3000 Years of Abundant Hemlock in Upper Michigan

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Abstract

Hemlock invaded the Great Lakes Region about 5500 years ago, colonizing lower Michigan and the Upper Peninsula as far west as Iron River. Over the past 3000 years it has become much more abundant in the eastern Upper Peninsula and has extended its range slowly westward and southward into Wisconsin. In the Sylvania Wilderness in Gogebic County, Upper Michigan, fine-scale paleoecological studies record hemlock's invasion of individual forest stands about 3000 C-14 years ago. Hemlock invasion was patchy as it became established in forests previously dominated by white pine, red maple, and oak. Pollen records from modern hemlock stands show that hemlock increased within a few centuries to become an abundant species, but white pine remained co-dominant for 1000-1500 years. Pollen records from two hardwood stands now dominated by sugar maple and basswood show that hemlock has never become abundant in these stands. Pollen evidence from mixed stands and from the edges of hemlock stands indicate marked fluctuations in the ratio of hemlock to sugar maple, with sugar maple abundance responding positively to disturbance by fire or by wind. Following clearcutting 50-60 years ago both hemlock stands and hardwood stands in western Upper Michigan have been succeeded by hardwoods, and the mosaic of hemlock and hardwood patches is no longer visible. We conclude that in the absence of disturbance hemlock stands can persist for many centuries, including the Medieval warm period (900-1300 AD) when the climate was as warm as today, and the Little Ice Age (1450-1850 AD) when the climate was colder. Although hemlock seedlings are not abundant in hemlock stands today, there are enough hemlock trees in the understory to assure continued canopy recruitment for several centuries.

Hemlock Entry To Michigan

Hemlock-northern hardwood forests developed in Upper Michigan during the last 5500 years. Small, isolated populations of hemlock may have been established before 6000 years ago by long-distance dispersal of seeds from Ontario, where hemlock had become abundant earlier. These colonies may have been similar to small outlying populations of hemlock today in Minnesota, 50-100 km beyond hemlock's range limit (Calcote 1986). As the result of regional changes in climate starting about 5500 years ago, hemlock began to spread throughout the eastern Upper Peninsula. By 4800 years ago, hemlock populations had expanded throughout the eastern half of the peninsula, and the range limit was moving westward rapidly to include the Huron Mountains, the base of the Keweenaw peninsula, and Iron River.

After the initial expansion of hemlock, the range limit remained stable at Iron River, presumably because climate was still limiting to the west, and also because hemlock populations here as well as elsewhere in eastern North America declined to low levels 4800 years ago. The

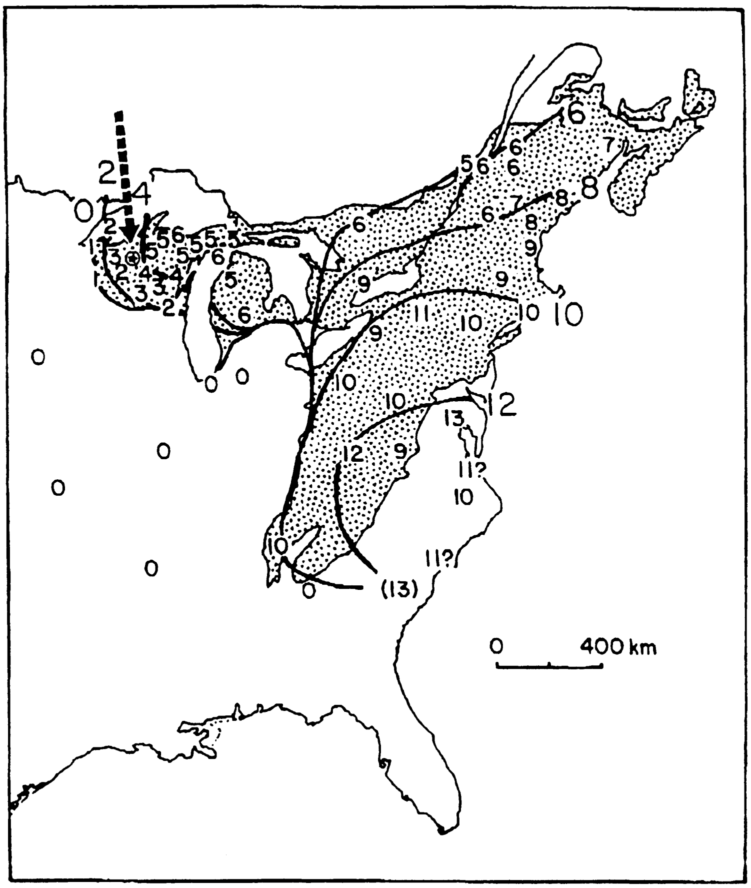

Figure 1: Hemlock migration in eastern North America. Lines are isochrones marking the approximate location of the hemlock range limit at 2000-year intervals during the Holocene. Arrow marks the location of the Sylvania Wilderness. (Reprinted from Davis *et al.* 1994, Blackwell Science Publications)

simultaneous, sudden decline in all parts of hemlock's range has been considered evidence for the outbreak of a pathogen, perhaps similar to the chestnut blight in this century (Davis 1981, Allison et al. 1986). Hemlock began to expand its range again about 4000 years ago, slowly extending its range westward across Michigan and southward into Wisconsin, reaching its present range boundary about 1000 years ago.

The late-Holocene expansion of hemlock in Upper Michigan was accompanied by population increases in Northern Hardwood species, such as yellow birch, sugar maple and basswood. Sugar maple and basswood had been present, although rare, for several thousands of years before the arrival of hemlock. The history of yellow birch is less well-known, but it appears to have expanded throughout Upper Michigan starting 3000 years ago. These changes are best documented at the Sylvania Wilderness, where fossil pollen grains in sediments accumulating in small forest hollows provide records of tree abundances at the stand scale. Pollen in small sites like these, which are only a few meters in diameter, records variations of tree abundances within 50-80 m (Sugita 1994, Calcote 1995). This fine spatial resolution is essential for understanding the history of the mosaic of hemlock and hardwood patches, 5-30 ha in size, which is a conspicuous feature of old-growth forest in western Upper Michigan (Pastor and Broschart, 1990; Davis et al., 1996).

Establishment of Hemlock Stands at Sylvania

At the Sylvania Wilderness in western Upper Michigan, hemlock first invaded forest stands between 3500 and 3000 years ago. Hemlock invaded forests that had been dominated by white pine, oak and red maple (Davis et al., 1994). Ratios of fossil hemlock to sugar maple pollen in small hollows from four hemlock stands are shown in Fig. 2. The changes in ratios to high values, characteristic of hemlock stands today, indicate that in these stands hemlock increased within a few centuries of invasion to become dominant (Fig. 2). Yellow birch also increased, and white pine declined, although it remained common for varying lengths of time — 1000 to 2000 years, depending on site. Within hemlock stands at Sylvania today yellow birch is often quite common, and cedar, red maple, sugar maple, fir and white pine are

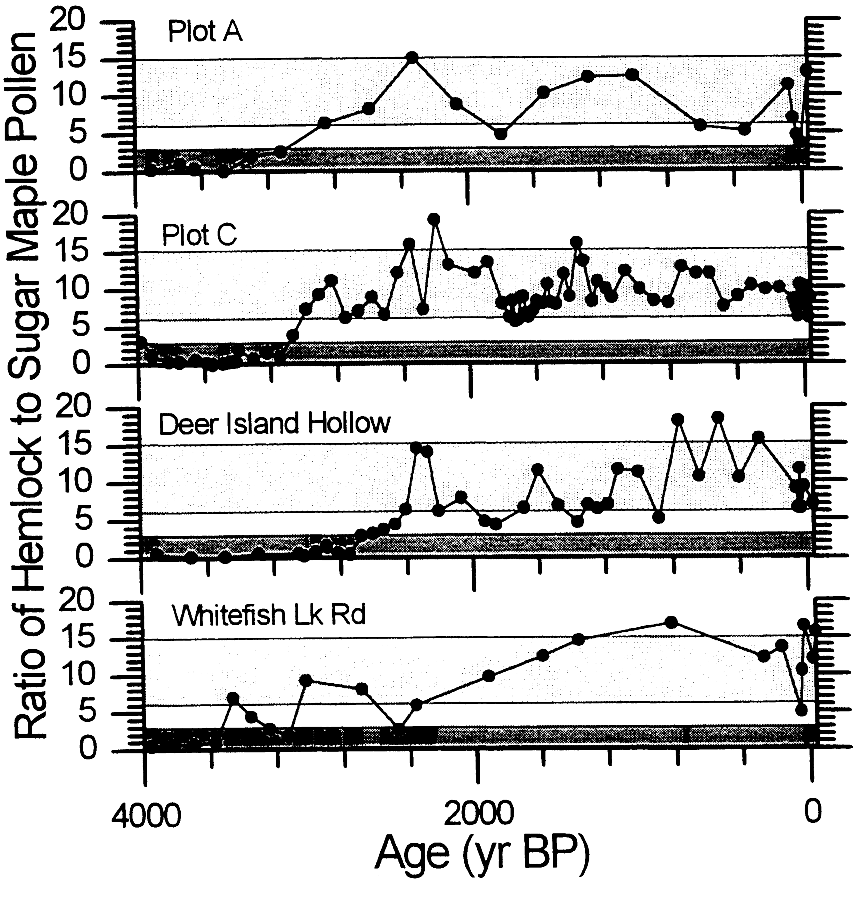

Figure 2. Ratio of hemlock to sugar maple pollen in sediments from small hollows in 4 present-day hemlock stands over the past 4000 years. The ratios of hemlock/sugar maple pollen characteristic of surface samples from hemlock stands (6-15) are shown by light shading, while darker shading indicates the low values (0-3) characteristic of surface samples from hardwood stands. In all four stands, the ratio changes between 3500 and 2500 C-14 years ago, when hemlock began to grow at Sylvania.

sometimes present. Basswood is less common (Frelich et al. 1993). Spies and Barnes (1985 a, b) have provided more detailed species lists for hemlock stands, and Ferrari (1993) has described the ground flora and nutrient cycling.

Many forested areas within Sylvania were *not* invaded by hemlock 3000 years ago. It is still unclear whether physical factors, biotic factors or just chance determined which stands were not invaded. The histories of several of these stands have been documented by fossil pollen in small hollows. Long records in three hardwood stands show that sugar maple and basswood were replacing red maple and pine at the time hemlock was increasing elsewhere in the forest. Yellow birch also increased, its local abundance depending on disturbance history (Frelich and Graumlich 1994). Hemlock has never been abundant in these three hardwood patches and may never have invaded these stands at all. Instead, they gradually developed the species abundances characteristic of current hardwood stands. Hardwood trees create a light environment that encourages the growth of sugar maple seedlings, and their nutrient-rich litter results in greater nutrient availability, enhancing sugar maple and basswood recruitment beneath a hardwood canopy. In hemlock stands, in contrast, the microclimate, low light during the springtime and low nutrient availability cause sugar maple seedlings to grow poorly, thus giving hemlock seedlings a competitive advantage (Ferrari 1993). These feedbacks can maintain hemlock and hardwood patches for thousands of years (Frelich et al. 1993).

Effect of Disturbance

Changes in stand types have occurred along the borders between hemlock and hardwood stands, and in mixed hemlock-hardwood stands. Fossil pollen records indicate that several mixed and border stands have had fluctuating relative abundances of hemlock and hardwood trees throughout the past 3000 years. Fluctuations are perhaps to be expected, since the mixture of feedbacks may allow hemlock and hardwoods to recruit with equal probability (Frelich et al. 1993). In every case where a layer of charcoal suggests a local fire, or a sharp peak in the abundance of birch pollen provides evidence of past disturbance by wind, sugar maple abundance increased nearby within a few decades. Tree ring evidence from the living forest corroborates this observation, suggesting that within the past 50 years, following patchy wind disturbance events, hemlock trees in a mixed stand have been replaced by patches of young sugar maple (Parshall 1995). Replacement of hemlock by maple has not occurred within the center of a nearby hemlock stand, however (Parshall 1995). Thus past disturbances at Sylvania, rather than favoring hemlock establishment, as has been observed in Menominee County, Wisconsin (Maissurow 1941), have tended to favor sugar maple.

Massive logging of both hemlock stands and hardwood stands outside the borders of Sylvania has also led to reproduction of hardwoods. Logging has had the effect of lessening landscape diversity, as the forest mosaic of hemlock stands, hardwood stands and mixed stands (Pastor and Broschart 1990) is reduced to hardwood forest alone (Hix and Barnes 1984, Davis et al. 1996).

Climatic changes that have occurred since hemlock started to grow in Sylvania appear to have had relatively little effect on hemlock stands. A gradual increase in moisture balance has occurred over the past several millennia, causing the expansion of bogs and a rise in lake levels (Brugam *unpublished data*, Futyma 1982, Futyma and Miller 1986). The late-Holocene rise in water table had already begun at Sylvania at the time of hemlock invasion and has continued since then, causing increasing numbers of hollows to begin to accumulate sediment. An increase in moisture may have been the climatic factor that allowed hemlock to extend its range westward into Sylvania in the first place (Brugam et al., in review), and it apparently allowed hemlocks to compete successfully with pine until hemlock had replaced almost all of the white pine within hemlock patches. Hemlock dominance was achieved at different times in different stands, but once hemlock was the dominant species stands generally remained dominated by hemlock. A decline in fire frequency 3000 years ago, evidenced by the decreased quantity of charcoal in hollow sediments (Davis et al. 1991), is probably associated with moister climate augmented by the microclimate of hemlock stands, where humidity is characteristically higher than in other kinds of forest (Godman and Lancaster 1990).

Changes in temperature during the past 1000 years are documented in other parts of the world (LaMarche 1973, Webb 1989, Wigley 1989). During the Medieval Warm period (900-1400 A.D.), for example, temperatures were as high as during the modern reference period (1940-1970), while during the Little Ice Age (1450-1850 A. D.) annual temperatures in the North Atlantic region were 1-1.5 ° C lower. The cooling caused advance of montane glaciers at many places throughout the world. These same glaciers have retreated in response to world-wide warming (about 0.6 °C) since 1880 A.D. (Bradley, 1989). In Minnesota the prairie forest border moved westward during the Little Ice Age (Grimm 1983), and forest composition in Michigan's Lower Peninsula was affected, with changes in species abundances that suggest lower temperatures (Bernabo 1981). We do not yet have any direct evidence, however, of climatic changes during this period in the Upper Peninsula.

Changes in climate may result in changes in species abundance in the forest if competitive abilities of species are altered (Davis 1986, Woods and Davis 1989). For example, hemlock recruitment may increase during cooler or wetter periods. We have inspected the pollen data for changes in species abundances in hemlock stands that could be correlated with the climatic changes during the past 1000 years inferred in other regions. However, the pollen records from four hemlock stands (Fig. 2) indicate that hemlock was abundant in all four stands before 1000 years ago. The ratio of pollen taxa used in Fig. 2 that supports this conclusion is correlated with the amount of hemlock in modern forest stands in Sylvania (Calcote *unpublished data*). Other evidence indicates that hemlock in one stand increased relative to pine 500 years ago, during the Little Ice Age. The longevity of these stands argues against the hypothesis that climatic changes during the Little Ice Age caused the establishment of hemlock stands (Stearns 1988, Mladenoff and Stearns 1993).

Evidence to date suggests that hemlock stand composition has not been very sensitive to the presumed temperature changes of the past 1000 years. However the nature of these climatic changes in the Great Lakes region is not known in detail. Studies of hemlock tree-rings point to moisture as the limiting climatic variable for growth within the Great Lakes region (Cook and Cole 1991). If future greenhouse climate in the Great Lakes region involves a decrease in moisture as well as a rise in temperature, the effects on hemlock distribution will be much greater than if temperature alone is affected (Davis and Zabinski 1992).

Size Class Distribution in Hemlock Stands in Sylvania

The size structure of trees in hemlock stands suggests that recruitment of hemlock saplings has been poor over the past 50 years. Heavy browse by deer is a frequent cause of mortality of hemlock saplings tall enough to project above the snow. However, the abundance of subcanopy hemlock trees within hemlock stands (Fig. 3) suggests that replacement of canopy hemlock by other hemlocks will continue for another century or more, regardless of hemlock seedling establishment and survival.

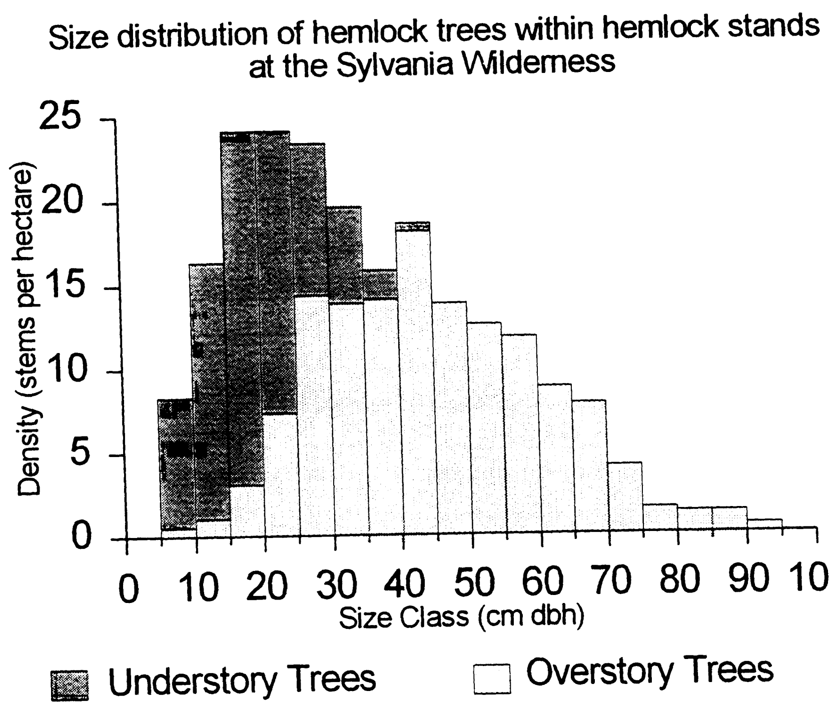

Figure 3: Size distribution of hemlock trees within hemlock stands. Data are from permanent Plots A and B, near Clark and Whitefish Lakes in Sylvania.

Future of Hemlock at Sylvania and Surrounding Forests

The history of hemlock stands suggests that the best management strategy for preservation of hemlock is protection from disturbance. In the absence of disturbance, hemlock stands are likely to persist for several hundreds of years even if temperatures rise by a degree Celsius. If browsing levels declined to allow recruitment of saplings, hemlock stands might persist indefinitely unless truly dramatic changes in climate, especially a change in levels of moisture, were to occur. Disturbance by selective logging, however, rather than releasing hemlock from suppression and helping it to reach a canopy, instead opens a stand to light, mimicking the effects of wind disturbances in the past. At Sylvania wind disturbance along the border of a hemlock stand has promoted the recruitment of sugar maple, converting the hemlock stand to a mixed stand where maple has increased likelihood of replacing hemlock.

If deer browse continues at the present high levels, recruitment of hemlocks in the smallest size classes will remain rare. Eventually, when all subcanopy hemlock trees have reached the canopy or have died without replacement, even the centers of hemlock stands will be affected. But, if browsing were to decrease for even a few decades, a generation of hemlock seedlings could reach the sapling stage within hemlock stands, greatly increasing the probability that hemlock will continue to reproduce itself and maintain its abundance in hemlock-dominated forest.

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