Post-Settlement History of Human Land-Use and Vegetation Dynamics of a Tsuga Canadensis (Hemlock) Woodlot in Central New England

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Post-settlement history of human land-use and vegetation dynamics of a *Tsuga canadensis* (hemlock) woodlot in central New England

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Summary

1. The landscape transformation of central New England resulting from deforestation (1750–1860), broad-scale agriculture (1790–1860), and extensive reforestation (1860–present) has exerted a major effect on the structure, function and pattern of the modern forests. However, relatively little is known of the specific nature and extent of these vegetational transformations.

2. Palaeoecological, dendrochronological and historical studies of a primary woodland were undertaken to document the characteristics of the pre-settlement forest, the sequence and type of human activities, and the pattern of subsequent vegetation change. The woodland remained forested throughout the settlement period but was used as a woodlot source of fuelwood, tanbark and building materials. At present the old-age structure of the forest and dominance by shade-tolerant *Tsuga canadensis* (hemlock) gives the appearance of a mature and stable community.

3. The woodlot has changed profoundly in structure and composition during the past 300 years as a result of human activity, natural disturbance and forest development. Ownership history is complex, involving at least 18 different owners from 1740 to 1907. Human land-use includes forest clearance and agriculture in the surrounding area, and repeated cutting of the woodlot. Wind damage, ice breakage and the loss of chestnut to blight are the major natural disturbances.

4. The pre-settlement forest was comprised of old-growth northern hardwoods, hemlock and *Pinus strobus* (white pine). Frequent cutting resulted in the development of a sprout chestnut forest that persisted until a decrease in cutting and the onset of the chestnut blight allowed the emergence of hemlock as the dominant species.

5. The modern forest, although seemingly mature and stable, is unlike any preceeding vegetation and is a poor analogue for the pre-settlement forest. Many of the species that were common before European settlement are rare on the site today and uncommon in the landscape.

6. The forest landscape of central New England effectively conceals the extent of the historical changes that have occurred. An interdisciplinary approach is necessary to evaluate the forces underlying these changes, the nature of the vegetation transformations, and their consequences in the modern landscape.

Key-words: deforestation, forest dynamics, human disturbance, palaeoecology, primary woodland

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Introduction

The complete transformation of the landscape of eastern North America by logging, land clearance and agriculture during the eighteenth and nineteenth centuries has been well recognized by historians and ecologists (Torrey & Allen 1906; Fisher 1933; Raup 1966; Cronon 1983). In central New England, 50–80% of the forested uplands were converted to pasture, hay fields and tilled land by the mid-1800s and supported thriving agricultural activity based on livestock and crop production (Bidwell & Falconer 1941; Black & Brinser 1952). In the late 1800s and early 1900s, urban manufacturing jobs and homesteading opportunities in the fertile mid-western United States lured the population from eastern farms and triggered broad-scale reforestation. Across the New England states 60–85% of the land currently supports forests and in many rural upland towns less than 5% of the landscape remains open (Fig. 1; Baldwin 1942). This legacy of past land-use has affected the structure and composition of the present vegetation (Spurr 1956), its response to natural disturbance processes (Foster & Boose 1992), and its soil and ecosystem characteristics (Fisher 1928; Aber *et al.* 1991). Thus, any attempt to understand modern forests and ecosystem processes requires an understanding of this historical past.

Despite the widespread appreciation of the land-use history and second-growth origins of forests in New England, a detailed understanding of the consequences of this history on the modern landscape has not emerged. Early agricultural and forestry practices generally have been lumped by ecologists into broad general categories and discussed with little regard for spatial precision. Land-use history is often differentiated into gross temporal divisions (e.g. pre-settlement, subsistence agriculture, commercial agriculture, land abandonment and modern periods) that may obscure the complexity and regional variation in these activities (Pruit 1981; Merchant 1989). Major questions remain to be addressed, including:

1. What was the structural and compositional nature of the pre-settlement forests, what type of landscape pattern did these forests form, and what disturbance processes affected them?

2. What are the spatial and temporal characteristics of the human activities that altered these forests and what were the direct environmental and vegetational consequences of these processes?

3. What lasting effects of human and forest history can be detected in the modern landscape?

4. How have these historical consequences shaped our investigations and interpretation of community and ecosystem processes?

The present study seeks to address these broad questions for a specific site in central New England.

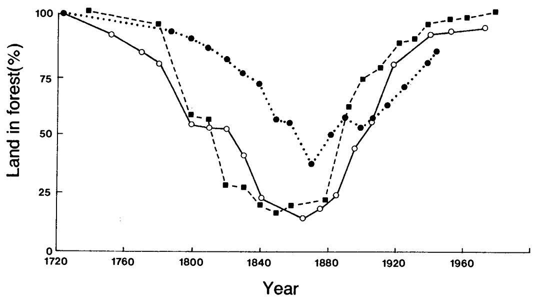

Fig. 1. Historical changes in the extent of upland forest area in the state of Massachusetts (●), town of Petersham (○), and the Prospect Hill tract of the Harvard Forest (■). Modified from Foster (1992).

We utilize a range of palaeoecological, dendrochronological and historical techniques, and capitalize on a wealth of accumulated information concerning the history of forest land at the Harvard Forest in Petersham, Massachusetts. Our study investigates the history of a *Tsuga canadensis* (hemlock) forest (Hemlock Woodlot), portions of a primary woodland (*sensu* Peterken 1981) that remained forested throughout the settlement period but was cut for timber, fuelwood and tanning bark. Currently this woodlot is one of the older stands in this region and has been studied as a possible analogue of the pre-settlement vegetation (Raup & Carlson 1941; Spurr 1956).

Study area

The Harvard Forest is located in north-central Massachusetts in the town of Petersham. The region forms part of the Eastern Highlands of central New England, an undulating upland generally exceeding 250 m a.s.l. Local topography is characterized by a series of north–south ridges and valleys with a relief of approximately 100 m. Soils are largely acidic and formed from glacial till derived from granodiorites and gneisses. The annual temperature is 8·5 °C, the frost-free season averages 5 months, and the annual precipitation is 105 cm with 150 cm of snow (Rasche 1953). Approximatley 90% of the upland area is forested with species typical of the transition hardwood forest zone (Westveld 1956) including *Quercus rubra*, *Acer rubrum*, *Betula lenta*, *Betula papyrifera*, *Fraxinus americana*, *Pinus strobus* and *Tsuga canadensis* (Nomenclature according to Fernald (1970)).

The Prospect Hill tract of the Harvard Forest occupies the northernmost and highest portion of the major ridge extending through Petersham. The tract comprises 380 ha and ranges in altitude from 270 to 420 m a.s.l. The Hemlock Woodlot lies in the centre of the tract in a relatively flat lowland that includes the adjacent Black Gum Swamp, other small wetlands, and lowland forests dominated by *Tsuga canadensis* or *Acer rubrum* (Fig. 2). Variability in relief, depth to bedrock, and the local presence of a fragipan create a highly dissected pattern of soil drainage. The poor suitability of the moist and rocky soils for agriculture appears to be the major factor dissuading farmers from clearing the Hemlock Woodlot or adjoining forests (Raup & Carlson 1941; Spurr 1956; Foster 1992).

Methods

MODERN VEGETATION

A detailed map of a 60-m × 120-m area extending from the edge of the Black Gum Swamp across the Hemlock Woodlot was constructed to locate

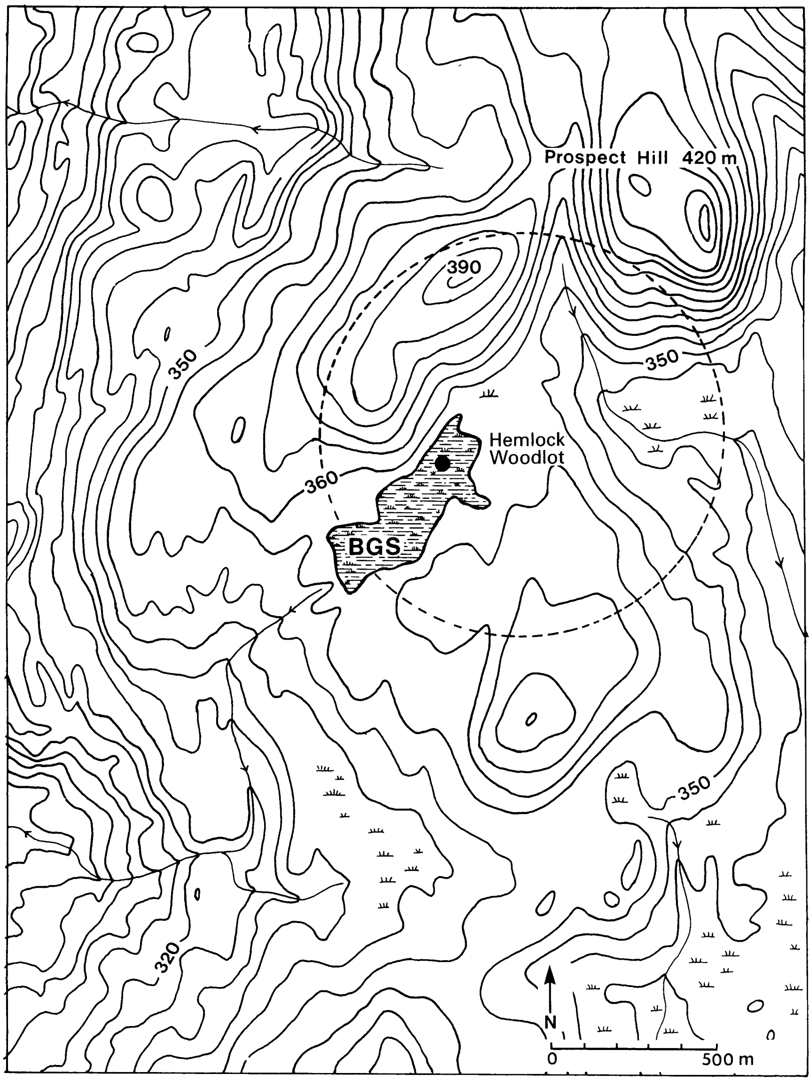

Fig. 2. Topographic map for the Prospect Hill tract of the Harvard Forest showing the location of the Hemlock Woodlot and Black Gum Swamp (BGS). The 500-m-diameter area depicted in subsequent maps (Fig. 8) is outlined. The location of the coring site in the Black Gum Swamp is indicated by a dot.

accurately coring sites, trees, stumps, and tip-up mounds. The plot was surveyed and permanently marked at the borders and trees were mapped using a triangulation technique modified from Rohlf & Archie (1978) (E. Boose & A. Lezberg, unpublished). All objects were permanently marked with either metal tags (trees), or wooden stakes (stumps and tip-up mounds). Trees (stems greater than 5-cm d.b.h.) were classified by species, canopy position, diameter at breast height (d.b.h.), and condition (dead, moribund or alive). Stumps were measured for diameter and height, identified to species where possible and described as cut or broken.

DENDROCHRONOLOGICAL ANALYSIS

Within the 60-m × 120-m plot the 95 largest trees (approximately 30% of the total) were analysed for age and abrupt changes in diameter increment in order to reconstruct the establishment and growth of the overstory. All trees were cored as close to the ground as possible, ranging from 15 to 50 cm above the ground surface. Measurements of annual growth increments were made under a stereomicroscope. Total age was determined and cores were divided into segments of differential growth based on abrupt transitions in ring width (≥50% change in growth over 2–3 years). Average annual growth increment for each segment was determined by dividing the segment length by the number of years. Relative growth rates for each segment of each tree core were assigned to one of five categories of growth based on the comparison of average segment growth rate to average total core growth rate. These include: greatly reduced growth, moderately reduced growth, average growth, moderately increased growth and greatly increased growth. Stand age structure was examined for synchrony of establishment dates.

FOREST AND LAND-USE HISTORY

The history of human activity and vegetation cover was compiled from diverse sources. The ownership history of the Hemlock Woodlot was derived from proprietors' grants, deeds and tax valuation lists. Deeds, sale records and early maps provide information concerning general land-use activity (e.g. woodlot, pasture, tillage and timber rights) that was supplemented by earlier studies (Fisher 1933; Raup & Carlson 1941; Spurr 1956; Foster 1992) to describe the timing of land abandonment, agricultural use and logging activity. Vegetation surveys provide maps and detailed descriptions of forest types for 1909, 1937, 1956 and 1988. A map series of the area within 500 m of the centre of the Hemlock Woodlot was compiled to show changes in vegetation cover (1840–1900) and forest types (1909–1988).

PALAEOECOLOGICAL ANALYSIS

Three sites were selected for stratigraphic analysis of pollen. The upper 50 cm of peat was analysed in the Black Gum Swamp, 200 m south-west of the centre of the Hemlock Woodlot. Previous work has shown that this section contains a regional record of post-settlement history plus a short segment of the pre-settlement record (Zebryk 1991; Foster & Zebryk 1993).

Local vegetation dynamics in the Hemlock Woodlot were examined in two monoliths of the humus profile recovered from sites 40 m apart in the centre of the stand (see Fig. 2). The organic humus was cut down to mineral soil (*c.* 20 cm) and 15-cm^2 monoliths were removed, wrapped in plastic and aluminum foil, and transported to the laboratory where they were frozen. A 2-cm-thick slice from the centre of each frozen core was removed with a band saw and sampled at contiguous 1-cm intervals to remove 1-cm^3 samples.

Pollen samples were processed according to the acetolysis procedure of Faegri & Iversen (1975) as modified by E.J. Cushing (personal communication). A minimum of 300 arboreal pollen grains was counted along evenly spaced transects at 400× magnification, or 1000× for difficult identifications.

Data were analysed in three ways. Standard pollen diagrams were constructed for each profile. Detrended correspondence analysis (DECORANA; Hill 1979) was used to reduce the complexity of these data through the ordination of samples and species based on pollen percentages. Dynamics and differences in the vegetation histories inferred from the two humus profiles were explored further by examining stratigraphic changes in the relative abundance of different pairs of species for the two profiles. This two-dimensional analysis facilitated the comparison of the two stratigraphies, and provided a detailed analysis of changes in the relative abundance of different species by defining temporal patterns of change.

Results

PALAEOECOLOGICAL STUDIES

Regional vegetation change

Major changes in the upland (i.e. non-wetland) vegetation in the Prospect Hill area may be interpreted from the pollen stratigraphy at Black Gum Swamp (Fig. 3, cf. Zebryk 1991; Foster & Zebryk 1993) in four zones:
I. pre-settlement forest (50–33 cm; before AD 1650);
II. extra-regional (i.e. Connecticut River Valley and eastern Massachusetts) settlement and low-intensity agriculture (33–23 cm; *c.* 1650–1740);
III. regional land clearance and extensive agriculture (20–10 cm; *c.* 1750–1860);
IV. farm abandonment, regional reforestation (10–0 cm; *c.* 1860–present).

These zones and the associated vegetational changes correspond well to the known and reconstructed cultural and vegetation history (Raup & Carlson 1941; Foster 1992).

Pollen percentages in the zone of pre-settlement forest are relatively stable. *Pinus* and *Tsuga* are high than at any subsequent period, whereas *Betula* is lower. The inferred upland vegetation is mixed hardwood–conifer forest composed of *Fagus grandifolia*, *Quercus*, *Betula*, *Acer rubrum*, *Castanea dentata* and *Fraxinus americana* with *Pinus* and *Tsuga*. Shrubs and herbs, including ruderals, are very poorly represented.

The next zone is interpreted as representing the early settlement period in eastern Massachusetts and the Connecticut River Valley. Agricultural clearance is suggested by the appearance of Gramineae, ruderals (*Ambrosia*, Compositae, Rosaceae), *Pteridium*, Cupressaceae (cf. *Juniperus communis*), and *Comptonia*.

Zone III is interpreted as indicating regional land clearance and agricultural expansion in central Massachusetts (1750–1860). There was an apparent decrease in forest cover indicated by a decline in most dominants of the pre-settlement vegetation and great increase in weeds including Compositae, *Ambrosia*, Gramineae and *Rumex*. *Betula* continues with high percentages, and aggressively sprouting species such as *Castanea and Acer rubrum* increase.

An apparent increase in the extent of forests across the uplands in Zone IV is indicated by an increase in *Quercus*, *Pinus*, *Tsuga*, *Fraxinus*, *Acer rubrum* and *Acer saccharum* and a decrease in *Betula*, ruderals (*Ambrosia*, *Rumex*, Rosaceae) and old-field and pasture species (Gramineae, Cupressaceae, *Juniperus*, *Ostrya*, *Pteridium*, Cyperaceae). *Fagus* never increased from its post-settlement low and

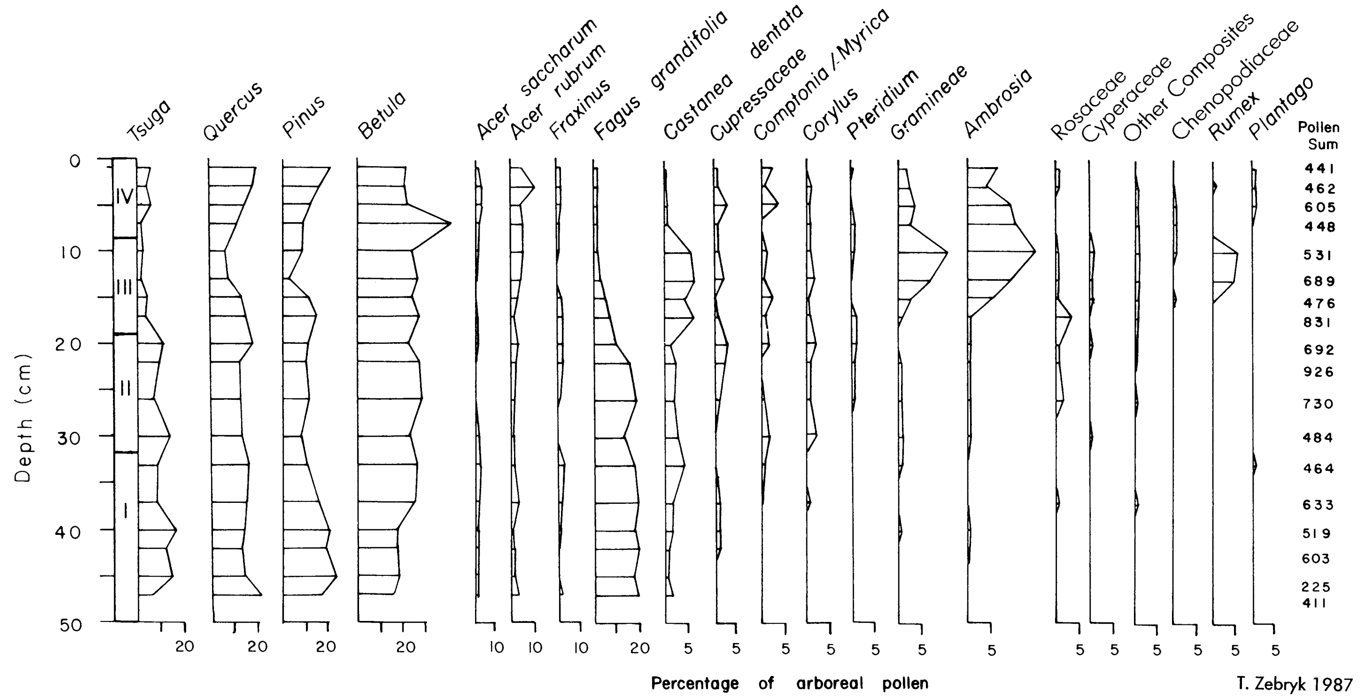

Fig. 3. Pollen diagram for the upper 50 cm of peat in the Black Gum Swamp, Harvard Forest, Mass. Pollen zones referred to in the text are indicated to the right of the depth scale.

Castanea was reduced to <1% by the blight in 1910–15 (Kittredge 1913).

Local vegetation history

The pollen stratigraphies from the two humus monoliths exhibit marked changes in the abundances of different taxa (Figs 4 and 5). Although some closed-canopy sites may receive considerable pollen from extra-local and regional pollen (Calcotte & Davis 1990; Schoonmaker 1992), the large magnitude of the changes in comparison to the Black Gum Swamp, plus high percentages of poorly dispersed grains (e.g. *Castanea*, *Fagus*, *Tsuga* and ferns) indicate

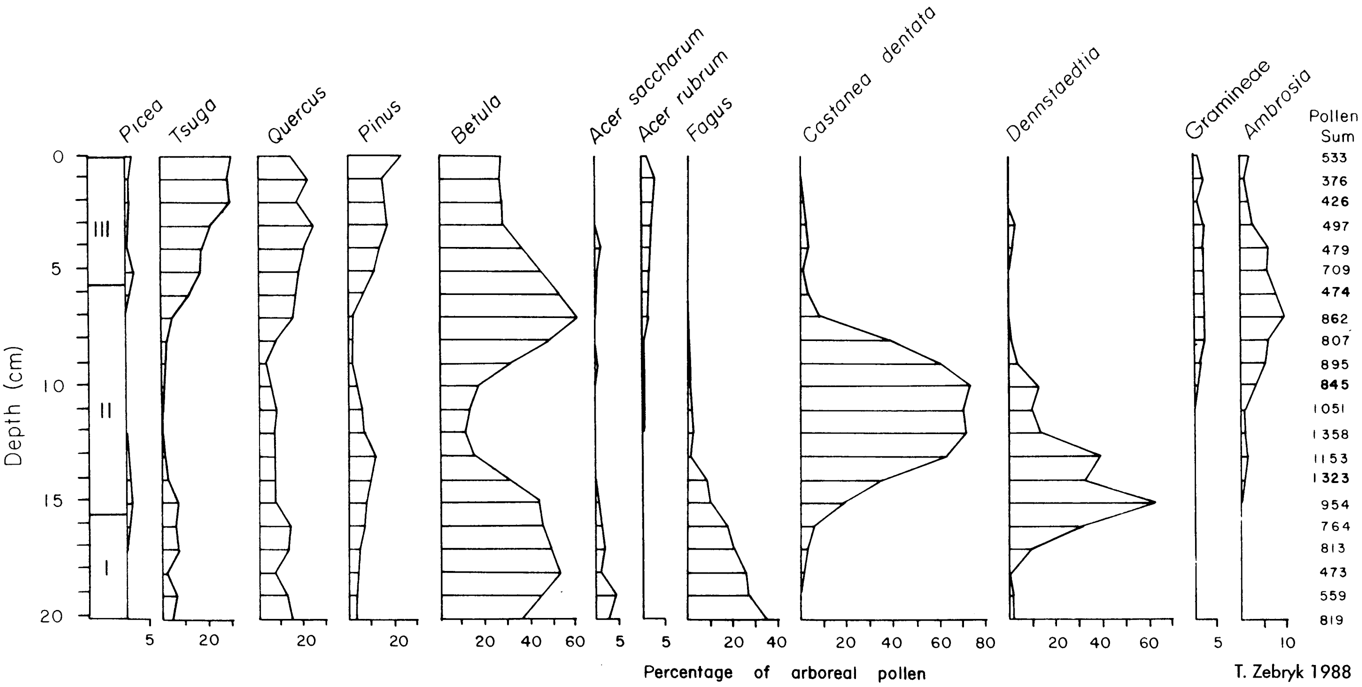

Fig. 4. Pollen diagram for the humus monolith from HWI in the Hemlock Woodlot, Harvard Forest, Mass. Pollen zones are indicated to the right of the depth scale.

that the humus soils collect pollen rain from the local vegetation. The presence of pollen from taxa presumably not located on the site (e.g. Gramineae and *Ambrosia*) enable correlation with regional diagrams such as that from the Black Gum Swamp. The close correspondence between the two humus stratigraphies verifies the reproducibility of local pollen records and suggests that the vegetation changes were similar within this small portion of the woodlot (Fig. 6).

Three zones may be distinguished in the humus stratigraphies based on: (I) the early period of very low *Castanea* abundance, (II) the broad expansion, peak and decline of *Castanea*, and (III) the upper period of very low *Castanea* values (Figs 4–6). The lower zone includes substantial pollen of *Betula*, *Fagus* and *Quercus* and lesser amounts of *Tsuga*, *Pinus strobus* and *Acer saccharum*. This assemblage suggests a northern-hardwood–*Tsuga*–*Pinus strobus* forest (cf. Nichols 1913; Westveld 1956) with the *Quercus* and *Betula* presumably represented by *Quercus rubra*, *Betula alleghaniensis*, *B. lenta* and *B. papyrifera*, respectively. Based on the very low abundance of *Castanea*, falling values of *Fagus* and rising values of *Betula* this zone corresponds to BGS Zone II (early post-settlement) or the end of BGS Zone I (pre-settlement). HW Site II appears to include more early samples than Site I.

In HW Zone II *Castanea* rises to greater than 70% of the arboreal pollen and eventually falls to very low levels. Concomitant with the high *Castanea* values are increases in Gramineae and *Ambrosia*. Throughout this zone there is a decrease and then rise in *Picea*, *Tsuga*, *Quercus*, *Pinus* and *Betula*

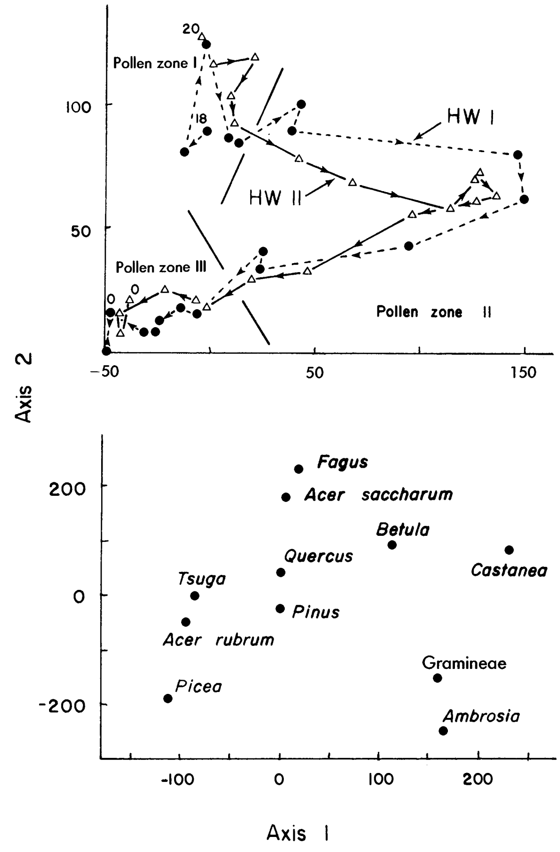

Fig. 6. DECORANA analysis of samples and taxa positions on the first two axes for the humus soil sites in Hemlock Woodlot, Harvard Forest, Mass.: (—•—) HWI; (–△–) HWII (cf. Figs 4 and 5). Adjacent stratigraphic samples are connected with lines and arrows indicating direction from the bottom to top of the cores. Samples falling into the three pollen zones for the woodlot diagrams are indicated.

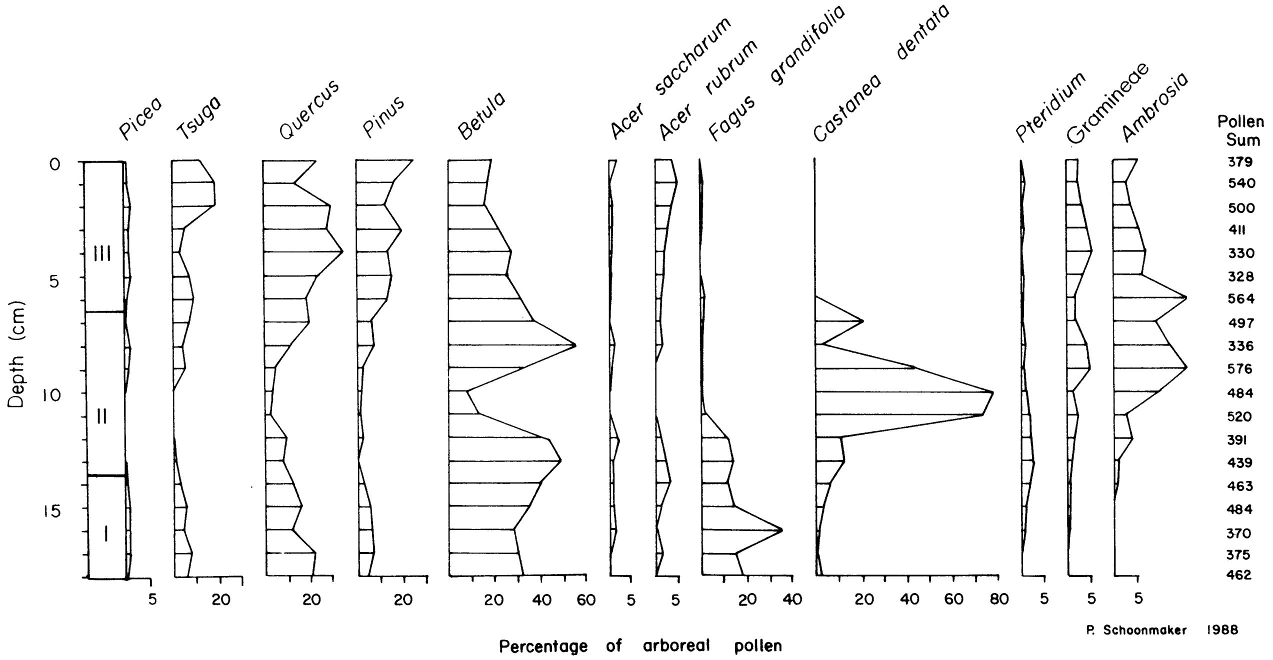

Fig. 5. Pollen diagram for the humus monolith from HWII in the Hemlock Woodlot, Harvard Forest, Mass. Pollen zones are indicated to the right of the depth scale.

and decline in *Fagus*. This zone is correlated with BGS Zone III, marking the intensive regional deforestation and agricultural period of the nineteenth century. Locally in the Hemlock Woodlot, this period appears to be associated with intensive cutting of the forest canopy and widespread sprouting of chestnut.

Following the fall in *Castanea* both cores show a peak in *Betula* followed by a gradual increase in *Picea*, *Tsuga*, *Quercus*, *Pinus* and *Acer rubrum* (HW Zone III). *Fagus* never recovers and occurs sporadically in both stratigraphies. *Acer saccharum* does not return to levels reached in the lower profile whereas *Ambrosia*, and to a lesser extent Gramineae, decrease throughout this upper section. Recent increases in *Pinus* pollen may represent the maturation and development of nearby (*c*. 300 m) plantations of *Pinus* planted in the 1920s.

Graphs depicting the relative abundance of different pairs of taxa in the humus stratigraphies enable the examination of the relative dynamics of various species and the comparison of the records from the two sites (Fig. 7). The graphs for many species pairs from the two sites confirm the similarity of the stratigraphies on a taxon level as movement and location of samples are very similar. Close similarities exist between the behaviours of samples from 14, 10 and 6 cm deep in HWI and 12, 10 and 4 cm in HWII, respectively, suggesting that they are temporally synchronous. This conclusion indicates that organic accumulation rates have been variable but roughly similar at the two sites. Species pairs exhibit a number of interesting relationships including (i) a strong tendency towards reciprocity (e.g. *Betula* and *Castanea*) or (ii) replacement (e.g. *Castanea* and *Tsuga*, *Pinus* and *Fagus*), and (iii) parallel trends in abundance (e.g. *Pinus* and *Quercus*, *Betula* and *Fagus* in the lower part of the cores).

LAND-USE HISTORY AND VEGETATION PATTERN

Information on the settlement history and forest clearance for the period 1738–1860 may be reconstructed from ownership records and deed transfers and the scattered vegetational information contained therein. Like most properties in the northern part of Petersham, the Hemlock Woodlot changed hands frequently; a total of 18 separate owners possessed the property between its original survey for the second Proprietor's Grant of 1738 (cf. Raup & Carlson 1941) and 1907 when it was purchased by Harvard University (Appendix 1; Foster 1992). The size of the parcel and the amount of accompanying land in possession of the owner varied greatly over time. Originally a 47-ha grant, the lot was split to 7·7 ha in 1793. Throughout the 1800s the individuals who owned the area evidently used it as a source of lumber, cordwood, poles or tannin for the nearby leather tannery (Foster 1992). The woodlot represented 15–100% of their holdings. In deeds from 1793 to 1885 the area is referred to as forested and it is mapped as woodland in the township map of 1830 (Raup & Carlson 1941). This information strongly suggests that the stand remained forested throughout the settlement period (Raup & Carlson 1941; Spurr 1956; Foster 1992).

Beginning in 1892 the owners of the woodlot combined it with surrounding lots into a large holding (⩾250 ha). This change in lot size is significant as it signals a general shift throughout the region away from intensive agriculture on small holdings to combined agriculture, forestry and land speculation on larger land areas. On these large holdings in the late nineteenth century there was less energy expended and less heterogeneous diversification of the landscape (Black & Brinser 1952; Foster 1992).

Historical records since 1830 document major changes in the vegetation cover as controlled by land-use and ownership patterns. On the 1830 township map the Hemlock Woodlot, Black Gum Swamp and adjoining lowland forest stand out as one of the isolated woodlands within an agricultural landscape (Fig. 8). This uncleared forest occupied soils of poor drainage and restricted areas of well-drained soil within lowlands. Steep slopes and more-gentle uplands to the north-west and south-east were in open pasture and mowings with interspersed tilled fields (Foster 1992).

Throughout 1900 the surrounding agricultural land was reforested as farming activity declined (Fig. 8). Around the Hemlock Woodlot pastures and mowings to the east and then north-west were abandoned first, followed by small pastures and tilled fields to the south. By 1900 essentially all land within 500 m of the Woodlot centre was reforested by natural successional processes. In comparison, approximately 85% of the Prospect Hill tract was forest, as was 80% of Petersham.

Information compiled by researchers at the Harvard Forest adds considerable detail to the vegetation maps for the twentieth century. The Woodlot was mapped in 1909 as part of a broad hardwood forest adjacent to a small stand of *Tsuga canadensis* with adjoining forests of *Pinus strobus* on abandoned old fields and *Picea* forest on the Black Gum Swamp (Fig. 8). Stand descriptions indicate that the Woodlot was comprised of sprout hardwoods (*Castanea dentata*, *Quercus rubra*, *Acer rubrum* and *Betula* spp.) with an understorey of *Tsuga* (Harvard Forest Archives, unpublished data). Abandoned pastures were occupied by poor hardwoods, principally *Betula populifolia* and *Acer rubrum*.

By 1937 many of the old-field hardwoods had been converted to *Pinus* plantations by the forestry staff at the Harvard Forest, leading to an increase

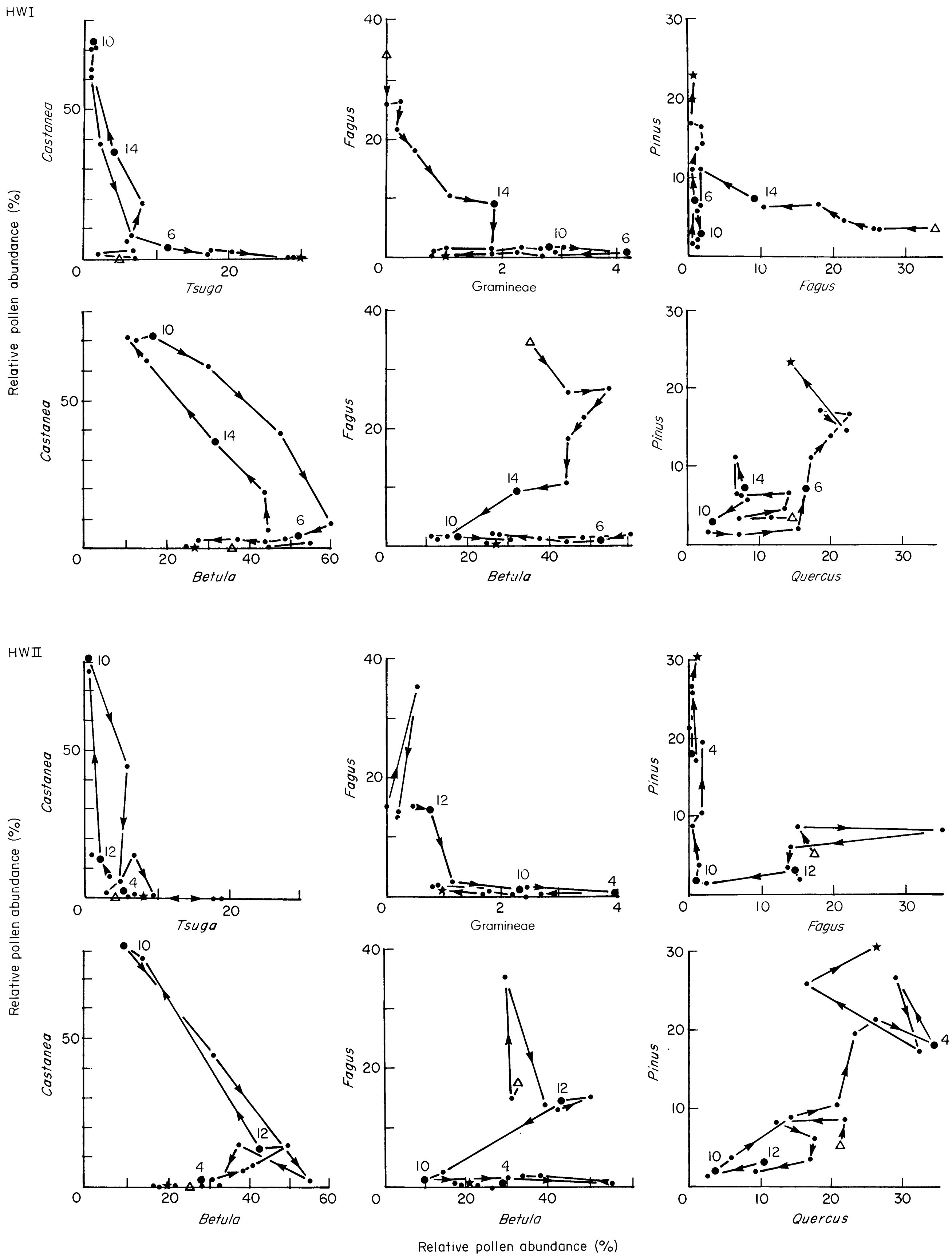

Fig. 7. Graphs depicting stratigraphic differences in the relative pollen abundances of different taxa at HWI and HWII in Harvard Forest, Mass. Adjacent stratigraphic units are connected by a line. Arrows indicate direction of more recent sample. Numbers indicate the location of samples at 14, 10 and 6 cm for HWI and 12, 10 and 4 cm at HWII. Open triangles indicate the position of the lowermost sample and stars mark the uppermost sample.

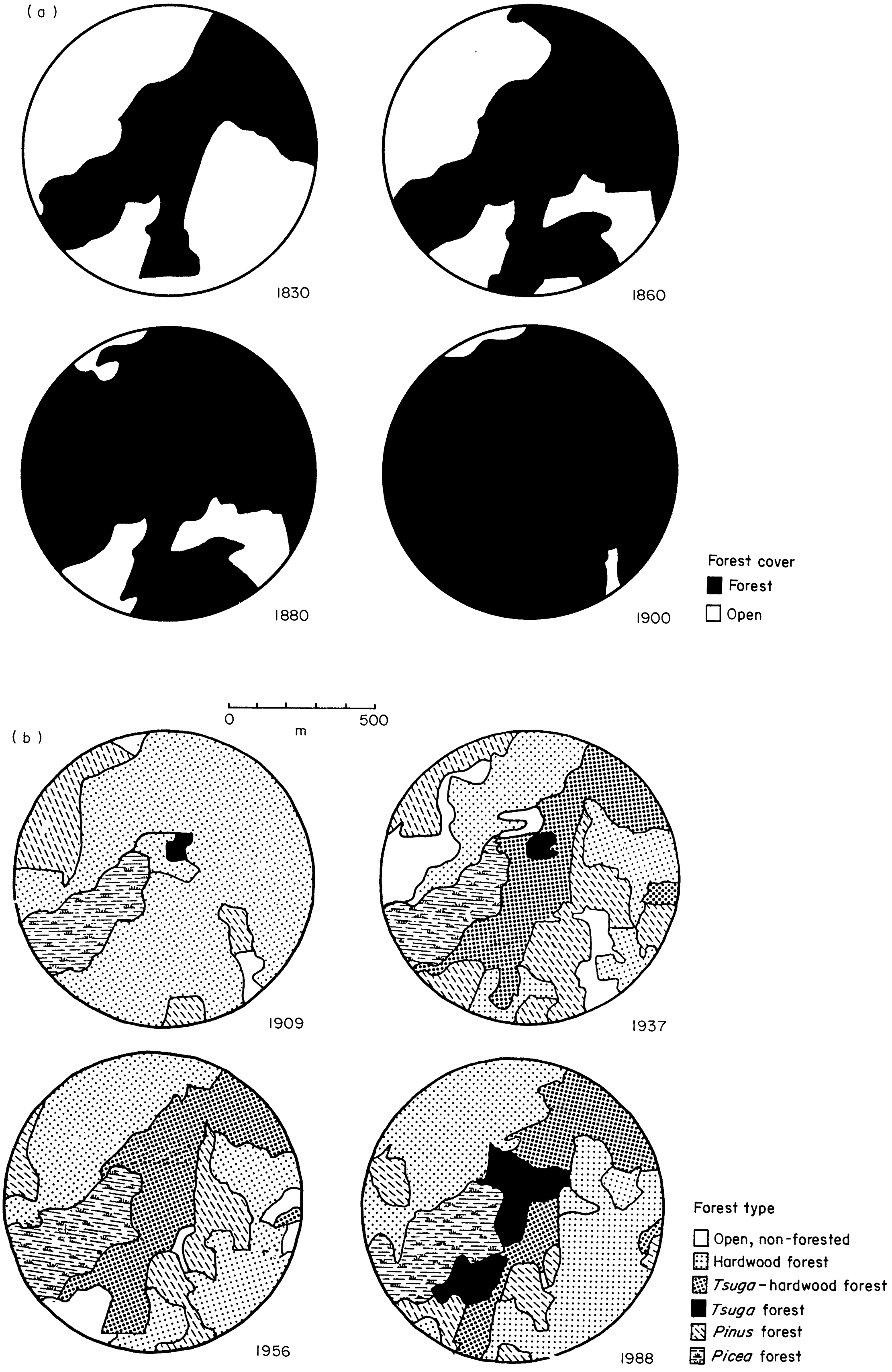

Fig. 8. Maps depicting (a) forest cover (1840–1900) and (b) forest types (1909–1988) within 500 m of the Hemlock Woodlot, Harvard Forest, Mass. Refer to Fig. 2 for location and topographic information.

in *Pinus* and open areas ready for planting. In the Hemlock Woodlot cordwood cutting and elimination of *Castanea* by blight had released the understorey *Tsuga* to form a *Tsuga*–hardwood forest. Since 1937 there has been a continual increase in the area of *Tsuga*–hardwood and *Tsuga* forest such that they occupy nearly all of the uplands that had been in forest cover in 1840 (Fig. 8). *Pinus* forest decreased during this period due to the impact of a hurricane in 1938 and other natural disturbances, although local plantations of *Pinus* established in the 1920s are currently mature (Foster 1988). Within the hardwood forest there has been a decrease in *Betula populifolia* and increase in *Quercus rubra* and *Acer rubrum* (Spurr 1956; Foster 1992).

Historical information on logging activity in the Hemlock Woodlot extends back to the 1870s with the extensive cutting of hardwoods and *Tsuga canadensis* (Appendix 2). Subsequently the stand has been thinned at least three times to remove *Castanea* poles (1893, 1900 and 1913) and damaged lightly by an ice storm in 1921, the hurricane of 1938 and by a moderate windstorm in 1941. The stand was thinned or salvaged for cordwood in 1930, 1940, 1949 and 1957. During the past 30 years the windthrow of a group of four or five *Tsuga* on the edge of the stand and single tree gaps within the stand are the only disturbance.

MODERN VEGETATION

The Hemlock Woodlot was mapped in 1990 as part of a 4-ha *Tsuga* forest (Fig. 8) with a basal area of 40 $m^2 ha^{-1}$ and density of *c.* 760 stems ha^{-1} for living trees and 257 stems ha^{-1} for standing dead trees (Table 1). *Tsuga* is dominant in density (65%) and basal area (62%) and is well represented in all size categories. *Pinus strobus* occurs as a small number of large stems, *Acer rubrum* and *Picea rubens* have many small stems. *Betula lenta*, *Quercus rubra*, *Betula papyrifera* and *Fagus grandifolia* occur in lesser numbers. *Castanea* stumps are scattered across the area.

AGE STRUCTURE

The age distribution of the forest is highly asymmetrical and indicates an even-aged stand with a few older individuals (Fig. 9). Approximately 6% of the trees are spread across the age classes from 150 to 220 years, 85% occupy the range from 100 to 150 years, and 8% are less than 100 years old. A peak in establishment (43% of the trees sampled) occurred from 1865 to 1880. *Tsuga canadensis* occurs in all age classes and *Picea rubens* has a wide range in ages, whereas all of the *Pinus strobus* and *Acer rubrum* sampled are less than 125 years old. No trees date to the period from 1830 to 1860.

CHANGES IN GROWTH RATE

Dendrochronological analysis enables the identification of decadal periods in which trees in the Hemlock Woodlot show major changes in rate of

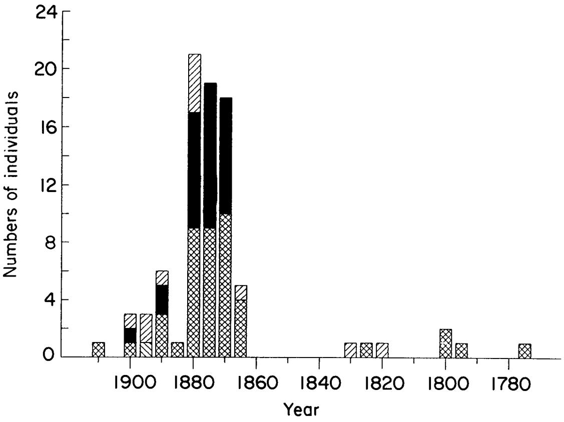

Fig. 9. Age distributions of the 95 largest trees in the 60-m × 120-m plot in the Hemlock Woodlot, Harvard Forest, Mass., showing *Tsuga canadensis* (▩), *Pinus strobus* (■) and other species (▨).

Table 1. Current vegetation of the Hemlock Woodlot, Harvard Forest, Massachusets, as based on a complete tally of a 60-m × 120-m mapped area

	Density (stems ha^{-1})		Relative density (%)		Basal area ($m^2 ha^{-1}$)		Relative basal area (%)	
Species	live	dead	live	dead	live	dead	live	dead
Tsuga canadensis	497	171	0·65	0·64	24·69	5·44	0·62	0·53
Pinus strobus	57	32	0·07	0·12	9·14	3·24	0·23	0·32
Picea rubens	50	21	0·07	0·08	2·02	0·47	0·05	0·05
Acer rubrum	101	22	0·13	0·08	2·82	0·21	0·07	0·02
Betula lenta	36	3	0·05	0·01	0·57	0·04	0·02	<0·01
Quercus rubra	8	3	<0·01	0·01	0·59	0·36	0·01	0·04
Betula papyrifera	4	0	<0·01	0	0·25	0	<0·01	0
Betula alleghaniensis	6	1	<0·01	<0·01	0·07	0·01	<0·01	<0·01
Fagus grandifolia	4	4	<0·01	0·02	0·06	0·19	<0·01	0·02
Total	763	257	1·00	1·00	40·21	9·96	1·00	1·00

growth. Because of the overwhelming dominance of *Tsuga canadensis* and *Pinus strobus* in the stand, growth responses in these species are identified separately, whereas all other species are grouped (Fig. 10). A large percentage of the trees present show an increase in growth rate ('release') in the periods: 1870–80, 1910–30 and 1940–50. These releases correspond to episodes of heavy cutting (1870–78), *Castanea* blight (1913–20), and the 1938 hurricane (Appendix 2), which presumably all resulted in improved light conditions for understorey trees and saplings. Many of the larger and emergent *Pinus strobus* were damaged by the 1938 hurricane and exhibit a decline in growth (1930–40). These same *Pinus strobus* recover in the period 1940–50, thus showing a 'release'. In addition to the decline in growth rate in 1930–40, there are decreases in 1880–1910 and 1950–70. The period of reduced growth rate in the nineteenth century is attributed to suppression by rapidly growing sprout *Castanea*. In the period 1950–70 the only known disturbance was a selective removal of a few hardwood trees. Continued competition within the stand could also explain the trend of reduced growth.

Discussion

STAND HISTORY AND THE DEVELOPMENT OF THE MODERN FOREST

The development of the current stand is the result of repeated disturbance by cutting, selective mortality, and natural disturbance that altered the abundance of taxa in the original forest and eventually led to the establishment and gradual ascendency to the canopy by *Tsuga canadensis*, *Pinus strobus* and hardwoods. During the past 250 years the stand has undergone remarkable transformations in structure and composition. Within this period the dominant species in the canopy have changed at least three times.

Pollen evidence from humus soils suggest that the original forest in the Hemlock Woodlot was dominated by northern-hardwood species, with *Fagus grandifolia*, *Betula alleghaniensis*, *B. lenta*

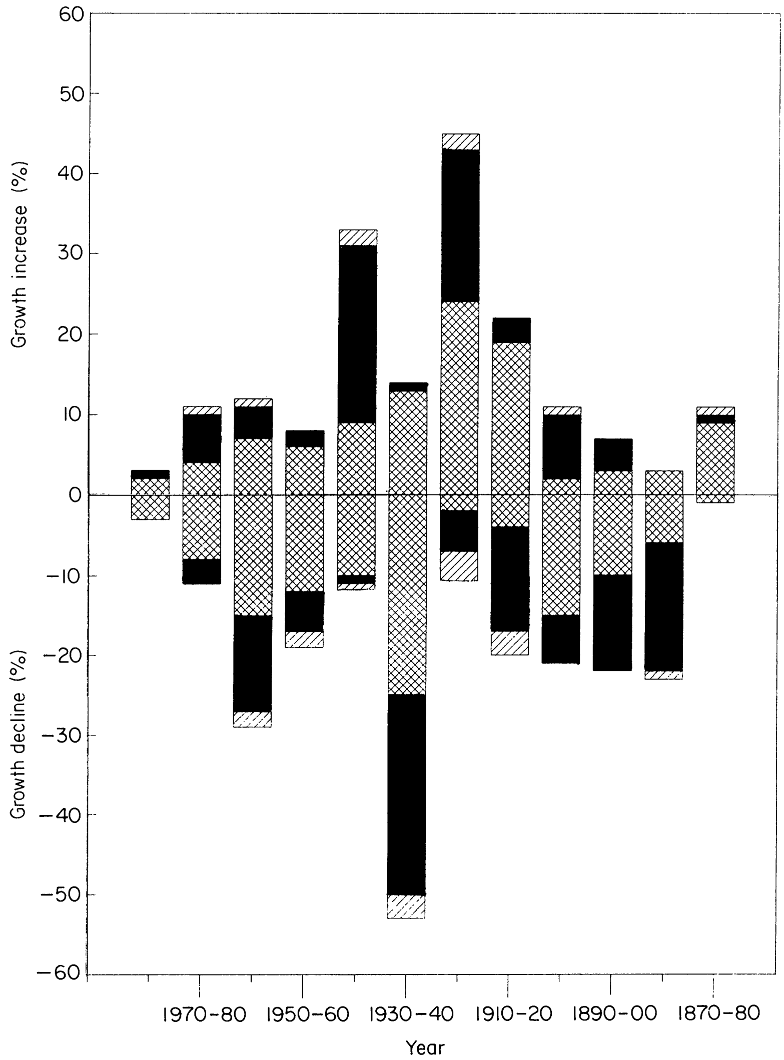

Fig. 10. History of growth increases and decreases in the Hemlock Woodlot, Harvard Forest, Mass., compiled from the 95 largest trees on the 60-m × 120-m plot. Taxa indicated include *Tsuga canadensis* (▩), *Pinus strobus* (■), and other species (▨).

and *Quercus rubra* accompanied by *Acer saccharum* (Foster & Zebryk 1993). *Tsuga canadensis* and *Pinus strobus* were present. This assemblage resembles the northern-hardwood–*Tsuga*–*Pinus strobus* forest, which is characteristic of moist, low-lying sites sheltered from major disturbance in the modern vegetation (Nichols 1913). Related studies indicate that more than 1000 years had elapsed since the last fire in this area (Foster & Zebryk 1993) and therefore the stand was presumably old-growth and of uneven age. Pollen assemblages of upland taxa recorded in sediments from the adjoining Black Gum Swamp suggest that *Quercus*, *Betula*, *Fagus*, *Acer rubrum*, *Castanea*, *Fraxinus*, *Pinus strobus* and *Tsuga* were common taxa across the uplands. Thus an interpretation of the pre-settlement landscape would include mixed hardwood–conifer forests of *Quercus*, *Betula*, *Castanea*, *Acer rubrum*, *Pinus* and *Tsuga* on the uplands, northern-hardwood–*Tsuga*–*Pinus strobus* forest on the lowlands and *Picea* forests on peaty sites.

Widespread deforestation and agricultural expansion in the late eighteenth century transformed the landscape as nearly all tree taxa characteristic of the pre-settlement forest declined and *Castanea* and *Acer rubrum* increased (Figs 4 and 5). The Hemlock Woodlot was heavily logged and sprout *Castanea* replaced the original forest of northern hardwoods, *Tsuga* and *Pinus strobus*. *Castanea*, which was present in the original stand, was able to capitalize on the open conditions following cutting due to its very rapid growth rate and sprouting ability (Paillet 1988) and was maintained in this forest by repeated cutting for cordwood, poles and tannin. Sprouted *Castanea* begins to flower within a decade so that its pollen representation was maintained through cutting cycles. This local dominance and increase by *Castanea* was evidently paralleled on a regional basis across central New England (Bromley 1935; G. Whitney, unpublished).

The limited extent of woodland cover in the mid 1800s when wood was a major fuel source led to the very intensive use of woodlot areas such as the Hemlock Woodlot. The modern stand origins are traceable to the late 1800s following the last major episode of cutting and paralleling the broad-scale abandonment of farmland and decrease in intensive landscape management. The majority of the trees established following a series of very heavy cuttings in the interval 1870–80, when most of the Prospect Hill area was logged (Foster 1992). The small number of trees pre-dating this event and the establishment of essentially all of the *Pinus strobus*, a species of moderate shade tolerance, suggest that the site was very open at this time. A few trees date to earlier episodes of logging (1765, 1790 and 1830) or possibly the 1815 hurricane (Spurr 1956).

Following the establishment episode in 1870–80 and a modest period of rapid forest growth, there ensued a 40-year period of slow growth in *Pinus strobus* and *Tsuga canadensis*, largely as a result of suppression by the much more rapidly growing *Castanea*. *Castanea* was able to outcompete and suppress the conifers and other hardwoods until it was stricken by the blight.

Hardwoods (*Quercus*, *Betula papyrifera* and *Acer rubrum*), *Pinus strobus* and *Tsuga canadensis* formed the canopy and grew rapidly during the decades after the *Castanea* blight (Fig. 10; HF Archives, unpublished). An ice storm damaged some larger *Quercus* in the stand in 1921 and cordwood thinning of hardwoods occurred in 1930; both events favoured the growth and dominance of *Tsuga* and *Pinus strobus*. A description of the stand after hardwood thinning indicates that the stand was comprised of *Tsuga*, *Pinus strobus*, *Quercus rubra* and *Betula papyrifera* with a crown density of 60% and canopy height of 15 m (HF Archives, unpublished). In 1938 the site was relatively sheltered from the hurricane by its lowland setting; however, field observations and the decrease in growth of many trees suggest that the canopy was damaged (HF Archives). *Pinus strobus* was affected more than *Tsuga canadensis* due to its predominance as an emergent tree and concentration of foliage on exposed branches (Foster 1988). Many subordinate *Tsuga* responded with increased growth immediately (1930–40) and all of the impacted *Pinus strobus* recovered and increased their growth rate in the next decade. In 1946 the stand was described as *Tsuga* (67%), *Pinus strobus* (16%), *Quercus rubra*, *Acer rubrum* and *Picea rubens* (each 5%) and 15–20 m tall (HF Archives, unpublished).

Since the hurricane, selective thinning of primarily hardwoods has led to a continued increase in the relative abundance of *Tsuga*. Thus the longevity of this species, its shade tolerance and ability to respond readily to increased light resources, and the selective removal of hardwoods by cutting, pathogens, ice and wind have resulted in the domination of the stand by *Tsuga*. This process of gradual increase of the classic climax species has been hastened by the selectivity of the natural and especially human factors.

As a result of the differential response of species to the sequence of disturbances that affected the stand, the modern forest is unlike any other that has occupied the site (Figs 4 and 5; Foster & Zebryk 1993). Thus, the appearance of old age, maturity and deep solitude in the *Tsuga* stand give a deceptive impression of stability. Contrary to the earlier suggestions of some ecologists (e.g. Raup 1956), the modern forests on a stand or landscape level have not reverted back simply to a composition and relative abundance typical of their pre-settlement occurrence. Rather, the major cumulative impact of land-use activity has been the nearly complete local elimination of sugar maple, beech and chestnut.

One striking result of the study is a realization that little evidence of the prior vegetation, including the original forest, or past land-use is apparent in the modern landscape. Despite the relatively short time-course of the history of changes that occurred (*c.* three centuries), the modern forest and the approximately 90 years since the last major transformation of the stand effectively obscure these changes. The few stumps that are visible are highly decomposed, difficult to distinguish as cut or natural and difficult to identify without intensive microscopy. This great deceptiveness in the appearance of the forest to the modern investigator highlights the utility of diverse approaches to understanding and characterizing forest communities.

Conclusion

Ecologists are becoming progressively sensitized to the importance of the effect of history on the structure and function of modern communities and ecosystems. However, the present study provides some indication of the extreme complexity of this historical activity and outlines how naively that we as ecologists generally deal with it. Over a period of 160 years the Hemlock Woodlot had 18 different owners. This decadal turnover of ownership provides opportunity for great heterogeneity of land-use practice as the objectives and attitudes of the individuals change. An added element of complexity was the relatively small size of individual land holdings, which led to great fragmentation and diversity of effects on a landscape scale.

For the Hemlock Woodlot this complexity of ownership pattern led to a relatively high frequency of disturbance. Heavy cuttings occurred at least three times and repeated light cuttings an additional six or seven times. The conclusion is that it is inevitable that ecologists will simplify greatly the history of inferred human impacts on the forest. However, a consideration of the extensive and variable nature of human use of the landscape suggests that we bear in mind some understanding of this complexity.

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Appendix 1. Ownership history of the Hemlock Woodlot in Harvard Forest, Petersham, Mass. For each owner the area of the Hemlock Woodlot and total area of land owned on the Prospect Hill tract is provided. If deed records stated that the woodlot was forested this is indicated with an asterisk* after the lot area

		Area (ha)	
Date	Owner	Lot	Total
1738	Proprietor's Grant II to Ephraim Haughton	46·9	46·9
1739	Benjamin Miles	46·9	46·9
1751	Josiah Hinds and Silas Bennett	46·9	46·9
1759	John Chandler, Jr	56·7	56·7
1761	David McClellan	40·2	45·7
1793	James Jackson, Jr	7·7*	24·2
1820	Joel Sanderson	7·7*	19·3
1829	Aaron Brooks, Jr	7·7*	7·7
1830	Lewis and John Peckham	7·7*	59·8
1839	Asa Clark	7·7*	18·7
1856	Jacques Goddard	7·7*	34·3
1873	William Hodges	7·7*	44·8
1885	Mary Russell	7·7*	44·8
1892	Adonai Shomo	246·5	246·5
1897	D. Ambrose Leonard	320·5	320·5
1898	Catherine Leonard	320·5	320·5
1906	James Brooks	342·5	342·5
1907	Harvard University	342·5	342·5

Appendix 2. History of the Prospect Hill Hemlock Woodlot, Harvard Forest, Petersham, Mass. The date and type of disturbance or human activity is listed. Unpublished references from the Harvard Forest Archives are cited by file number

Date	Event	Reference
1738	Land granted to proprietors	
1765	Heavy cutting of adjacent *Tsuga* stand	HF 1946-A
1790	Light cutting of adjacent *Tsuga* stand; *Castanea* stumps noted in deed of 1793	HF 1946-A
1815	Light damage from hurricane	HF 1946-A
1820	Deed notes lot as 'pine woodland'	
1830	Light cut of *Castanea* and *Pinus strobus*	HF 1931-D; HF 1946-A
1870–78	Heavy cutting of *Castanea*, hardwoods and *Tsuga*	HF 1946-B
1893	*Castanea* poles cut	HF 1946-B
1900	*Castanea* poles cut	HF 1931-D
1913	*Castanea* poles cut	HF 1946-B
1914–20	*Castanea* blight	Kittredge (1917)
1921	Ice storm; tops broken on 85-year-old *Quercus*	HF 1931-D
1930–32	Cordwood thinning (36 cords from 3.0 acres): *Quercus rubra*, *Acer rubrum*, *Fraxinus americana*, *Betula lenta*, *Betula papyrifera*, *Castanea dentata* and *Betula alleghaniensis*	HF 1931-D
1938	Patchy hurricane damage; small groups of hardwoods and *Pinus strobus* uprooted; *Tsuga* little damaged	HF 1940-C
1940–41	Salvage cutting of scattered downed trees; 80–90% *Tsuga* left, scattered *Quercus rubra*, no *Pinus strobus*	HF 1940-C
1941	December gale from east; windthrow hardwoods on windward side and adjacent to canopy gaps	HF 1940-C
1949	Chestnut salvage and some hurricane salvage	HF 1949-A
1957	Partial cut to remove hardwoods, favour residual *Tsuga*	HF 1957-B