Pollen in Laminated Sediments Provides Evidence For a Mid-Holocene Forest Pathogen Outbreak
Author(s): Taber D. Allison, Robert E. Moeller, Margaret Bryan Davis
Reviewed work(s):
Published by: Ecological Society of America
Stable URL: http://www.jstor.org/stable/1939835
Accessed: 06/04/2012 11:23

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at http://www.jstor.org/page/info/about/policies/terms.jsp
JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

POLLEN IN LAMINATED SEDIMENTS PROVIDES EVIDENCE FOR A MID-HOLOCENE FOREST PATHOGEN OUTBREAK

Taber D. Allison, Robert E. Moeller, and Margaret Bryan Davis

The populations of two major forest tree species, American chestnut (Castanea dentata) and American elm (Ulmus americana), have been devastated by pathogens introduced in this century (Kuhlman 1978, Sinclair and Campana 1978, Anagnostakis 1982). The fossil pollen record in eastern North America shows a rapid decline of eastern hemlock (Tsuga canadensis) 4850 14C yr BP and may be evidence for a catastrophic pathogen outbreak similar to the chestnut blight and Dutch-elm epidemics.

Davis (1981) hypothesized that the prehistoric decline of hemlock was caused by the outbreak of a pathogen similar in epidemiology to the exotic pathogens that devastated chestnut and elm. Three lines of evidence supported the pathogen hypothesis. First, the decline was synchronous throughout the range of hemlock, within the limits of precision of 14C dating (Davis 1981, Webb 1982). Second, the decline occurred throughout a 1.5 × 106 km2 region where different climatic factors limited hemlock’s growth and reproduction. For example, the decline occurred in the mountains of New Hampshire, where hemlock is limited to the warmest part of the elevational gradient (Davis et al. 1980), and in Michigan, where moisture is apparently limiting (Brubaker 1975). Third, the concentra-

1 Manuscript received 30 August 1985; revised 30 December 1985; accepted 27 January 1986.
2 Natural Resource Ecology Laboratory and Department of Range Science, Colorado State University, Fort Collins, Colorado 80523 USA.
3 Permanent address: Universidad Nacional de Mar del Plata, Balcarce, Argentina.

ECOL. 67(4): 1986, pp. 1101–1105
© 1986 by the Ecological Society of America
FIG. 1. (A) Chestnut pollen, as percent of total tree pollen, versus depth at Pout Pond, New Hampshire, before and after the introduction of the chestnut blight (indicated by arrow). Samples 1–2 cm thick were prepared from a frozen core using standard pollen analysis techniques. The smoothed curve (dotted line) traces a 75% decrease within 5 yr. The age scale is not linear, reflecting the change in sediment compaction with depth. (B) Hemlock pollen grains versus depth for the region of the hemlock decline. Hemlock pollen was counted along transects across thin sections that were cut perpendicular to the bedding plane of embedded sediment. The smoothed curve (dotted line) corresponds to a 75% decrease within 7–8 yr. The arrow indicates the beginning of the hemlock decline at 126.66 cm depth. (C) Hemlock pollen grains versus depth in thin cross sections of embedded sediment from the region of hemlock recovery. The data in (B) and (C) are counts from one transect at each depth, but are not directly comparable, as statistically significant differences exist between lamination thicknesses in thin sections from these sampling levels. Each count in (B) includes, on average, 3.8 laminations, while each count in (C) includes, on average, 4.2 laminations. The calendar year age scales for (B) and (C) are approximations determined by interpolating between radiocarbon dates calibrated in calendar years (Klein et al. 1982). Occasional gaps occur in the count sequence of (B) and (C) due to separation of sediments during the embedding process or due to previous removal of sediment for pollen analysis (T. D. Allison, personal observation).

(Swain 1973). Sediment in the frozen core was laminated in the upper 10 cm (estimated age 0–30 yr) and at levels deposited before settlement in 1810 AD. Contiguous segments of sediment 1–2 cm thick were cut from the core and prepared for pollen analysis according to the methods of Faegri and Iverson (1975). Pollen was counted in transects across microscope slides at 640×; ~350 arboreal pollen grains were counted on each slide.

Chestnut pollen percentages fell from 3% to <0.5% of total tree pollen, and chestnut pollen concentrations declined from 46,000 to 5700 grains/g dry mass, at 11.5 cm below the surface. The decline in chestnut pollen deposition occurred between samples that differ in mean age by 7–8 yr (Fig. 1A).

Data similar to those from Pout Pond were obtained from Linsley Pond, Connecticut (Brugam 1978); in both sites the absence of benthic invertebrates preserved fine-scale stratigraphy. In the Linsley Pond core, chestnut pollen averaged 8.8% of total tree pollen in samples from 30–70 cm depth. It dropped from this value at 30 cm to 1.7% of total tree pollen at 27 cm depth; this 3-cm depth interval was estimated to cover 9 yr. The percentage of chestnut pollen remained low (\( \bar{X} = 1.8\% \)) throughout the younger sediments (27–0 cm) (Brugam 1978 and personal communication).

Given these results for the decline of chestnut, we hypothesized that a decline in hemlock fossil pollen deposition within 7–9 yr would support the hypothesis that a pathogen or similar agent was involved. Previous
TABLE 1. Summary of radiocarbon dates for sample depths included in the pollen diagrams of Pout Pond and Mirror Lake, New Hampshire (Fig. 3).

<table>
<thead>
<tr>
<th>Sample no.</th>
<th>Depth (cm)</th>
<th>14C age (yr BP)</th>
<th>Age (calendar years)*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pout Pond</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>GX-8492</td>
<td>82–84</td>
<td>2710 ± 145</td>
<td>790–1045 BC</td>
</tr>
<tr>
<td>GX-8494</td>
<td>149–151</td>
<td>5995 ± 180</td>
<td>4585–5220 BC</td>
</tr>
<tr>
<td>Mirror Lake</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>I-5394</td>
<td>300</td>
<td>3170 ± 155</td>
<td></td>
</tr>
<tr>
<td>I-5395</td>
<td>400</td>
<td>3750 ± 180</td>
<td></td>
</tr>
<tr>
<td>I-4732</td>
<td>600</td>
<td>4960 ± 155</td>
<td></td>
</tr>
</tbody>
</table>

*The 90% confidence interval of the equivalent age in calendar years (Klein et al. 1982).

Pollen analyses of Pout Pond sediment (Davis 1981; T. D. Allison, personal observation) showed a decline of hemlock pollen percentage from 23% of total pollen to 10% between 126 and 127 cm, coupled with a 72% decline in hemlock pollen concentration (from 153 000 grains/cm² to 43 500 grains/cm²). The estimated age at this depth, based on interpolation between radiocarbon-dated samples (Table 1), is 4867 radiocarbon yr BP. The age estimate agrees closely with dates of the decline recorded in other lakes and bogs (Davis 1981, Webb 1982).

We obtained a detailed record of these changes by examining the laminae within the Pout Pond core. Cubes of sediment were removed from various depths in the core and embedded in Carbowax PEG 1000 (Tippett 1964). Thin sections (30 μm) were cut perpendicular to the bedding plane of the laminae with a microtome and mounted in immersion oil on slides for viewing under a light microscope.

Laminations deposited between 83 cm and 150 cm (including the hemlock decline at 127 cm) are couples 100–200 μm thick consisting of a layer of dinoflagellate and chrysophyte cysts and a layer of pollen-containing organic sediment (Fig. 2). The annual periodicity of the laminations is confirmed by the agreement between the number of couples between 83 and 150 cm depth (3848 couples; SD of estimate = 70.3) and the number of calendar years (3540–4430 years; midpoint = 3935). The latter was determined from the difference between the 90% confidence intervals of the calendar year equivalents of radiocarbon dates at 83 cm and 150 cm depths (Table 1) (Klein et al. 1982). We estimated the total number of laminations between 83 cm and 150 cm by counting couples per millimetre thickness in thin sections from six 1 cm thick samples collected at ≈10-cm intervals. A mean sedimentation rate (in years per millimetre) was determined for each sample; the number of years elapsed between samples was estimated by interpolating between two sample depths.

Fig. 2. Thin section of laminated sediment from Pout Pond, New Hampshire, showing >7 yr deposition of dinoflagellate and chrysophyte cysts. Dotted line equals 100 μm. (Taber D. Allison, University of Minnesota, Minneapolis, Minnesota, USA.)

We determined the detailed stratigraphy of the hemlock decline by counting hemlock pollen in situ on thin sections. Hemlock pollen was tabulated along transects whose length ran parallel to the bedding plane of the laminations. The transect height (the diameter of the microscope field) included 3–4 laminations. Hemlock pollen was identified by shape and wall sculpturing. Each of our pollen counts is the number of pollen grains in one transect, and represents deposition over 3–4 yr. Pollen counts are equivalent to concentrations in a volume of sediment equal to 0.03 mm (the thickness of the thin section) x 0.65 mm (the transect height) x 10 mm (the length of the transect).

Pollen influx (grains per square centimetre per year) can be calculated by dividing pollen counts by the sedimentation rate (in laminations per unit transect height). For example, we estimated a sedimentation rate of 5.9 laminations/mm at the depth of the hemlock decline. Each transect, 0.65 mm high, contained an average of 3.8 laminations (years). A count of 36 hemlock pollen grains per transect, therefore, was equivalent to 9.5 pollen grains·0.3 mm⁻²·yr⁻¹. If one assumes a uniform distribution of pollen in the cube of sediment from which the thin section was made, this deposition rate can be converted directly to an influx value: 3167 grains·
cm$^{-2} \cdot$yr$^{-1}$. This figure is higher than that for the influx of hemlock pollen (2500 grains $\cdot$cm$^{-2} \cdot$yr$^{-1}$) estimated from 1-cm$^3$ samples using conventional pollen analysis techniques (T. D. Allison, personal observation). Our result is not surprising, however, because hemlock grains that extended beyond the plane of the thin section were sectioned and counted, enlarging the effective sampling width of the thin section.

The mean number of hemlock pollen grains per transect decreased by 75% within a 7–8 yr period (Fig. 1B); this is comparable to the rate of decline of chestnut pollen observed in younger sediment from Pout and Linsley Ponds. Hemlock pollen was rare in Pout Pond sediment deposited 100 or more years after the initial decline, but hemlock pollen persisted until the beginning of the recovery, recorded at the 103–106 cm depth interval. This pollen may represent continued local presence of hemlock at low densities.

Pre-decline levels of hemlock pollen deposition were again reached at 97 cm, $\approx 500$ yr after the recovery began and 1900 yr after the initial decline (Figs. 1C, 3). The recovery of hemlock pollen was much slower than its previous decline. Davis (1981) suggested that evolutionary changes were responsible for the recovery—either the development of host resistance or an attenuation of pathogen virulence analogous to the hypovirulent strain of the chestnut pathogen (Anagnostakis 1982).

Pollen counts per transect in Fig. 1B and C are not directly comparable, as sedimentation rate was 6.5 laminations/mm during the recovery, compared to an average 5.9 laminations/mm at the depth of the decline. This difference results in slightly inflated pollen counts per transect during the recovery compared to counts made at depths before and during the decline. In terms of annual hemlock pollen deposition, a count of 20 grains per transect at the depth of the recovery would be equivalent to 18 grains per transect at the depth just before the decline. Thus, hemlock pollen influx at 101 cm depth (1580 grains $\cdot$cm$^{-2} \cdot$yr$^{-1}$) was lower than the deposition rate just before the decline (3167 grains $\cdot$cm$^{-2} \cdot$yr$^{-1}$).

The rapidity of the hemlock decline has not been observed previously because lake sediments seldom retain fine-scale stratigraphy. For example, although the hemlock pollen stratigraphies of Pout Pond and Mirror Lake, New Hampshire, are similar (Likens and Davis 1975, Davis 1981), sediment mixing has destroyed the detailed record at Mirror Lake. The decline in hemlock pollen deposition at Mirror Lake is spread over 35 yr despite a rapid rate of sediment deposition (7–8 yr/cm) and sampling at contiguous 1-cm intervals (Fig. 3). Experimental studies at Mirror Lake by Moeller et al. (1984) show that biological mixing now extends 7 cm below the sediment-water interface; these studies predict that an instantaneous change in pollen deposition would be recorded as a gradual change over 4–8 cm of sediment, equivalent to 30–60 yr.

The rapid decline in hemlock pollen observed in the laminated sediments of Pout Pond, and its similarity to the recent decline of chestnut pollen, are strong circumstantial evidence for the pathogen hypothesis. The spontaneous appearance of a serious forest pathogen presents an interesting contrast to the chestnut blight, which was introduced to North America by humans. The recovery of hemlock pollen 2000 yr after its decline suggests that natural processes might eventually result in a similar population recovery of chestnut.

Acknowledgments: We thank R. Brugam for the use of his data from Linsley Pond. We also thank E. J. Cushing, A. A. Middledorp, M. Schwartz, D. Cook, R. Calcote, R. N. Mack, and two anonymous reviewers for their comments, which greatly improved this manuscript. Funding was provided by the National Science Foundation, DEB 80-12159.

Literature Cited


1 Manuscript received 1 August 1985; revised 23 January 1986; accepted 24 January 1986.

2 Department of Ecology and Behavioral Biology, University of Minnesota, Minneapolis, Minnesota 55455 USA.

3 Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania 19103 USA.