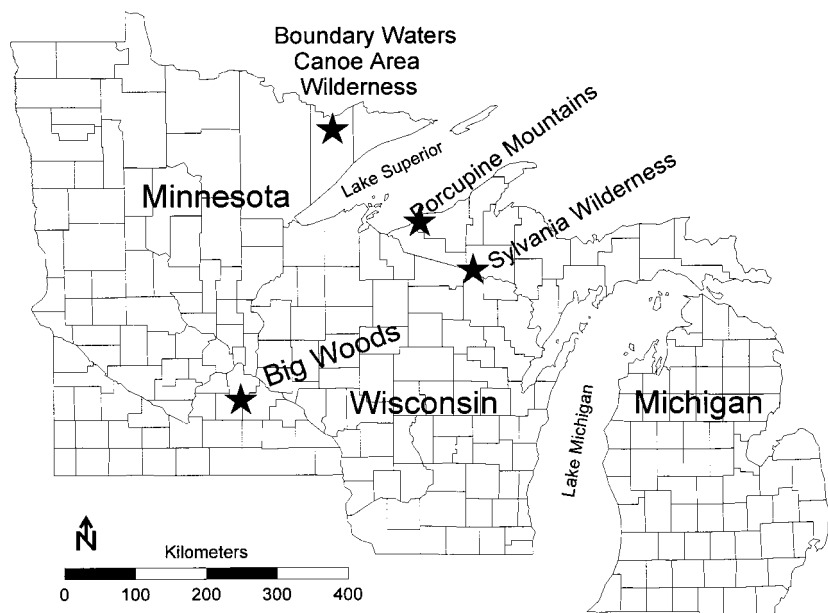


Figure 1.2. Location map of the Lake States Region, showing the major study areas.



Figure 1.3. Young quaking aspen stand typical of second-growth forest in the Lake States. Photo: University of Minnesota Agricultural Experiment Station, Dave Hansen.



Figure 1.4. Mixed aspen, white spruce and balsam fir forest was/is common in the northern Lake States region prior to European settlement and today. Photo: University of Minnesota Agricultural Experiment Station, Dave Hansen.

clearing followed by burning of slash that occurred between 1850 and 1940 in the Lake States. In northern parts of Minnesota and Michigan, forests of spruce and jack, red or white pine (Figures 1.5, 1.6, 1.7) yielded to aspen, while in northern Wisconsin and parts of northern Michigan, hemlock–hardwood or hardwood forest (Figure 1.8) was converted to aspen. Lowland conifer forests (Figure 1.9) have seen relatively little conversion to aspen or other forest types, due to the undesirable sites they occupy.

Climate

The climate of the Great Lakes Region is humid continental. Summers are short and cool; average July temperatures range from 17 °C in northern Minnesota to 19–20 °C in the Upper Michigan study areas, to 22 °C in the oak–maple forests of southern Minnesota. Winters are long and cold; average January temperatures range from −17 °C in northern Minnesota to −6 to −8 °C in Upper Michigan and southern Minnesota (National Oceanic and Atmospheric Administration 1980). It should be noted that there is a strong lake effect and that temperatures within



Figure 1.5. The southernmost occurrence of upland black spruce forest occurs in Minnesota's Boundary Waters Canoe Area Wilderness. Photo: University of Minnesota Agricultural Experiment Station, Dave Hansen.



Figure 1.6. Even-aged jack pine forests occur after fire on sandy and rocky sites along the southern margin of the boreal forest. Photo: University of Minnesota Agricultural Experiment Station, Dave Hansen.



Figure 1.7. An old-growth red pine stand at Itasca State Park, Minnesota. Photo: University of Minnesota Agricultural Experiment Station, Dave Hansen.



Figure 1.8. Sugar maple stand typical of the 'Big Woods' region of Minnesota and the northern mesic forests of Wisconsin and Michigan. Photo: University of Minnesota Agricultural Experiment Station, Dave Hansen.



Figure 1.9. Lowland black spruce on sphagnum peatlands are extensive in northern Minnesota, Wisconsin and Michigan. Photo: University of Minnesota Agricultural Experiment Station, Dave Hansen.

10 km of the Great Lakes may be higher during the winter and lower during the summer than indicated above (Eichenlaub 1979). Continentality (an index of annual temperature range) in Upper Michigan is nearly the same as the New England coast of Maine (Trewartha 1961). Mean annual frost-free period ranges from about 90 days in the northern part of the region (although about 120 days near Lake Superior), to 160 days in the southern part (Phillips and McCulloch 1972). Day lengths range from about 8–9 hours on December 22 to 15–16 hours on June 21.

Annual precipitation ranges from 800 mm to 900 mm over the region and is much higher during the summer months than winter months, except near Lake Superior, where it is fairly evenly distributed throughout the year (Eichenlaub 1979). Measurable precipitation (0.25 mm or more) falls on 130 to 160 days per year near the Great Lakes, which is the same range as maritime areas in the Pacific Northwest and New England, USA (Court 1974). Away from the Great Lakes, most precipitation falls during intense convective storms during summer months, so that measurable precipitation falls on only 100 days. Only 5–10% of months in Upper Michigan can be considered to have severe or extreme drought (Court 1974). About 25–35 thunderstorm days occur annually in the

region (Court 1974), but owing to accompanying rain, these result in only 1–5 lightning fires per 400 000 ha per year (Schroeder and Buck 1970). Annual snowfall is 1–2 m away from Lake Superior, but in Lake-effect snowbelts, average snowfall may be as high as 4 m, and occasionally up to 7 m of snow falls in one winter in the Porcupine Mountains (Muller 1966, Eichenlaub 1979). The ground is snow covered on and off from December to March in the southern part of the region, and continuously from late November until mid April in the northern part. The region receives about 60% of possible sunshine during the summer months and only 30–40% of possible sunshine during the winter months (Visser 1954).

The principal primary forest remnants

Hemlock–hardwood forests of Upper Michigan

In Upper Michigan there are two large areas of forest that have escaped logging. The largest is the Porcupine Mountains Wilderness State Park, on the coast of Lake Superior near the western end of Upper Michigan (Figure 1.2). Braun (1950) presents a description of the vegetation of the Porcupine Mountains and calls the area ‘a vast hardwood forest containing the most extensive primeval tracts remaining on the continent.’ It should be noted, however, that some of the area has (since 1950) been logged. Even though acquisition of the area was authorized in 1944, not all of the property was immediately purchased. Large-scale logging operations, which did not reach western Upper Michigan until the 1940s, were under way as the park was being purchased. Today, the park contains approximately 14 500 ha of forest which was never logged, although about 1500 ha had some fallen timber salvaged after a windstorm struck the area in 1953. The second-largest area (6073 ha) of primary forest is in the Sylvania Wilderness Area in Ottawa National Forest (Figure 1.2). Sylvania is a township on the Wisconsin–Michigan border 80 km from Lake Superior which was held as a private preserve until being sold to the United States Forest Service in 1966. The only trees removed were in a forest thinning near roads and a few pines on the lakeshores.

The principal advantage of conducting studies of forest dynamics on a few large blocks of remnant forest (as opposed to many small ones) is that a bias toward old-growth stands with large trees is avoided. Many of the small remnant forests, such as smaller state parks, scientific areas and Nature Conservancy preserves, were selected for purchase specifically because they contained old-growth forest. Young forests developing after

natural catastrophes were probably not considered for purchase because the forest was not recognized as being much different from the ubiquitous second-growth. In general, these small areas do not contain young virgin sapling and pole-sized stands as do the large blocks of forest which were preserved for other reasons.

The principal vegetation type on all these forest remnants is northern mesic forest as defined by Curtis (1959). Sugar maple dominates most of the forest inland from Lake Superior, and mixes extensively with hemlock near the lake. Occasional stands of hemlock are also found inland, especially in Sylvania. Lesser amounts of yellow birch, red maple, basswood and white pine occur throughout the area (Braun 1950). All other tree species are of local or sporadic occurrence. Elevations in the Porcupine Mountains range from 182 m on the surface of Lake Superior to about 600 m at 5 km inland. Glacial Lake Duluth covered parts of the area until approximately 8000 ybp (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 loam and silt loam soils predominating on gentle north slopes (0–10%). Farther inland, bedrock comes near the surface and topography is more rugged, with slopes up to 30% in steepness on the predominating north slopes. Soils are still generally 1 m or more deep in these upland areas and are of loam or sandy loam texture. South slopes in both areas have very steep or vertical outcrops of bedrock unsuitable for development of forests, although a few gently sloping south-facing hills are present. Soils include coarse-loamy, mixed, frigid Alfic Fragiorthods and Entic Haplorthods (Michigan State University 1981). Observations of thickness of root mats of recently fallen trees indicate that fragipans occur at depths of 50–100 cm. In the uplands, Lithic Haplorthods and Lithic Borofolists also occur locally.

The topography of Sylvania is quite different from the Porcupine Mountains. 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 m to 550 m in elevation and contains many small lakes and bogs. The drift is deep (>30 m), red color, slightly acidic, and of sandy loam texture. The upland forest soils at Sylvania are spodosols and most are classified as coarse-loamy, mixed, frigid Alfic Fragiorthods or Alfic Haplorthods (Jordan 1973).

Near-boreal forests of northeastern Minnesota

A small extension of boreal forest extends from Canada into northeastern Minnesota (Weber and Stocks 1998). Because it is on the very southern

edge of the boreal forest and contains a few scattered stands of species not usually considered boreal, Heinselman (1973) coined the term 'near-boreal forest,' which I adopt here. The boreal tree element includes jack pine, black spruce, and aspen, mixed with balsam fir, white cedar, white spruce, and paper birch in older stands. The non-boreal element exists in stunted form here at the northern edge of the range, including white and red pine, red maple, northern red oak, bur oak, and pin oak. Red maple and the oaks in particular can be in the form of a shrub or small tree, unlike the large sizes (1 m diameter at breast height, dbh) they reach further south. Near-boreal forests include the following types: (1) fir–birch forest on relatively good soils; (2) jack pine–black spruce on coarse shallow soils over granitic bedrock, as well as several other jack pine-dominated types; (3) red maple, aspen, birch and fir on moist but not wet sites; (4) red pine on shallow rocky soils, especially common along lakeshores; and (5) birch–white pine forests, common along lakes and streams regardless of the soil type. A variety of conifer swamp forests with black spruce, tamarack or a mixture of the two also occurs.

The Boundary Waters Canoe Area Wilderness lies within the near-boreal forest zone (Figures 1.1, 1.2), centered at about 48 °N latitude, and 91 °W longitude. It contains about 439 000 ha of land and water and was set aside as a wilderness area off limits to logging by the United States Congress in 1978. Of this, 335 000 ha is forested, and 169 000 ha (50% of forest) has never been logged (Heinselman 1996). The stand-origin dates for the entire 160 000 ha that was never logged were mapped by Heinselman (1973, 1996), and the community makeup of this tract was also sampled by Ohmann and Ream (1971). Fourteen major fire years, with large stand-killing fires, have occurred since 1595, including four (1863–64, 1875, 1894, and 1910) that account for nearly three-quarters of the forest area.

'Bigwoods' forests of southeastern Minnesota

These forests were at the edge of the prairie–forest border in the southwestern part of the Lake States (Figure 1.2). Early survey data indicated a large patch about 8000 km² in size that was dominated by a mixture of red oak, white oak, American elm and sugar maple (Grimm 1984). This patch was typical of forests along the prairie border in the Mid-western United States, in that the oaks were more abundant along the prairie edge, and the maple and elm more abundant in the interior of the forest, and the forested area was often on the northeast side of some sort of topographic feature that served as a fire break (Grimm 1984, Leitner *et al.*

1991). Soils were relatively deep loams to sandy loams on top of glacial drift.

At this point, only a few small scattered remnants of Bigwoods vegetation exist, which may comprise 1% of the original forest (Minnesota Biological Survey 1995). These remnants are tiny compared with the Porcupine Mountains or Boundary Waters Canoe Area Wilderness. As they are the only representatives of a formerly large forest, however, their importance goes beyond their size. Because of fire suppression during the past century, sugar maple has increased in abundance, while oaks have decreased in many stands, such as that in Figure 1.8.

Summary

The Lake States are in a unique zone of sharp climate change so that a large variety of forest types is present. A large body of scientific information exists on the response of these forests to disturbances. In this book, I synthesize these findings so that Lake States forest dynamics can be compared with analogous forests in the world's cool-to-cold temperate zones. Lake States forests include oak and beech-maple forests analogous to those in western Europe, Japan, southern South America and New Zealand; hemlock forests similar to those in eastern Asia; red and white pine forests with analogs in northern Korea, China, and northern Europe; vast peatland larch and spruce forests, analogous to those in Siberia; and fire-adapted near-boreal forests of jack pine and black spruce, similar to those across southern Canada, northern Scandinavia, and northern Japan. Several large primary forests still exist in the Lake States so that the dynamics of forests with minimal human influence can be compared with other regions where human influence has had more impact. Enough detail on the Lake States forest history, composition and dynamics is presented to facilitate comparison with other forests. I hope to enable readers to qualitatively predict forest response to disturbances in any of these other temperate conifer-hardwood forests around the world.