The Summer Drought Related Hemlock (Tsuga canadensis) Decline in Eastern North America 5,700 to 5,100 Years Ago

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Abstract

High resolution paleoecological analyses from Shepherd Lake, Ontario, Canada, show that 10 to 100 year lake level fluctuations due to climatic change were responsible for alterations in the aquatic biodiversity 5,700 to 5,100 years ago. Thermophilic aquatics such as the Bushy pondweed *Najas flexilis*, charophyte algae and aquatic invertebrates indicate water level fluctuations of several meters, which were likely linked to a warm, dry summer climate. Pollen analysis and radiocarbon dating at Wilcox Lake shows a hemlock decline at 5800 years ago that lasted 1,000 years. Multiple regression analysis indicates that the decline coincides with a drop in mean annual precipitation from 830 to 700 mm. From fossil pollen analysis the impact of these droughts on the upland forest is poorly visible, except for the hemlock decline during the first half of the 6th millennium ago. The two-phased reduction of hemlock from 30% tree cover to less than 5% within centuries is found in large parts of northeastern America. Our results imply drought-weakened hemlock trees and stands, and that drought may have triggered local insect calamities, such as hemlock looper attack. However, this also implies that climatic change and not a pathogen-pest attack was responsible for the synchronous decline of hemlock all over its range in eastern North America. Reconstructing and understanding the hemlock decline is, therefore, of interest to the public and to ecosystem managers when anticipating the effect of pathogen-pest attacks combined with climatic change.

Introduction

Hemlock (*Tsuga canadensis* (L.) Carriere) is a prominent forest tree in the northeastern United States and adjacent Canada. Although hemlock wood is economically unimportant today, hemlock stands have amazing beauty and an important cultural value for humans. However, in the past few years an increasing number of stands have become threatened by the woolly adelgid (*Adelges tsugae* Annand), an introduced insect pest from Asia which has defoliated and killed stands (McClure 1987, Orwig and Foster 1998). It is, therefore of interest to know if similar and comparable large scale hemlock mortality has occurred since its expansion from its ice age refuge to its present range in eastern North America.

Over the past 60 years pollen analysis has revealed forest history of the postglacial period. In southern Ontario, for example, the major expansion of hemlock occurred between 9,000 and 8,000 years ago based on calibrated radiocarbon dates. Pollen studies done within the hemlock range also show that after a rise in importance it had a dramatic and rapid decline, which began 5700 to 5600 years ago (i.e. 4,900 to 4,800 radiocarbon years ago). Thereafter, it took at least a thousand years for it to recover, and at most locations hemlock never became as prominent as it was before its decline. This catastrophic decline from 30% to less than 5% within decades has been known and recognised since the first pollen studies done by Auer (1930) in Canada and by Deevey (1939) in the United States who wrote: "During period C2 conditions in southern Connecticut became slightly more xerophytic, as illustrated by a rise in hickory and the somewhat less striking decline of hemlock''. Even if other studies also revealed a hickory maximum during and after the hemlock decline and attributed this to xerothermic conditions in-between two phases of mesic climatic conditions (Niering 1953), the drought hypothesis for the decline was not pursued further at that time; it took another 25 years before Margaret Davis (1981) proposed possible explanations for such a decline. She favoured the hypothesis of a pathogen or pest attack by hemlock looper (*Lambdina fiscellaria*, Lepidoptera), especially when comparing the rapidity of the demise to pathogen attacks occurring during the 20th century, such as the extirpation of chestnut (*Castanea dentata*) due to introduced chestnut blight in eastern North America (Andersen 1974). She pointed out that this explanation was the most probable due to a lack of evidence as to other causes, e.g. climatic change, fire, windstorms and/or prehistoric human activities. First attempts failed to find direct evidence of the pathogen or pest, e.g. the chitinous insect remains (Allison et al. 1986), but some authors of textbooks accepted that hemlock looper was the reason for the decline (e.g. Delcourt and Delcourt 1991). It took several years to get the first evidence of an increased abundance of hemlock insect pests during the decline (Bhiry and Filion 1996). However, until now the question of why a pathogen-pest attack should have occurred around 5,700 years ago and not centuries before or after was not asked. Recently drought, based on sedimentological evidence, was proposed as a triggering mechanism for the potentially explosive but unproven massive presence of hemlock looper in billions of individuals (Yu and McAndrews 1996; Yu et al. 1997). On the other hand, research on the consequences of the reduction in hemlock stands became important during the last few years only, showing that trees such as birch (*Betula* spp.), beech (*Fagus grandifolia*), pine (*Pinus* spp., especially *P. strobus*) and maple (*Acer* spp., especially *A. saccharum*) were filling the canopy gaps formed by dying hemlock (e.g. Fuller 1998) and that the hemlock decline had only a slight effect on lake trophy and biodiversity (Boucherle *et al.* 1986; Hall and Smol 1993). Therefore, and because the hemlock decline was of such importance for prehistoric biodiversity, we here assess mortality-triggering mechanisms by using high-resolution

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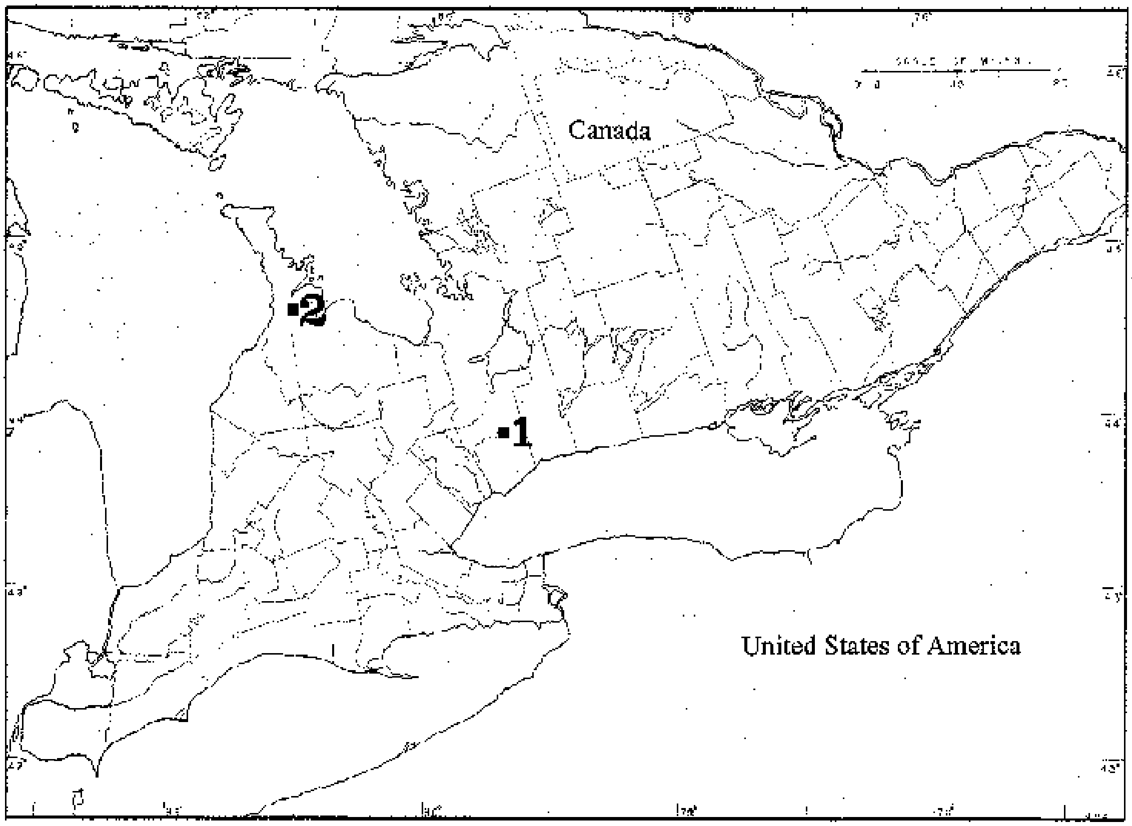

Figure 1.—Location map: Wilcox Lake is at 43°56'24"N, 79°25'58"W, 295 m asl, and Shepherd Lake is at 44°39'30" N, 81°08'30" W, 235 m asl. in southern Ontario, Canada.

pollen and macrofossil data from two sites in southern Ontario. Assessing and clarifying the mechanisms of a near-extinction of hemlock 5,700 to 5,100 years ago may therefore add to our understanding of former forest dynamics and of future threats to hemlock by the woolly adelgid and climatic change.

Materials and Methods

For the present study we chose two lakes: Wilcox Lake is 30 km north of Toronto on the Oak Ridges Moraine and Shepherd Lake is 150 km north-west of Toronto on the Bruce Peninsula (Fig. 1). Wilcox Lake (44 ha) is a kettle lake which formed during the late Pleistocene ca. 15,000 years ago. The cool-temperate climate is typified by the record at Richmond Hill (230 m asl) where the 1951-1980 means were: for January temperature -7.4°C, for July temperature 20.5°C and for annual precipitation 805 mm that is evenly distributed throughout the year (Environment Canada 1982a, b). Judging by remnant woodlots the original mixed forest was dominated by sugar maple (*Acer saccharum*), beech (*F. grandifolia*), red oak (*Quercus rubra*), white oak (*Q. alba*) white ash (*Fraxinus americana*), birch (*Betula papyrifera, B. allegheniensis*), basswood (*Tilia americana*), ironwood (*Ostrya virginiana*), large toothed aspen (*Populus grandidentata*) and, formerly, white elm (*Ulmus americana*) together with white pine (*Pinus strobus*) and hemlock (*Tsuga canadensis*). Local wetland forest included white cedar (*Thuja occidentalis*), tamarack (*Larix laricina*), red maple (*Acer rubrum*), silver maple (*A. saccharinum*) and black ash (*Fraxinus nigra*).

Shepherd Lake (15 ha) was formed after the retreat of the Glacial Lake Algonquin approximately 11,500 years ago; it lies between low drumlins formed on Silurian dolostone. The lake is surrounded by grazing land and a few cereal crop fields as well as woodlots much like those around Wilcox Lake except that white spruce (*Picea glauca*) and balsam fir (*Abies balsamea*) are prominent. In the lake the Bushy pondweed (*Najas flexilis*), as well as some stonewort algae (*Chara* sp. and *Nitella* sp.) build up dense mats, indicating the lake to be oligotrophic to mesotrophic. The lake has only a very small inlet and outlet indicating rather stagnant water. At the nearby climate station of Wiarton the mean January temperature is -7.1°C, the mean July temperature is 18.5°C and the mean annual precipitation of 965 mm with a peak in November and December (Environment Canada 1982a, b) due to the effect of nearby Lake Huron. A core of uniform calcareous organic gyttja sediment was taken in 1997 from the lake's center in 1.25 m of water depth with a modified Livingston piston sampler (Wright 1967). Ten Radiocarbon dates were measured on terrestrial plant remains at the

Table 1.—Radiocarbon dates from Shepherd Lake, Ontario, performed at the University of Utrecht (The Netherlands).

Depth (cm)	^{14}C-age (BP)	Calibrated age range (years ago)	University of Utrecht No. (UtC)
387	2570 ± 50	2,751-2,715	7154
446	3049 ± 41	3,337-3,173	7215
531	4007 ± 41	4,521-4,414	6129
555.5	4400 ± 110	5,254-4,847	6130 (not used for interpolation)
570.5	4250 ± 170	4,986-4,536	6131
601	4900 ± 70	5,716-5,589	6132
615	5040 ± 60	5,896-5,722	6133
664	5860 ± 50	6,739-6,644	7216
752	7572 ± 100	8,411-8,195	7068
806	8187 ± 47	9,216-8,993	7155

University of Utrecht (The Netherlands), allowing an accurate dating of the sediments and of paleoecological events (Table 1).

For the macrofossil analyses sediment slices of 1 cm thickness representing 15 cc of sediment each were processed following Haas (1996). Sieving of sediment samples was done using 2000, 1000, 500, 250 and 125 mm mesh sieves. Residues were analyzed for plant and animal remains. Pollen samples were prepared following Moore et al. (1991). Pollen determinations were done following McAndrews et al. (1973) and by using the reference collection of the Royal Ontario Museum, Toronto. The pollen sum, generally over 500 per sample, was calculated using total pollen, but by excluding pollen of aquatic plants and spores of bryophytes and ferns.

Results

Figure 2 shows a simplified pollen percentage diagram from Wilcox Lake with the regional zonation since the deglaciation 14,000 years ago (McAndrews 1981). Hemlock migrated from a southern refuge to the upland around Wilcox Lake about 9,000 years ago coincident with climatic warming and moistening. It also indicates an abrupt hemlock decline beginning 5,800 years ago, which is synchronous with other localities in northeastern North America. Canopy gaps formerly occupied by hemlock were filled by maple, pine, and oak. It took a 1,000 years for hemlock to recover, although it never gained the same importance in forests again.

Coincident with the hemlock decline, the annual precipitation dropped from 830 to 700 mm, the sharpest drop since hemlock migrated. At the western limit of hemlock the annual precipitation is 700 to 740 mm. In addition to reconstructing climate using the pollen record we also use local aquatic plants and animals as indicators of climatic change (Haas 1996). Figure 3 shows a selection of plant and animal macrofossils found in Shepherd Lake sediment dating 8,000 to 2,600 years ago. As expected, macrofossils from upland plants such as trees are rare at the center of Shepherd Lake 150 m away from the shore. A few leaves, anthers and cone-scales of hemlock were found.

However, note that the first hemlock macrofossils were present shortly after 7,000 years ago, suggesting that the tree had migrated later to the Bruce Peninsula, which is north of Wilcox Lake (Fig. 1). Hemlock remains between 6,200 and 5,200 years ago indicate trees grew on the nearby drumlins. After 5,200 years ago hemlock fossils are rare, which confirms the near-extinction of hemlock indicated by fossil pollen. In contrast, aquatic plant fossils are more common than remains from upland trees. Bushy pondweed (*N. flexilis*) and charophyte algae dominated the postglacial period. Charophyte data are only partially shown, but the most prominent species was *Chara foliolosa*, a southern species which ranges northward to within 300 km of Shepherd Lake. Both species are typical for shallow water conditions where the water is less than 4 m deep, and thus indicate shallow water at the center of the lake (Haas 1996, Haas et al. 1998) where they were both extremely abundant around 5,700 years ago. *N. flexilis* is an annual plant that reproduces only from seed; it needs warm water conditions of more than 19°C for some days to germinate and to subsequently produce seeds (Haas 1996). This temperature is normally reached in late June to early July where the water is less than 4-m deep, i.e. where there is no thermocline. Such shallow, warm water seems to have prevailed 6,000-5,600 years ago, with a distinctive peak around 5,700 years ago perhaps lasting only a few decades. Given the location in the core and the today's water level this also means that the lake level of Shepherd Lake was at least 2-4 m lower than today. This indicates an extremely warm and dry summer climate.

Several types of animal remains and the northern presence of *C. foliolosa* sustain this reconstruction of summer climate and lake levels, e.g. abundant caddisflies (Trichoptera), freshwater sponges (Porifera), bryozoans, water mites

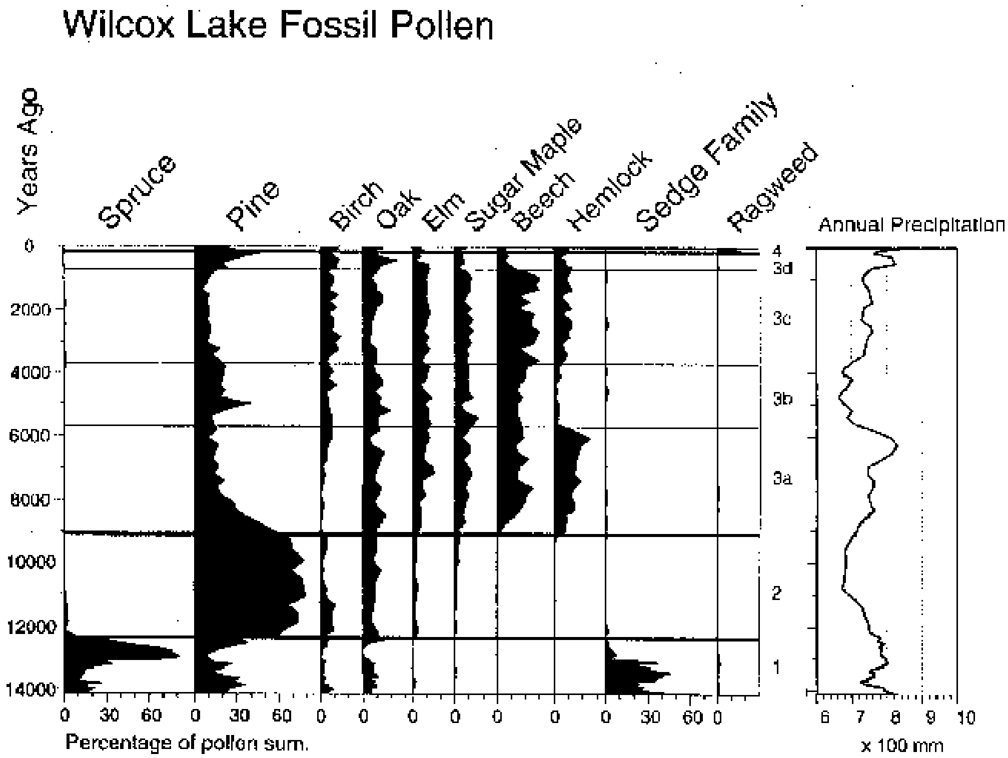

Figure 2.—Pollen percentage diagram from Wilcox Lake, Ontario, showing selected plant taxa. The complete counts are deposited in the North American Pollen Database. The pollen percentage sum is 200 tree pollen grains. Note the hemlock decline at 5,800 years ago. Annual precipitation is plotted as a three-point running mean of values calculated by the multiple regression equation of Bartlein and Whitlock (1993).

(Oribatida), and Ostracodes (Fig. 3). Interestingly, the abundance of charcoal and minerogenic particles does not change significantly in the dry period. This suggests that forest fire was unimportant during the mid-postglacial period at this latitudes, which confirms studies by Anderson et al. (1986) in Maine, and observations in Québec, Canada (C. Carcaillet, pers. communication). Other peaks of *N. flexilis* occurred around 6,300 and 5,300 years ago, and both peaks are paralleled by small peaks of animal remains, especially, Ostracodes. These peaks, spanning a few decades at most, were also the result of low water caused by drought. As *C. foliolosa* is only present in small amounts for this time period, this may point to the fact that such droughts were slightly less severe than the drought around 5,700 years ago.

Fig. 4 shows the corresponding pollen percentage diagram from Shepherd Lake for the period 5,900 to 4,400 years ago. The major event is the hemlock decline and minimum. Note that the total curve of non-arboreal-pollen (NAP, i.e. herbs), do not increase at this time (Fig. 4). Therefore, and because tree pollen did not change, the hemlock decline and succession happens within a dense forest where gaps are filled rapidly.

In detail, the hemlock (*T. canadensis*) decline happened in two phases. The first decline phase from over 35% to 25% occurred 5,700 years ago; it was followed by increased pollen of gap-filling tree species such as pine (*Pinus*) and birch (*Betula*) followed by a short, but intense recovery of hemlock before its second decline started 5,300 years ago. This decline was much stronger and spanned approximately 200 years. Thereafter hemlock did not recover for more than 1,000 years at Shepherd Lake, and in southern Ontario in general. This second decline provoked a succession of different tree species, especially beech (*F. grandifolia*), birch (*Betula*) and elm (*Ulmus*). Note that this change in forest diversity was also accompanied by some small peaks of herbs, such as sedges (Cyperaceae), grasses (Poaceae) and mugwort (*Artemisia*). Forest gaps must have been filled rather rapidly with trees within 10 to 20 years, the limit of stratigraphic resolution.

Discussion

The two hemlock declines at Shepherd Lake occur within seven centuries and coincide with major drought events shown by the macrofossil data. This implicates climate in the hemlock decline in northeastern North America. An insect pest attack could not be documented at Shepherd Lake, where no hemlock looper remains were found, and where insect remains from upland species are rare in general. This does not exclude hemlock looper which may have had a

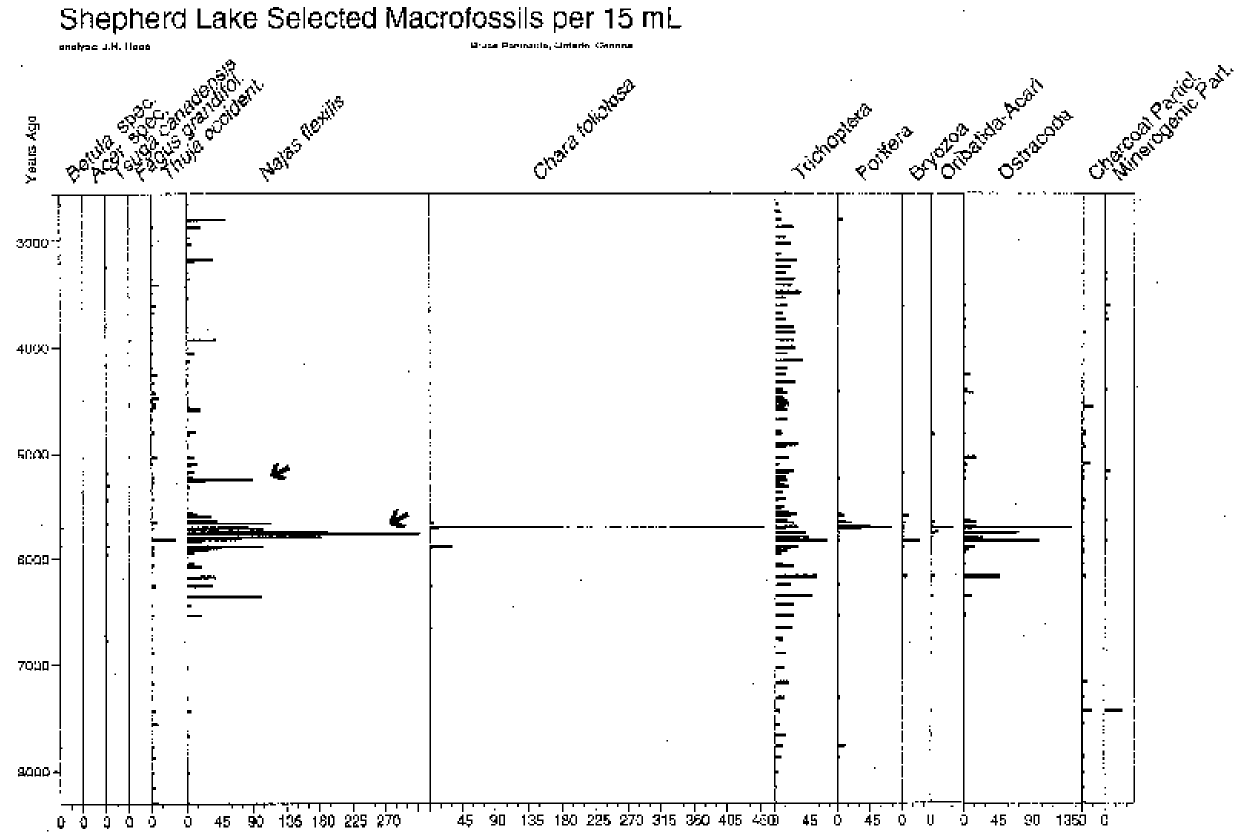

Figure 3.—Macrofossil concentration diagram from Shepherd Lake, Ontario, with selected plant and animal taxa 8,200 to 2,500 years ago. Note the peaks of *Najas flexilis* abundance around 5,800 and 5,300 years ago (arrows), as direct evidence for low lake-levels due to warm-dry summer climate.

destructive defoliation effect at other localities (Bhiry and Filion 1996), but it may indicate that these hemlock looper attacks were only of local importance, as they are in today's forests (Fowells 1965). Such pest attacks would be an indication for drought-weakened and dying hemlock trees. However, a triggering of local hemlock looper populations by climatic change is conceivable and would fit to the today's population behavior of hemlock looper, which never explode more than on a local scale (Fowells 1965). This would also explain why hemlock looper remains are only mentioned and found from a few paleoecological studies (for example Bhiry and Filion 1996, Lavoie et al. 1997).

Of course the droughts were not only present locally at Shepherd Lake or just in southern Ontario. For example, the sediment description of several bogs and lakes analyzed for pollen and macrofossils by Auer (1930) show sediment changes during the hemlock decline suggesting synchronous drought, e.g. from lake mud to bog peat or from fen peat to bog peat. Such records were not discussed in terms of climatic change. However, in recent years some studies indicated a major drought interval in North America during the first half of the 6th millennium ago (Valero-Garcés et al. 1997, Yu et al. 1997), but the resolution and dating quality of most of these studies was low.

To explain such a drought, we must invoke persistence of dry Pacific and/or arctic air masses. In addition, the summer drought events 5,700 to 5,100 years ago fit well to the reconstructed climate in central Europe (Haas et al. 1998) where a warm and dry period was reconstructed for 5,700 - 5,300 years ago within the Alpine arc of Switzerland and northern Italy. So, a general northern hemispheric dry period is indicated.

However, when assessing a climatic nature of the hemlock decline, it is important to assess the ecology of the species. Hemlock is one of the few tree species in North America which has a distinctive shallow rooting system that is susceptible to drought (Fowells 1965). In addition, low atmospheric humidity restricts hemlock growth. Normally the rooting system of seedlings or young trees is confined to the upper 20 cm of soil. A few days of severe summer drought may result in the near-complete mortality of hemlock saplings and populations (Fowells 1965; Godman and Lancaster 1990). It is therefore important to foresters today to keep hemlock litter moist by maintaining shade from adult hemlock trees or other tree and shrub species. Therefore, seedlings and young, immature trees would have suffered from drought periods 5,700-5,100 years ago. Such susceptibility has been described from different places in

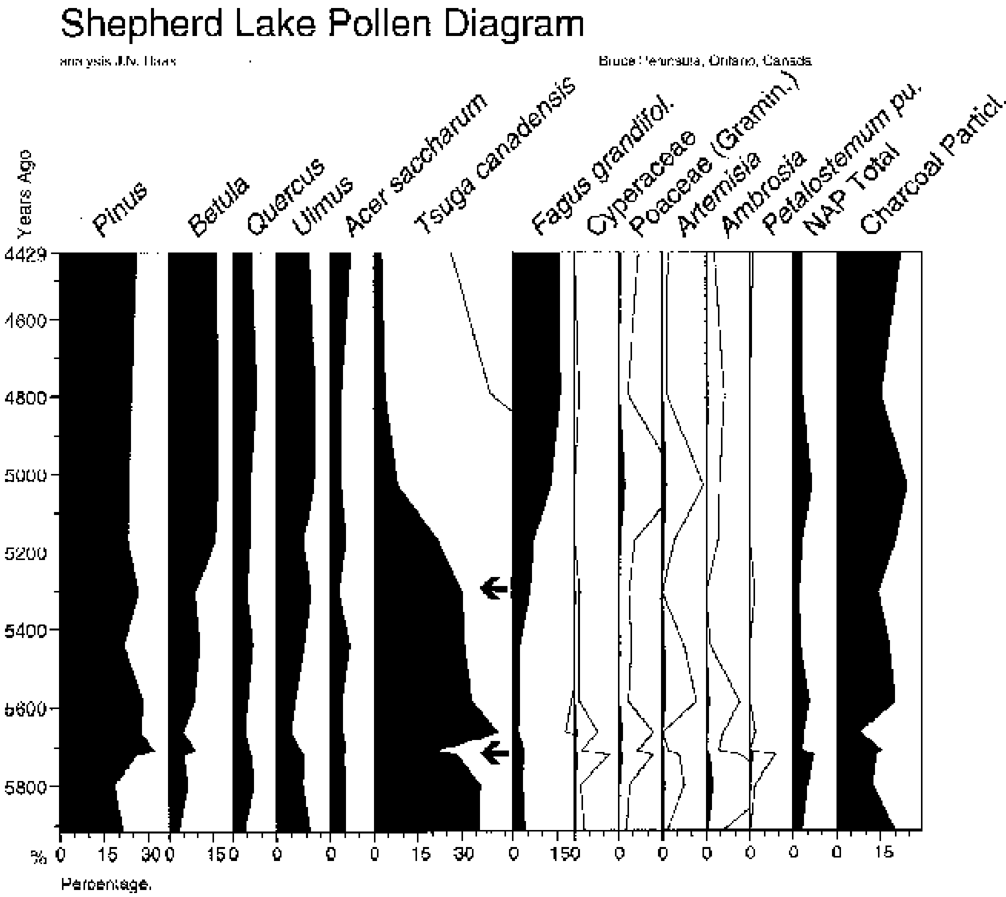

Figure 4.—Pollen percentage diagram from Shepherd Lake, Ontario, with selected plant taxa 5,900 to 4,400 years ago. Note the two-phased hemlock decline around 5,700 years ago, and after 5,300 years ago (arrows). NAP = Non-arboreal-pollen Total (i.e. herbs).

North America (Fowells 1965). Therefore there perhaps was a vicious circle during the 5,700 - 5,100 decline of hemlock: even if large hemlock trees may have survived the drought to be followed by normal mortality, their seedlings would not have survived, allowing other species to grow, which in their turn would have prevented extensive regeneration of hemlock when climate became wetter again. Soil moisture and atmospheric humidity are limiting factors at the natural range limit of hemlock towards the west and the south (Fowells 1965). Hemlock stands on shallow or coarse soils were at risk in former times, as they are today. Shady moist slopes and ravines, on the other hand, would have been places where hemlock survived severe droughts because of reduced, but still available soil moisture. These ecological characteristics of hemlock trees and stands today, therefore, contradict the hypothesis proposed by Filion and Quinty (1993) who attributed the decline to moister climate. Hemlock (Fowells 1965) and our results from Wilcox and Shepherd Lake demonstrate the contrary, and attribute the hemlock decline to drought.

The two-phase hemlock decline over 600 years between 5,700 and 5,100 years ago was also recently noted by Fuller (1998), but her few radiocarbon dates indicate the two declines to be 6,000 and 5,500 years ago, which is slightly too old in comparison with the more accurate dates from Shepherd Lake. Thus the decline of hemlock was a long-term process, provoking different kinds of gap-filling reactions by different tree species depending on the site conditions. It was a synchronous process all over eastern North America linked to drought and perhaps also to local pest attack, but the subsequent forest regeneration and tree population dynamics cannot be seen as a standard process, but were related to time and specific site conditions and geographic location.

Conclusions

Hemlock and hemlock stands were sharply reduced 5,700 to 5,100 years ago because of summer droughts. Seedlings and young hemlock suffered and died because of their shallow rooting system, as soil moisture and atmospheric humidity are the most important limiting factors for hemlock. Larger trees under moisture stress sustained a fatal, but local pathogen-pest attack, perhaps the hemlock looper although not all trees died. Such an attack was triggered by drought, but would not have been the reason itself for the decline of hemlock. Understanding such complex interactions between climate, plants and animals on a long-lasting scale is important when assessing the possible effect of future climatic change. It also shows that major mortality of hemlock populations occurred long before today's attack by pathogens such as the hemlock woolly adelgid. And it also indicates that hemlock survived climatic stress and pathogen attack 5,700 to 5,100 years ago, and that the recovery took more than 1,000 years.

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