

Recent successional processes investigated by pollen analysis of closed-canopy forest sites

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Abstract

Forest succession was investigated by pollen analysis of two mor-humus sections and of peat from a 3 m-diameter hollow under mixed conifer-hardwood forest in north-central Massachusetts, USA. The humus profiles recorded a major forest perturbation caused by the removal of *Castanea dentata* by the chestnut blight (1910–1912), and the peat from the hollow extended the record beyond the time of colonial settlement (1733). *Fagus grandifolia* was a forest dominant before 1733 but declined abruptly upon settlement. *Castanea*, a late Holocene immigrant to the area, rapidly increased its pollen representation after settlement until the epidemic of the chestnut blight. Forest succession following the loss of *Castanea* involved the successive rise to dominance of *Betula*, *Quercus*, *Acer rubrum*, and *Tsuga canadensis*. These vegetational changes conform to observations made during studies of forest-stand composition by other workers. Allogenic factors such as logging, disease, and wind have initiated major compositional change, which has been modified by autogenic successional processes such as the gradual rise to dominance of *Tsuga canadensis* around one of the humus sections. The two humus sites resolve fine-scale pattern in former vegetation such as differences in the distribution of *Pinus strobus* and *Castanea* over 200 m, the distance between the mor-humus sites. These within-forest sites permit investigations of fine-scale vegetational patterns and processes that are of interest to forest ecologists.

Introduction

Studies of forest succession require data covering long periods because of the life-span of most forest dominants. However, direct observational data of this sort are rarely gathered (Christensen 1977; Christensen & Peet 1980; Hibbs 1983; Leak 1987; Scheiner & Teeri 1981; Veblen & Lorenz 1987), and inferences are often drawn from composition and structural characteristics of contemporary forest

stands, spatial chronosequences (Cowles 1899), or plot dissection data (Henry & Swan 1974; Oliver & Stephens 1977).

Stratigraphic pollen data represent samples of vegetation covering long time-periods, but most pollen data have been gathered from peatlands and lakes that integrate vegetation patterns over large regions at time-scales too coarse to detect local, short-term successional changes. Mor-humus deposits, which are found within certain forest types, may contain well-preserved pollen in an orderly time-sequence, yielding records of forest change

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over hundreds of years (Aaby 1983; Andersen 1984). In this paper, we present pollen data from two humus deposits and from a small forest-hollow in an area of mixed conifer-hardwood forest in north-central Massachusetts, U.S.A. (Fig. 1), and we interpret these data in terms of recent successional change.

The study site is in the Harvard Forest, Petersham, in which much data have been collected describing recent forest change over 10s or 100s of years (Spurr 1956; Oliver & Stephens 1977; Hibbs 1983). These investigations have emphasized the initial floristic composition model of succession (Egler 1954) and the role of disturbance in influencing changes in forest composition. Oliver & Stephens (1977) presented the major allogenic factors that have affected forests

in this region over the past 150 years. These factors include logging, hurricanes, fires, insects, and the spread of *Castanea* blight. Hibbs (1982, 1983) in an analysis of forest compositional changes following a hurricane in 1938 emphasized the delayed expansion of *Tsuga canadensis* and the role of *Pinus strobus* in these predominantly hardwood forests. Our pollen data are used to assess independently these changes and to examine the relative roles of autogenic and allogenic processes in recent forest development. We also look for evidence of pattern in the vegetation prior to and following the loss of *Castanea*. The small forest-hollow was examined to extend the period under investigation beyond the time range of these other studies.

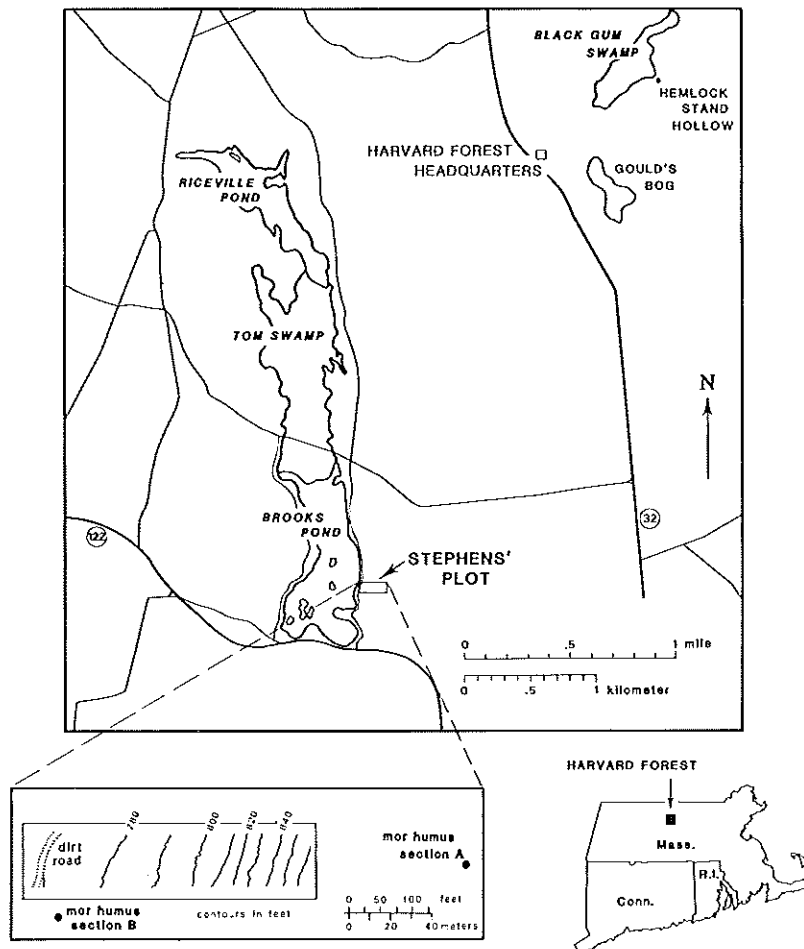


Fig. 1. Map of study area in the Harvard forest (Petersham, Massachusetts) showing location of Stephens' Plot, the mor-humus sampling sites (inset at lower left from Stephens 1956) and the small forest-hollow.

Mor humus is a dry, acidic accumulation of partially decomposed leaf litter of low biological activity (Muller 1878). The absence of earthworms results in minimal mixing of layers, and most pollen is immobilized in organic aggregates (Munaut 1967). Slow decomposition from fungal digestion and comminution by soil arthropods concentrates, with time, the highly resistant pollen exines in lower layers. Mor humus is typically associated with acidic, free-draining soils, such as podzols, and is found under trees producing a leaf litter of high polyphenolic content (Davies *et al.* 1964). Mor-humus accumulations of up to 120 cm representing several thousand years have been found on undisturbed Scandinavian lake islands (Bradshaw & Hannon unpubl.). This humus type contrasts with mull humus in which rapid decomposition and mixing destroy any temporal sequence and create unfavorable conditions for pollen preservation. The existence of shallow mor-humus deposits within the Harvard Forest permitted the use of this type of unconventional pollen analysis in the present study.

Mor humus and small, wet hollows within closed-canopy forests can be assumed to collect pollen chiefly derived from trees growing within 20–30 m based upon the studies of Andersen (1970) and Heide & Bradshaw (1982). In a study of contemporary pollen-tree relationships in the northern hardwood forests of Wisconsin and Michigan it has been shown that the *Betula* pollen-type is over-represented relative to the abundance of birch trees in the local vegetation, *Quercus* and *Pinus* are proportionately represented, and *Tsuga* and *Acer* are under-represented (Heide & Bradshaw 1982). Where no birch, pine, or oak trees occurred within 20 m of the pollen sampling site, percentage pollen values of up to 20% were recorded, indicating the good dispersal properties of these pollen types. These studies are important in establishing the relative abundance and location of former tree populations around mor-humus sampling sites.

Study area

The study was conducted in the Harvard Forest, Worcester County, Massachusetts, USA (42°32'N

Lat.; 72°11'W Long.). The small hollow, Hemlock Stand Hollow (HSH), was 3 m in diameter and lay within Compartment II, Prospect Hill Tract. The two mor-humus sections (A, B), ca 4.5 km southwest, lay within Compartment VI, Tom Swamp Tract. Section A lay at the top of a small hill at 280 m (elev.) in coarse-textured, well-drained soil; section B lay 200 m west at 240 m (elev.) at a more mesic site, ca. 30 m east of the shore of Brooks Pond. The mor-humus sections were adjacent to the study plot of Stephens (Oliver & Stephens 1977). Our study areas are parts of the forest known never to have been ploughed for agriculture, although they were extensively cut and used to graze farm animals. At present they are adjacent to extensive areas of secondary forest.

The vegetation of Harvard Forest is in the transition region between deciduous forest and mixed conifer-northern hardwoods forest and includes among its dominants *Acer rubrum*, *Betula lenta*, *B. papyrifera*, *Pinus strobus*, *Quercus alba*, *Q. rubra*, and *Tsuga canadensis*, in association with the less common *Fagus grandifolia*, *Fraxinus americana*, and *Prunus serotina*. Trees in a circular plot of 0.13 ha (diameter = 20 m) adjacent to HSH were (in decreasing order of basal area): *Pinus strobus*, *Tsuga canadensis*, *Quercus rubra*, *Picea rubens* (planted), *Betula papyrifera*, and *Acer rubrum* ($\Sigma = 93\%$ of total). In a plot of the same size around Section A, *Q. rubra*, *B. lenta*, *A. rubrum*, and *T. canadensis* were the dominants ($\Sigma = 90\%$), whereas around section B, *T. canadensis*, *A. rubrum*, *Q. rubra*, and *B. lenta* were the leading species ($\Sigma = 91\%$).

Methods

Field

At each sample site the ground was probed to determine the greatest depth of organic deposit. At HSH a pit was dug to a depth of 45 cm at which point coarse sand was encountered. Samples for pollen analysis were obtained by pushing glass vials into a clean wall of the pit along a vertical line at 1-cm-intervals. At sites A and B humus and soil samples were taken from clean faces in shallow pits dug to the

B soil horizon using a metal spatula to transfer soil materials into vials. The sample interval was 0.5 cm.

Basal areas of trees greater than 10 cm circumference were measured at a height of 1.3 m within circular plots (20 m radius) around or adjacent to the sample sites.

Laboratory

Pollen was concentrated from 1 cm³ subsamples employing successive treatments of 10% KOH, 40% HF, and acetolysis solution (Faegri & Iversen 1975). Residues were washed through a 196 μ m-mesh sieve after KOH digestion, and were mounted in silicone oil (1000 cs) after dehydration in tertiary butyl alcohol. Counts were made at a magnification of $\times 400$ following equally-spaced traverses over entire coverslip areas. We counted alternate samples, working for the most part side-by-side in order to ensure uniformity of pollen identification. Counts were made to a minimum of 500 pollen and spores. The calculation sum was all pollen and spores in a given sample. Paired gymnosperm guard-cells were calculated as a percentage of the calculation sum plus the number of guard-cell pairs. Numbers of charcoal fragments $> 23 \mu$ m were also tabulated, and the raw

counts are presented in Figs. 2 and 3. Only principal pollen types and summary categories are included in the diagrams; complete data in tabular form are available from the authors.

Results

Humus sections

The sections consisted of 7.5 cm (A) and 8 cm (B) of organic or organic/inorganic soil. Pollen was abundant and was well preserved in the upper humus but included 10–15% degraded pollen (*sensu* Cushing 1967) in samples consisting of mixtures of humus and inorganic particles. The numbers of pollen types identified were consistently high throughout both profiles (A = 32 ± 5.3 , B = 35 ± 4.7 : mean \pm std. deviation), suggesting that the poorer preservation evident in the lower samples did not introduce a bias through differential loss. Observations of the flora near the sample sites suggest that most of the pollen recovered had a local origin except for certain pollen types generally present in small amounts, e.g., *Ambrosia*, *Rumex*, *Plantago lanceolata*, *Cerealia*, and *Artemisia* ('Other long-distance types', Figs. 2, 3), which originated beyond the forest stand.

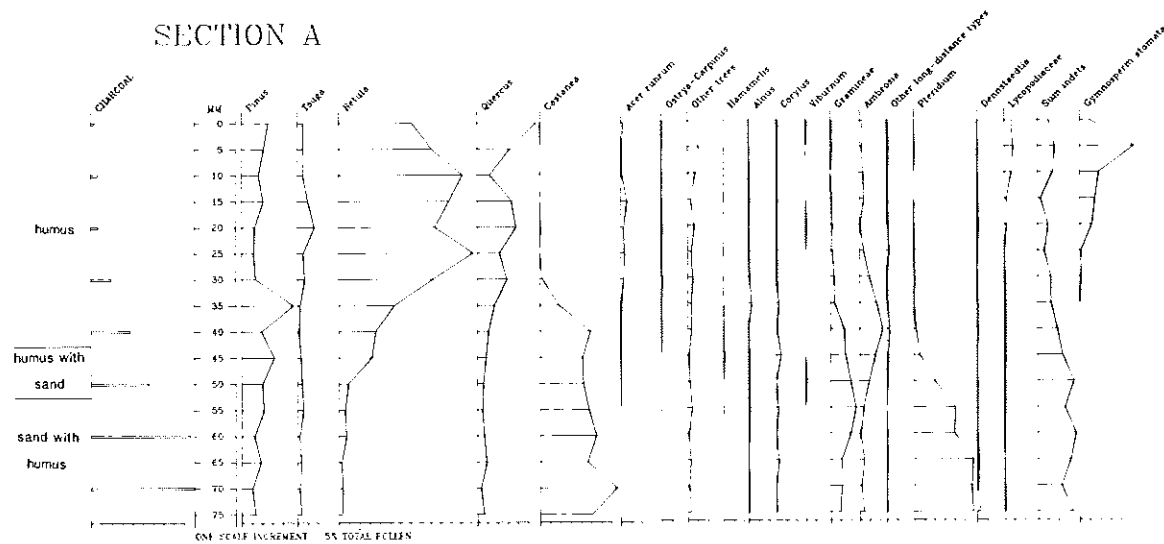


Fig. 2. Pollen diagram for mor-humus section A. For each level the pollen types are in percentages, whereas charcoal abundance is the number of fragments $> 23 \mu$ m encountered while counting to the pollen sum.

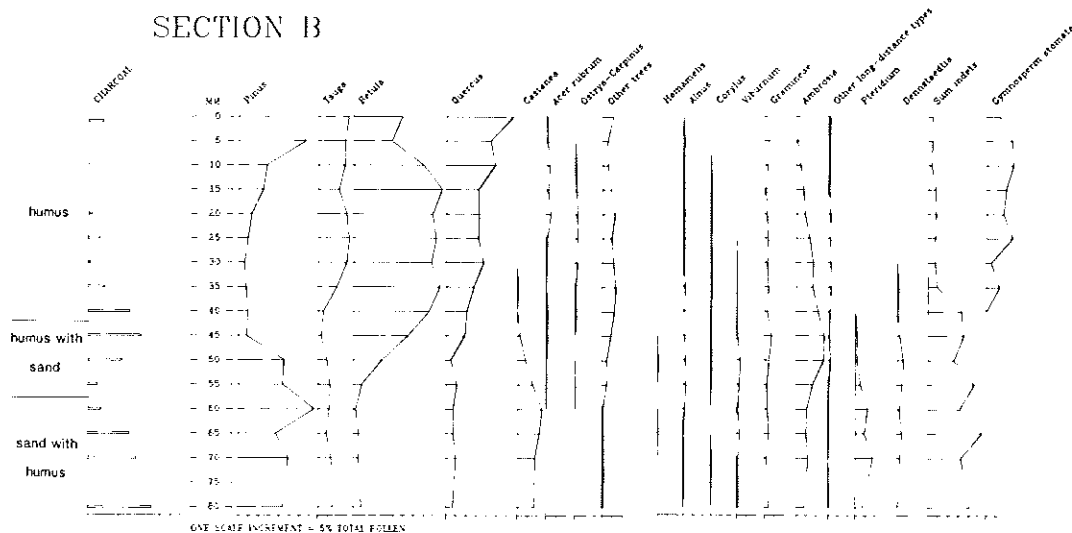


Fig. 3. Pollen diagram for mor-humus section B. For each level the pollen types are in percentages, whereas charcoal abundance is the number of fragments $>23 \mu\text{m}$ encountered while counting to the pollen sum.

There is an overall correspondence between the mor-humus pollen records (Figs. 2, 3), including groups of pollen types with similar qualitative relationships but with different percentage values at each site. For purposes of discussion we have subdivided the diagrams into three phases, which are discussed individually.

Castanea phase ($A = 4-7.5 \text{ cm}$; $B = 6-8 \text{ cm}$)
Castanea pollen was the most abundant arboreal type in this phase in section A. *Castanea* pollen was also continuously present in section B but had lower values than in section A. *Pinus* pollen (probably from *P. strobus*, but its pollen was not always readily distinguishable) was co-dominant with *Castanea* in section B, but values of $<10\%$ in section A are probably of long-distance origin based upon the observations of Heide & Bradshaw (1982). The area around B also supported a rich pteridophyte flora in this phase, including *Dennstaedtia punctilobula*, other Polypodiaceae, *Osmunda*, and *Lycopodium* (mostly *L. lucidulum*). Pteridophyte spores and the presence of *Viburnum* pollen and *Sphagnum* spores perhaps reflect the mesic nature of the site. At the top of the hill (section A), only Gramineae and Compositae (Tubuliflorae-type) pollen and *Pteridium* spores were prominent. The charcoal records reached their

maximum values at the base of both diagrams and at these positions in the profiles may represent accumulation over long time-periods. The lower pollen assemblages pre-date the spread of *Castanea* blight and the development of pure mor-humus. The assemblages represent typical forest-composition post-dating colonial settlement (1733) but prior to major agricultural abandonment in the mid-1800s based upon the distribution of *Ambrosia* pollen. The forests of this phase were probably open in structure and disturbed by human activity as well as possibly by grazing domestic animals.

Castanea decline ($A = 3-4 \text{ cm}$; $B = 4.5-6 \text{ cm}$)
 Both sections show signs of tree removal during this phase: *Castanea* in section A and *Castanea* and *Pinus* in section B. There are peak values of pollen originating from beyond the forest (e.g., *Ambrosia*, *Cerealia*). The loss of *Castanea* was the result of the fungal pathogen, *Endothia parasitica*, which was first noted in Petersham in the fall of 1910 and found to be universally distributed throughout the Harvard Forest by 1912 (D. R. Foster, pers. comm.).

Acer-Betula-Quercus-Tsuga phase ($A = 0-3 \text{ cm}$; $B = 0-4.5 \text{ cm}$)
 Sequential increases in *Betula*, *Quercus*, and *Tsuga*

pollen-percentages occur at both sites during this phase, although *Tsuga* attains values three-times higher in section B than in A, whereas peak *Betula* values in section A are 20% greater than in B. During this phase, *Acer rubrum* pollen-percentages reach a peak and then decline, but its values are consistently higher in section A than in B. *Pinus* pollen-percentages (mostly *P. strobus*-type) increase in section B across the top 2 cm, but such an increase is absent from section A where, across the corresponding interval, there is an increase in *Lycopodium* spores (mostly *L. obscurum*). Increases in numbers of guard-cell pairs (gymnospermous type) parallel increases in *Tsuga* pollen-percentages at both sites.

Contemporary vegetation

The same suite of tree species was recorded around each mor-humus section but in differing proportions (Table 1). In plot A, *Quercus rubra*, *Betula lenta*, and *Acer rubrum* were dominant, whereas in plot B, *Tsuga canadensis* was the principal tree. This corresponds well with the surface-pollen data (Table 1), but *A. rubrum* and *T. canadensis* are under-represented in the pollen record. Total plot basal area was greater around section A (38 m²/ha) than around B (25 m²/ha). A large *Castanea* stump was found close to mor-humus section A.

Small hollow

The HSH pollen record (Fig. 4) extends back to pre-settlement times, i.e., before the *Ambrosia* rise. The

Table 1. Tree basal areas within 20 m of humus sections and comparable surface-pollen data.

	Section A		Section B	
	Trees %	Pollen %	Trees %	Pollen %
<i>Acer rubrum</i>	25	2	12	1
<i>Betula</i> spp.	34	42	10	26
<i>Pinus strobus</i>	1	15	1	15
<i>Quercus</i> spp.	34	34	17	35
<i>Tsuga canadensis</i>	5	3	61	16

record can be divided into two phases, pre- and post-settlement.

Pre-settlement

Spectra below the *Ambrosia* rise are dominated by *Fagus* pollen, which declines in abundance as *Ambrosia* rises. Coincident with the decline in the *Fagus* curve is the loss of *Nyssa* pollen. Similar trends can be seen in the pollen diagram from nearby Gould's Bog (Davis 1958), which is in a basin of about 5 ha. Trees of *Fagus grandifolia* and *Nyssa sylvatica* are sensitive to fire damage, and the reduction in their abundance may be related to fires during the period of colonial settlement, such as those recorded by Oliver & Stephens (1977) in the Harvard Forest. Other tree pollen-types present in significant amounts included *Betula*, *Pinus*, *Quercus*, and *Tsuga*. The low but consistent percentage values of *Pteridium* spores suggest that the forest had an open canopy.

Post-settlement

The most notable feature of this phase is the decline to insignificant values of *Fagus* pollen coincident with the rise in *Ambrosia*. *Fagus* has a sparse and restricted distribution in the contemporary vegetation of the Harvard Forest. Increases in the representation of *Viburnum* (probably *V. acerifolium*, an upland, open-forest species) and *Hamamelis* pollen, and of *Dennstaedtia* spores, indicate a further opening of the canopy. *Castanea* percentages increase slightly as *Fagus* values decline, but a peak value is reached with increases in *Betula* and *Quercus* pollen-percentages as the forest canopy reforms, perhaps reflecting the local abandonment of fields and the onset of secondary succession. There is no *Castanea* pollen in the top sample, which presumably post-dates the loss of *Castanea* due to the chestnut blight. The Harvard Forest is situated near the late-Holocene range-limit of *Castanea* populations as judged by the occurrence of its pollen in low percentages in lake and peatland sediments (Gaudreau & Webb 1985). It is noteworthy that its population peaked only after the major forest-perturbation caused by colonial settlement of the region (Paillet 1988). Such a perturbation would have created an opportunity for the *Castanea* population to build up quickly and achieve local dominance.

HEMLOCK STAND HOLLOW

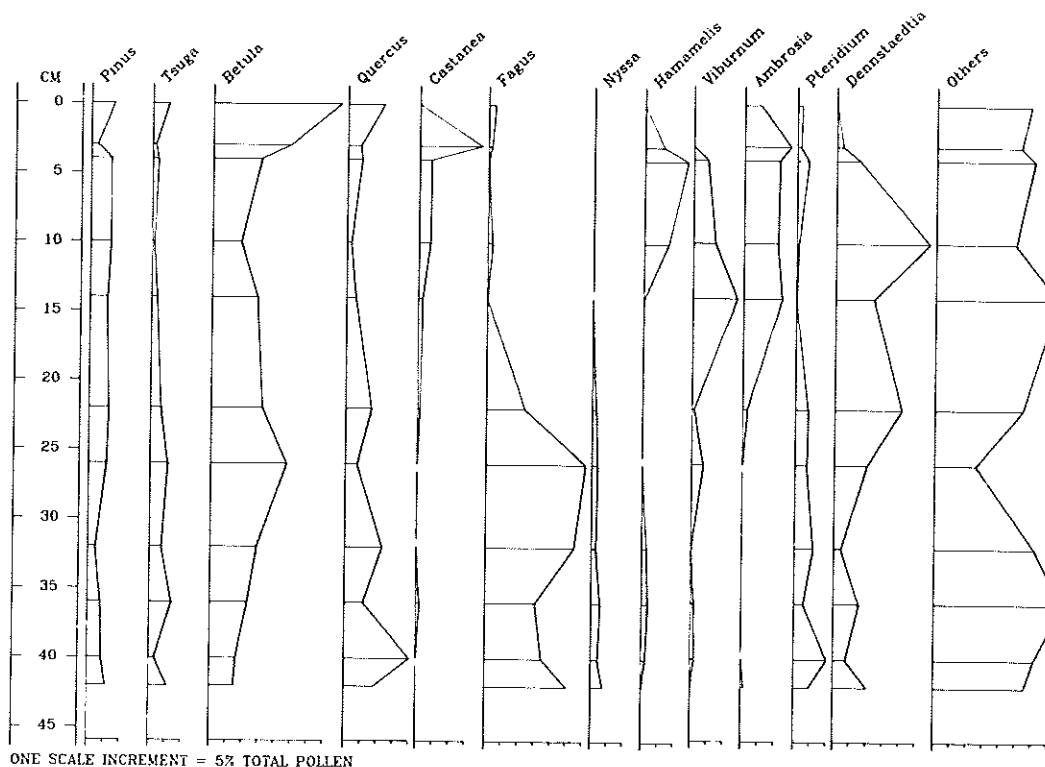


Fig. 4. Pollen diagram for Hemlock Stand Hollow. The only sediment type present was humified peat. Major contributors to 'Others' included Compositae, *Fraxinus*, Gramineae, *Ilex*, *Lycopodium*, *Carpinus-Ostrya*, *Salix*, and Polypodiaceae.

Discussion

The pollen diagrams from the humus sites cover a time-period comparable to that for the reconstructed basal areas (Fig. 5) of forest-dominants presented by Oliver & Stephens (1977) for an adjacent 0.36 ha rectangular plot (Stephens' Plot, SP). Oliver and Stephens related changes in basal-area estimates to the elimination of chestnut and to logging, allogenic events that are in part recorded in the mor-humus profiles.

The *Castanea* decline and the subsequent rise to dominance of *Tsuga canadensis*, *Betula lenta*, *Acer rubrum*, *Quercus rubra*, and *Q. alba* (Fig. 4) are discernible in section B and in SP, whereas in section A, *Betula* pollen became far more abundant than *Tsuga* pollen. In the present vegetation around site A, *B. lenta* and *A. rubrum* are dominants, and *Tsuga*

is of minor importance. Thus the pollen sites are resolving a former pattern in the forest vegetation not detectable in the single plot of Oliver and Stephens. In contrast, the 1854 logging operation that removed *Pinus strobus* and some *Castanea* (Oliver & Stephens 1977) was not recorded in the humus sections. Section B lost its *Pinus strobus* at the time of the *Castanea* blight and has detected recent increases in nearby *Pinus* populations. *Pinus strobus* was never an important tree at or close to site A.

The datasets imply that the forests prior to the *Castanea* decline were open in structure. SP had low total basal area, and the humus sections sampled significant proportions of pollen indicative of open ground. The humus sections alone illustrate the local pattern of *Castanea* dominance at the ridge top and *Castanea-Pinus* co-dominance at the lower elevation site. While the strong influence of allogenic events

STEPHENS' PLOT: BASAL AREA

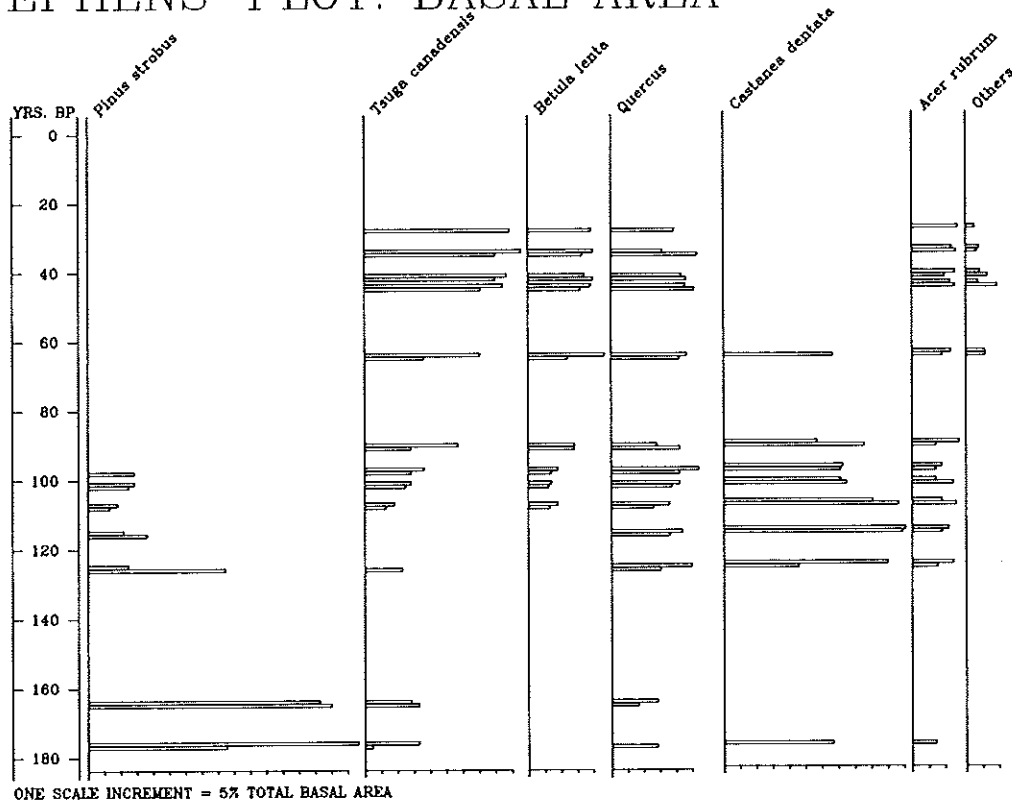


Fig. 5. Changes in basal areas (%) of forest dominants in Stephens' Plot over 180 years. Similar trends are expressed when the data are plotted in absolute units. (Based on data in Oliver & Stephens 1977.)

on recent forest history is clear in these three records, the humus sections additionally record an autogenic developmental sequence after the *Castanea* decline. This is best expressed in section B where it involves a rapid rise in values of *Betula* pollen, followed by more gradual increases in *Quercus* percentages, and then an increase in *Tsuga* pollen, which is reflected in the present-day dominance of *Tsuga* trees growing around site B.

Kelty (1986) documented the fast growth of hardwood species (particularly *Quercus rubra*) after a major canopy-disturbance in the Harvard Forest. The rate of increase of *Tsuga canadensis* basal area gradually accelerated as the growth of the hardwood canopy closed, and a similar process is probably recorded by the pollen from section B. Therefore, the present *Tsuga* dominance is not purely the result of an allogenic process but rather arises from a combi-

nation of allogenic factors and such autogenic factors as changing relative growth rates, shading, and competitive interactions. Jacobson & Bradshaw (1981) present a mor-humus profile from southeastern Massachusetts showing a similar sequence in which *Tsuga* has recently achieved dominance over *Quercus* and *Acer rubrum* after the *Castanea* decline. Such changes may therefore be of widespread regional occurrence.

The HSH diagram suggests that the *Castanea*-dominated forests themselves were a short-lived vegetation type because *Castanea* populations increased only after the major decline of *Fagus*, which occurred simultaneously with colonial landscape modification. These major changes took place during the past 250 years and indicate the dynamic nature of the post-settlement forests of the region. However, it may not be justified to infer that a simi-

lar high degree of change characterized earlier times.

Such major changes in forest dominants occurring over short time-periods are surprising to find in forests known never to have been clear cut and put into agriculture. The relative importance of predictable autogenic processes and chance allogenic factors in controlling forest composition has implications for the success of forest-simulation models describing forest change (Shugart *et al.* 1981).

Sites that collect time-sequences of pollen under closed forest canopies have certain assets and problems when compared to more conventional methods of studying successional processes. Our studies at Harvard Forest show that fine-scale patterns of vegetation change can be resolved over distances of 200 m within a forest. The records came from 8 cm of mor-humus and associated soil. Deeper and older deposits occur in northwestern Europe and perhaps at places in northern North America. Therefore, much potential remains for further investigations. However, mor-humus records do not permit age-class analyses and direct study of structure and density of vegetation. Further limitations include the taxonomic resolution of pollen data and the complex relationships between pollen and the abundance of tree species. Insights from the potentially long time-scale of mor-humus profiles, together with spatial precision, outweigh some of these problems.

Further insights into successional processes in the forests of central Massachusetts would result from the examination of humus sequences in a network of sites incorporating abandoned, reforested fields. Such a study would allow an evaluation of autogenic successional processes to complement the primarily allogenic factors that appear to have been operating in periodically-disturbed forests. Small, closed-canopy sites allow reconstructions of forest vegetation at a scale familiar to plant ecologists and permit the study of small-scale processes such as gap-phase dynamics. These sites also provide linkages between present vegetation and conventional, regionally-based pollen data from lakes and peatlands.

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