LATE HOLOCENE STAND-SCALE INVASION BY HEMLOCK
(TSUGA CANADENSIS) AT ITS WESTERN RANGE LIMIT

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Abstract. The movement of plant range limits in the past has been clearly documented as a response to changing climate, but the pattern and timing of local invasions that result from these plant migrations are not well understood. Sedimentary evidence from small forest hollows is used here to reconstruct the pattern of stand-scale invasion by eastern hemlock (Tsuga canadensis (L.) Carr.) at its current range limit in Wisconsin. Pollen records from lakes show a slowly increasing regional hemlock population over the past 2500 yr, as its range expanded from the east in response to cooler, wetter climate. In contrast, hemlock pollen in each of the forest hollows increased abruptly within the past 500 yr, demonstrating stand-scale dynamics at a time when regional changes were small. Moreover, this abrupt rise in hemlock is part of a two-phase sequence of local invasion. First, stands were initially colonized as much as 2000 yr ago, but the size of these local populations remained low for as long as 1800 yr. This pattern suggests that scattered, small populations grew beyond the continuous range limit of hemlock, which was tens of kilometers to the east. Second, these small hemlock populations expanded in size between 100 and 500 yr ago during a time of cooler, wetter climate, which was apparently limiting population growth. These results illustrate contrasting patterns of change between local and regional populations, and the importance of outlying colonies as sources of rapid population expansion when environmental conditions become favorable.

Key words: climate change; colonization; forest hollow; forest stand invasion; plant distribution; pollen; stomata; Tsuga canadensis; Wisconsin, USA.

INTRODUCTION

Climate is the predominant factor influencing plant distribution at subcontinental scales (Woodward 1987, Sykes et al. 1996), and changes in climate are accompanied by shifts in plant ranges (Webb et al. 1987, Huntley and Webb 1989, Prentice et al. 1991). This means that future climate change will lead to different plant distributions than occur today (Overpeck et al. 1991, Davis and Zabinski 1992, Iverson and Prasad 1998). As the range of a plant spreads across a landscape, individuals dispersing into previously unoccupied space must become established within the constraints of physical site characteristics and competition with resident vegetation. Our understanding of this local establishment process primarily emerges from observations of contemporary invasions, which have become a major component of recent global change (Vitousek et al. 1996, Pitelka et al. 1997). However, most of these invasion studies describe species that have been introduced by humans to areas outside their native ranges and, therefore, their migration or spatial spread does not solely represent a range shift in response to climate change.

Paloecological methods document plant invasions that have occurred over long time intervals in response to changing climate (Prentice 1988, MacDonald 1993, Jackson 1997). Most of these studies are restricted to plant migrations across large areas and over long time periods, because they use pollen preserved in lake sediments, which represents vegetation on landscape to regional scales (e.g., Huntley and Birks 1983, Davis et al. 1986, Bennett 1988; Huntley and Webb 1989, Jackson et al. 1997). Very small sedimentary basins, such as forest hollows, can be used to reconstruct past changes in forest composition on the scale of several hectares. This small spatial scale is appropriate for reconstructing colonization and population expansion of individual forest stands, and a group of forest hollows within a relatively small area can address differences in stand invasion in relation to range-limit dynamics (e.g., Bradshaw 1988, Björkman and Bradshaw 1996, Davis et al. 1998).

In this study, sedimentary records from forest hollows are used to reconstruct the invasion of eastern hemlock (Tsuga canadensis (L.) Carr.) into forest stands at its modern western range limit in Wisconsin. Previous studies of pollen from lakes have demonstrated a progressively westward movement of hemlock’s range limit over the past 6000 yr (Fig. 1) in response to a change in climate toward cooler, wetter conditions (Bartlein et al. 1984, Brugam and Johnson 1997, Davis et al. 2000). Hemlock pollen is present by 2500 yr ago in lakes along hemlock’s western range limit, but the

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abundance of hemlock pollen has risen very slowly since then (Fig. 1: Davis et al. 1986). This leaves open the question of how hemlock’s local- to landscape-scale population developed as its range limit reached its present location. Were hemlock stands colonized at the same time in the past, after which local populations grew slowly? Or were individual stands invaded at different times, each contributing modestly to the regional hemlock population? These two scenarios imply different patterns of spread across a landscape, ultimately affecting how quickly a species can respond to changing climate.

**STUDY DESIGN**

To address these questions, I focused on the development of four hemlock stands located within 12 km
of each other along hemlock’s western range limit (Fig. 1). Since hemlock trees are present in all four stands today, each site represents a separate example of stand invasion as the range limit of hemlock arrived to the region. Forest hollows provide a more local record of vegetation change than lakes because as the size of a sedimentary basin decreases, pollen produced from local sources becomes a larger component of total pollen deposited at a site (Jacobson and Bradshaw 1981, Prentice 1985, Jackson 1990, Sugita 1994, Jackson and Lyford 1999). For small lakes (20–100 m radius) like those shown in Fig. 1, variation in pollen can distinguish compositional differences in vegetation on the order of 100–1000 hectares. Pollen preserved in forest hollows (<10 m radius), on the other hand, is more closely related to vegetation on the order of a few hectares. Even though 50–60% of pollen may be derived from plants >100 m away, variation in forest composition within 100 m of the hollows is discernable (Jackson and Wong 1994, Sugita 1994, Calcote 1995, 1998, Jackson and Kearsley 1998).

An important consideration in this study is the ability to detect a small hemlock population because very few trees might be present at a site during the initial stages of invasion. Pollen percentages from forest hollows can resolve small, local population sizes, but only roughly. For example, hemlock pollen percentages as low as 0.5% may represent the presence of trees at a site, especially when regional populations are low, but they can also be as high as 1% in stands where hemlock trees are absent locally, but abundant regionally (Calcote 1986, Parshall 1999, Parshall and Calcote 2001). Here I interpreted 1% hemlock pollen as strong evidence for local presence in the early stages of invasion when the regional population is low.

Much stronger evidence for the local presence of trees comes from the presence of fossil stomata ( Hansen 1995, Clayden et al. 1996) because the leaves and needles from which stomata are derived disperse very short distances. In fact, the presence of hemlock stomata in forest hollow sediments today indicates that trees are present within 20 m (Parshall 1999), and fossil stomata are used here to define with high confidence that trees were present within the stand in the past.

Fossil pollen assemblages were also compared to pollen in surface sediments and associated forest composition data in order to evaluate past shifts in stand composition in relation to forests that exist today (Calcote 1998, Davis et al. 1998). Rather than relying on a single taxon, this approach integrates pollen from all of the important tree taxa, assuming that highly similar fossil-modern pairs are produced by similar forest stands. This method works well for areas with relatively homogeneous vegetation such as northwestern Wisconsin (Sugita 1994, Calcote 1998, Parshall and Calcote 2001).

### Study Area

The study area spans the western range limit of hemlock in northwestern Wisconsin (Fig. 1: Goder 1955, Finley 1976).  In the 1850s, hemlock comprised ~25% of all trees in this area, according to the U.S. General Land Office, which also provides occasional records of hemlock trees growing >50 km to the west (Finley 1976, Calcote 1986, Godman and Lancaster 1990). Other trees common in the presettlement upland forests include white pine (Pinus strobus), sugar maple (Acer saccharum), yellow birch (Betula alleghaniensis), American basswood (Tilia americana), and red pine (Pinus resinosa) (Stearns 1951, Curtis 1959, Finley 1976, Frelich 1995). Soil textural characteristics and drainage of the study area are largely controlled by sandy till and outwash features of the Copper Falls Formation, deposited during the last deglaciation (Hole 1976, Clayton 1984, Clayton et al. 1991).

Climate over the past 4000 yr has become progressively cooler and wetter in the Midwest and Great Lakes region (Webb et al. 1983, Bartlein et al. 1984, COHMAP 1988, Davis et al. 2000), leading to a rise in the regional water table (Futyma and Miller 1986, Winkler et al. 1986, Miller and Futyma 1987, Winkler 1988, Brugam and Johnson 1997). In addition to the migration of hemlock, the range limits of several other mesic species, including white pine and American beech (Fagus grandifolia), moved westward over the past 3000–4000 yr (Jacobson 1979, Bennett 1985, Davis et al. 1986, Woods and Davis 1989).

The direct impact of Europeans in northern Wisconsin was small until the late 1800s when logging activities began (Fries 1951, Williams 1989). The Rust-Owen Lumber Company owned most of the land in the study area and started cutting trees in the mid-1870s (Fischer 1964). Logging peaked in the 1890s, but operations continued until the 1930s when the land was acquired by the federal government and became the Chequamegon National Forest.

### Methods

All four forest hollows are seasonally to continually wet depressions, ~10 m in radius, and surrounded by closed-canopy forests with hemlock trees growing within 20 m (Fig. 1, Table 1). Sediment cores were collected from three of the hollows (Diamond, Drum-
TABLE 2. AMS (accelerator mass spectrometry) radiocarbon dates and their associated calendar dates identified by CALIB version 4.2 (Stuiver and Reimer 1993, Stuiver et al. 1998) at the four forest hollow study sites.

<table>
<thead>
<tr>
<th>Site</th>
<th>Depth (cm)</th>
<th>Material</th>
<th>¹⁴C age BP</th>
<th>Calendar age BP (2σ range)</th>
<th>Lab no.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Owen</td>
<td>15</td>
<td>wood</td>
<td>350 ± 50</td>
<td>350 (510–300)</td>
<td>Beta-117377</td>
</tr>
<tr>
<td>Diamond</td>
<td>29</td>
<td>charcoal</td>
<td>2410 ± 50</td>
<td>2360 (2710–2340)</td>
<td>AA-21375</td>
</tr>
<tr>
<td>Cutacross</td>
<td>16</td>
<td>wood</td>
<td>1490 ± 30</td>
<td>1350 (1420–1310)</td>
<td>OS-15671</td>
</tr>
<tr>
<td>Cutacross</td>
<td>26</td>
<td>wood</td>
<td>2295 ± 85</td>
<td>2340 (2710–2120)</td>
<td>AA-21376</td>
</tr>
<tr>
<td>Drummond</td>
<td>53</td>
<td>charcoal</td>
<td>3200 ± 100</td>
<td>3430 (3680–3170)</td>
<td>OS-16942</td>
</tr>
<tr>
<td>Drummond</td>
<td>40</td>
<td>needles, Pinus strobus</td>
<td>360 ± 40</td>
<td>350 (510–310)</td>
<td>Beta-119673</td>
</tr>
</tbody>
</table>

Note: Calendar ages and ranges are from intercepts of the calibration curve (Method A) and are rounded to the nearest 10 yr.

mond, Cutacross) using a 10-cm diameter piston corer, and from one hollow (Owen) using a 6.3-cm diameter acrylic tube. The sediments in each hollow are almost entirely organic, derived primarily from plant material shed by vegetation surrounding the basin.

The pollen record from Hemlock Lake, a closed basin ~1 ha (55-m radius) in size, is representative of other lakes in the region. The Holocene sediments are dominated by pine pollen, especially white pine, with lesser amounts of oak and birch (Davis et al. 2000). Birch pollen gradually increases ~4000 yr ago, and the first hemlock pollen grains appear 3000 yr ago. Continuous hemlock pollen accumulation over the past 2500 yr indicates the presence of hemlock trees on the landscape (Davis et al. 1986, Davis and Sugita 1997).

Sedimentary analyses

Surface and fossil sediments were prepared for pollen analysis using standard methods (Faegri and Iversen 1989). Pollen grains were identified at 400× magnification and counted until at least 400 tree pollen grains were encountered. Counts of stomata and marker grains were made on the same slides assessed for pollen until an equivalent of 1000 pollen grains was reached. Macroscopic charcoal fragments were counted in sediment samples prepared by soaking in KOH for at least 24 h and sieving through a 250-micrometer screen.

A date of AD 1890 was assigned to the level in the core corresponding to the period of European settlement, defined stratigraphically as a reduction in pine pollen, and an increase in ragweed (Ambrosia) and other herbaceous pollen. Plant macrofossils were selected from sediments at important stratigraphic horizons for AMS (accelerator mass spectrometry) radiocarbon analysis (Table 2). All dates are reported in the text as calendar years before present (BP), where “present” is AD 1950. Sediment ages for other depths were determined by linearly interpolating between radiocarbon dates, the date of European settlement, and the surface of the core.

Modern analogues

To expand the network of surface pollen samples from forest hollows already available for northwestern Wisconsin (Calcote 1995, 1998, Parshall and Calcote 2001), I collected additional paired samples of pollen and vegetation data, yielding a more inclusive range of modern forest stand types that exist in the region. Sites were assigned to stand types by classification of basal area for the 11 common upland trees, and a measure of dissimilarity, squared chord distance (SCD), was calculated to compare all pollen assemblages to each other (Prentice 1980, 1986, Overpeck et al. 1985, Grimm 1987). Fossil pollen assemblages are compared with this set of surface samples to infer past stand composition.

RESULTS

Surface sample analyses

Six different stand types were identified based on tree basal area around each pollen surface sample (Fig. 2). The dominant pollen types in surface sediments correspond well with the dominant trees identified in the stand type classification. Changes in past stand composition are interpreted from fossil pollen using threshold SCD values identified from these data and other similar studies (Calcote 1998, Davis et al. 1998, Parshall and Calcote 2001). SCD values <0.05 are strong evidence that fossil pollen assemblages were produced by analogous modern forest types. SCD values <0.1 also provide a reliable level of interpretation and serve here as weak analogues.

Sedimentary records

Owen hollow.—Pollen and stomata from Owen Hollow clearly demonstrate both the initial arrival of hemlock trees and their subsequent increase in abundance (Fig. 3). Hemlock pollen first appears ~2360 yr BP, followed shortly thereafter by hemlock stomata, which occur in all younger sediments. Hemlock pollen percentages increase to 10% of total pollen at 350 yr BP, and subsequent fossil pollen assemblages resemble those of modern hemlock stands. Coincident with this shift, ash pollen increases and pine pollen declines temporarily. The settlement period is represented in the top samples by a modest increase in ragweed and other herbaceous taxa, and a major decline in pine pollen.
from 50% to 25%. Charcoal is most abundant in the deepest sediments, when the stand was apparently dominated by white pine, and declines as hemlock stomata and pollen first appear. There are a few stumps present today, primarily white pine, but many of the hemlock trees at the site are >250 yr old, indicating that logging occurred but was not extensive.

Diamond hollow.—The stand history from Diamond Hollow shows a similar pattern of development to Owen Hollow (Fig. 4). Hemlock pollen is uncommon (<0.5%) before 2340 yr BP, and reaches 1% ~ 1350 yr BP, suggesting local presence of trees. Hemlock stomata first appear around 800 yr BP, well before the sharp increase in pollen that occurs just before European settlement. Like Owen Hollow, a shift in modern analogue similarity toward hemlock stands occurs at the same time that hemlock pollen percentages increase sharply. Charcoal concentrations are low throughout the core.

Cutacross hollow.—The core from Cutacross Hollow was started at 13 cm below the surface owing to fibrous and woody material at the top of the sediments. Hemlock pollen is extremely low (0.3%) before 3430 yr BP (Fig. 5), and surpasses 1% between 1500 and 2000 yr BP. The absence of all stomata from the sediments between 30 and 50 cm suggests that preservation was poor at this time, so hemlock may have been present but undetected. Hemlock stomata first appear at 520 yr BP, as both hemlock and birch pollen increases and white pine pollen declines. Modern analogues shift toward hemlock stands with the rise in hemlock pollen. A layer of small fragments of bark and wood just before this change likely represents a canopy disturbance just before the development of this hemlock forest. As at Owen Hollow, charcoal abundance is very high in the lower portion of the core where pollen assemblages are dominated by pine, and declines as hemlock pollen surpasses 1%.

Drummond hollow.—Hemlock pollen is low (<0.5%) in Drummond Hollow before 1260 yr BP, and doesn’t surpass 1% until 350 yr BP (Fig. 6). Hemlock pollen gradually increases after this time to reach 5% of total pollen by the settlement period. Stomata are only found around the time of settlement, but the absence of all stomata throughout much of the core suggests poor preservation conditions. Fossil pollen assemblages before 350 yr BP are similar primarily to the pine-oak-hardwood stand type, and show weak or no similarity to modern pine stands, which is a different pattern than the other three sites. Although this hemlock population has increased in size over the last three centuries, pollen percentages fail to show an abrupt increase as seen at the other sites. Ash pollen percentages increase sharply (>10% of total pollen) ~350 yr BP, coincident with a peak in birch pollen abundance and a brief decline in pine pollen abundance. This suggests that a canopy disturbance occurred just before the local hemlock population began to grow in size. Many
FIG. 3. Pollen, stomata, and charcoal in forest hollow sediments at Owen Hollow. Light shading is a 10× exaggeration. Dates shown are radiocarbon ages as in Table 2. Modern analogues are identified with circles representing similar fossil–modern pairs. Stand types and sites are arranged in the same order as in Fig. 2. Pollen is measured as a percentage; stomata are measured as number per milliliter; and charcoal is measured as number of fragments per 20 milliliters.

FIG. 4. Pollen, stomata, and charcoal in forest hollow sediments at Diamond Hollow. Light shading is a 10× exaggeration. Dates shown are radiocarbon ages as in Table 2. Modern analogues are identified with circles representing similar fossil–modern pairs. Stand types and sites are arranged in the same order as in Fig. 2.
**Fig. 5.** Pollen, stomata, and charcoal in forest hollow sediments at Cutacross Hollow. Light shading is a $10^3$ exaggeration. Dates shown are radiocarbon ages as in Table 2. Modern analogues are identified with circles representing similar fossil–modern pairs. Stand types and sites are arranged in the same order as in Fig. 2.

**Fig. 6.** Pollen, stomata, and charcoal in forest hollow sediments at Drummond Hollow. Light shading is a $10^3$ exaggeration. Dates shown are radiocarbon ages as in Table 2. Modern analogues are identified with circles representing similar fossil–modern pairs. Stand types and sites are arranged in the same order as in Fig. 2.
of the hemlock trees surrounding the hollow are >180 yr old (see also Stearns 1951), demonstrating that the stand was initially colonized by the early 1800s, before logging occurred. Charcoal values are low throughout the core, except in samples at the time of European settlement, which likely represents a human-caused ignition since this site is near the center of logging activities at the turn of the century.

**DISCUSSION**

The vegetation history derived from these forest hollows differs from the vegetation history derived from lakes along hemlock’s range limit. At Hemlock Lake, the gradual increase in hemlock pollen over the past 2500 yr contrasts with the relatively rapid and substantial increase in hemlock pollen deposited in forest hollows over the past 500 yr. These two distinct patterns arise from the different spatial scales represented by each basin. The forest hollows are recording changes in forest composition at the stand scale, while the lakes are recording changes in forest composition in the region (Jacobson and Bradshaw 1981, Prentice 1985, Calcote 1995). Apparently, the rapid growth of local hemlock populations was not a significant regional occurrence, since none of the lakes at hemlock’s range limit show much change. The small spatial representation of forest hollows captures a two-stage pattern of stand development not available from lake records, including initial colonization followed by stand expansion. In the following discussion I first evaluate the evidence available for this two-phase invasion sequence, then I address ecological factors that likely influenced both initial colonization and subsequent expansion of the stands.

*Evidence for colonization and stand expansion*

Although hemlock pollen occurs in the older forest hollow sediments, its very low abundance and inconsistent presence makes it doubtful that trees were growing near any of the sites before 2500 yr ago. This pattern corroborates the evidence from lakes in the region showing a landscape-scale hemlock population so small that it is not discernable from larger distant hemlock populations that existed to the east (Fig. 1: Davis et al. 1986, Davis 1987, Davis and Sugita 1997). Fossil stomata clearly document the earliest arrival of trees at Owen Hollow ~2000 yr ago, and the other sites show evidence of colonization at various times after this (Figs. 3–7). This agrees well with the first continuous presence of hemlock pollen in Hemlock Lake, and suggests that small, dispersed populations of trees were present on the landscape by 2000 yr ago.

The presence of stomata is the best evidence that trees were growing nearby, but their absence does not prove that trees were absent from a stand, because preservation conditions may have been poor, or trees were growing too far from the forest hollow to be detected. In several instances the absence of all stomata suggests that the date of first colonization is probably an underestimate. Hemlock pollen percentages surpassing 1% where stomata are absent is relatively strong evidence that hemlock trees were growing at Cutacross and Diamond by 1500 yr BP, and at Drummond by 700 yr BP. If both stomata and pollen evidence is consid-
ered, colonization occurred at all sites between 2000 and 500 yr BP (Fig. 7).

Stand expansion, on the other hand, is documented by a substantial rise in hemlock pollen and a shift in pollen assemblages to resemble modern hemlock stands, which includes a rise in birch and a decline in white pine pollen. Based on this evidence, initial colonization clearly predated stand expansion by several hundred to at least 1000 yr at three of four sites. A lag between initial colonization and population expansion is a reasonable scenario for hemlock. Hemlock's high tolerance of shade allows saplings to survive for >100 yr in a dark understory, and adult trees can persist at a site for >400 yr (Graham 1941, Hough and Forbes 1943, Godman and Lancaster 1990). Therefore, once trees become established, only a few generations are necessary to produce the pattern of low, persistent hemlock populations documented in this study.

Ecological factors associated with initial colonization

Before these hemlock populations grew in size, local populations were very small and the regional population was probably diffuse. How and why were these particular sites initially colonized? The increasing chance that seeds reached a site as hemlock's range limit continued to move closer to the area must have played a role. Site characteristics may have also influenced the chance of successful colonization, thereby affecting the rate of range expansion because hemlock's small seeds can disperse long distances (Davis et al. 1986, Davis 1987, Godman and Lancaster 1990). Although no one site factor was identified to be important in all four cases, several are worth discussing here, including a reduction in fire occurrence, favorable physical characteristics, and prior forest composition.

A decline in charcoal at Owen and Cutacross Hollows as hemlock trees first colonized these stands is good evidence that fire and hemlock's initial colonization were related (Figs. 3–6). There is no clear spike in charcoal abundance that would suggest a catastrophic fire facilitated hemlock establishment, as has been cited by some authors (Maissurow 1941, Eckstein 1980). Instead, the decline in charcoal indicates that an overall reduction in fire may have encouraged stand colonization by allowing hemlock seedlings to survive and eventually ascend to the canopy. A cooler, wetter climate following the mid-Holocene warm period would have decreased the frequency of fire, and although there are no long-term records of fire occurrence from lakes nearby, sites in south-central Wisconsin show a reduction in fire occurrence since 3000 yr BP (Winkler 1997).

Differences in physical characteristics among sites may have also influenced hemlock colonization, as is certainly true for modern outlying colonies that occur in cooler, moister northern slopes and ravines in Minnesota and southwestern Wisconsin (Adams and Loucks 1971, Rogers 1978, Calcote 1986). Hemlock trees appeared first at Owen Hollow, a site located only 50 m from the shore of a large lake. Lakeshores and bogs are good sites for hemlock establishment in modern old-growth forests (Pastor and Broschart 1990, Frelich et al. 1993), and were probably among the first areas colonized by hemlock in the past. Lakeshores have higher light availability, a greater amount of exposed mineral soil, and a more consistent source of moisture throughout the year, all potentially improving the chances for hemlock survival (Olson et al. 1959, Coffman 1978, Rogers 1978). The soils at Owen Hollow also have a larger component of fine-grained particles (Table 1), which retain water more effectively and reduce the chance of seedling desiccation.

The species composition of the resident forests may have also influenced colonization if some stand types are more resistant to invasion than others (Elton 1958, Mooney and Drake 1986, Crawley 1987). Stands that were colonized first (Owen, Cutacross, and Diamond) were dominated by pine, documented by both pollen analogues and the presence of pine stomata. In contrast, hardwoods comprised a large proportion of the stand around Drummond Hollow, the last site to be colonized. Davis et al. (1998) provide evidence for differential stand invasibility, observing that hemlock preferentially invaded pine stands over hardwood stands. The delayed colonization of hardwood stands could be related to the difficulty of hemlock establishment in hardwood litter and competitive interactions with hardwood seedlings and saplings (Friesner and Potzger 1934, Kavanagh and Kellman 1986, Frelich et al. 1993). Alternatively, there may be some unknown physical difference in site characteristics that is responsible for both a difference in stand type before hemlock arrival, and the ability of hemlock to establish and expand at the site.

Synchronous stand expansion suggests a common explanation

The synchronous expansion of these hemlock stands over the past 500 yr suggests that one or only a few factors explain their recent development. Human impacts are often the cause of such a clear change in forest composition, but they are not the direct cause here because population growth was initiated before European settlement. There is some indication that selective logging for white pine may have encouraged a secondary expansion at the turn of the century at the Drummond and Diamond sites. More recent logging or other canopy disturbance would tend to encourage the replacement of hemlock by hardwoods because of poor hemlock regeneration throughout forests of the Great Lakes (Tyrrel and Crow 1994, Parshall 1995, Davis et al. 1996). Deer browse is cited as one of the main reasons for this recent lack of regeneration (Anderson and Loucks 1979, Frelich and Lorimer 1985, Alverson et al. 1988), and a decline in deer populations over the
past 500 yr could have led to an increase in hemlock. However, there is no record available to test this hypothesis, and other factors might also explain hemlock's poor regeneration recently (Mladenoff and Stearns 1993).

Since all of the sites occur within a small area, a relatively large disturbance may have caused synchronous expansion. Fire has been suggested as a facilitating factor in hemlock stand establishment (Maisurow 1941, Eckstein 1980), but unlike the link between fire and initial colonization, there is no evidence that fire was associated with population expansion at these sites. Wind is a more common disturbance agent in the Great Lakes forests (Canham and Loucks 1984, Whitney 1986, Freligh and Lorimer 1991), and light to moderate wind disturbances over a period of time may favor hemlock's eventual accession to the canopy (Hough and Forbes 1943, Rogers 1978, Abrams and Orwig 1996). Canopy disturbances probably preceded local hemlock expansion at three sites. At Cutacross Hollow, the evidence consists of a layer of woody debris immediately underlying sediments with higher hemlock and birch pollen percentages (Fig. 5). At Owen (Fig. 3) and Drummond (Fig. 6) Hollows, ash and birch pollen percentages increase as pine pollen declines, which suggests mortality of white pine, and replacement by ash and birch, and then by hemlock.

A shift in climate toward cooler, wetter conditions could also explain the synchronous expansion of hemlock, since seed germination and seedling survival are susceptible to drought ( Olson et al. 1959, Godman and Lancaster 1990), and tree growth is favored by low summer temperatures and higher precipitation (Graumlich 1989, Cook and Cole 1991). As climate changed over the past 3000 yr, some critical threshold may have been crossed that increased the likelihood of local hemlock establishment and survival, leading to the shift in stand composition. The period between 500 and 150 yr ago, identified in many places around the world as the Little Ice Age ( Lamb 1982, Grove 1988, Baron 1995), was particularly cool and wet in the upper Midwest (Wahl 1968, Grimm 1983, Clark 1988, 1990) and may have further favored hemlock regeneration. There is no evidence for expansion of hemlock stands at other parts of its range, but populations that are climatically limited may be more responsive to small changes in climate. Furthermore, climate coupled with canopy disturbance would have been an effective mechanism for synchronous expansion at these sites (Stearns 1951, Mladenoff and Stearns 1993).

CONCLUSIONS

A change in climate toward cooler, wetter conditions over the past several millennia in the midwestern United States led to the westward expansion of several mesic species, and the development of the hemlock stands described here provides a unique example of how this kind of range expansion is expressed at the stand level. While hemlock pollen from lakes documents a slowly growing regional population over the past 2000 yr, pollen and stomata from forest hollows reveal that local hemlock populations were present for as long as 1800 yr, and then grew very quickly in size within the past 500 yr. This means that as hemlock's range limit reached its present location, the slow growth in its regional population was a composite of many local colonization and rapid population expansion events. Local stand expansion at other times over the past 2000 yr must have occurred elsewhere on the landscape to contribute to the slow regional rise found in lakes, but were not sampled here.

Before stand expansion, small populations of hemlock trees were apparently scattered across the landscape outside of its continuous range limit that existed tens of km to the east. Outlying colonies today occur more than 50 km west of hemlock's present range limit, and could serve as loci for future population expansion if the climate were to become cooler or wetter. Outlying colonies provide important sources of propagules for plants to extend their ranges into areas where climate is now favorable for colonization and expansion, and in doing so, plant migration can respond to changing climate more rapidly. Long-distance seed dispersal and rapid expansion of outlying colonies must have played some role in the rapid plant migrations that occurred during the early Holocene, and will likely be important for plant populations responding to climate change in the future (Pitelka et al. 1997, Clark 1998, Clark et al. 1998, Iverson and Prasad 1998, Higgens and Richardson 1999, Davis 2001).

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