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DISTURBANCE HISTORY, COMMUNITY ORGANIZATION AND VEGETATION DYNAMICS OF THE OLD-GROWTH PISGAH FOREST, SOUTH-WESTERN NEW HAMPSHIRE, U.S.A.

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SUMMARY

(1) The disturbance history, community organization and vegetation dynamics of old-growth forests in central New England are described using long-term data (1905–1985), age-structure analysis, tree-ring chronologies, stand ordination and fire-scar dating.

(2) The natural disturbance regime is characterized by frequent local events, such as windstorms, lightning, pathogens and fire, and by occasional broad-scale damage by hurricane winds. Site susceptibility to disturbance is controlled by slope position and aspect.

(3) Old-growth vegetation is organized along a complex gradient of soil depth, slope position, and frequency and intensity of disturbance. The even-aged overstorey and presence of shade-intolerant tree species suggests that large canopy gaps resulting from hurricanes and fire were historically important for stand initiation. More local disturbance results in tree-growth responses detected by dendrochronology.

(4) The effect of the 1938 hurricane on the old-growth forests was examined to understand landscape patterns, stand damage, and vegetation development following catastrophic winds. The post-hurricane landscape was a mosaic of differentially damaged stands controlled by physiography, wind direction and pre-hurricane vegetation.

(5) Succession follows the pattern of even-aged stand development. All trees establish within twenty-five years of disturbance. Most hardwood species grow rapidly into the canopy, whereas *Fagus grandifolia* and *Tsuga canadensis*, although establishing contemporaneously, grow slowly as shade-tolerant saplings beneath the hardwoods and then extend into the canopy following subsequent disturbance.

(6) The post-hurricane studies support interpretations, drawn from the old-growth stands, that disturbance processes have been historically important in this region. Disturbances operate in a heterogeneous manner in the landscape: gradients of frequency, severity and type of disturbance are controlled by physiographic and vegetational features.

INTRODUCTION

Questions concerning the historical role of natural disturbance in forests of central and northern New England and the long-term stability of these ecosystems have prompted vigorous discussion (Stephens 1956; Raup 1957; Siccama 1974; Davis 1981; Bormann & Likens 1979a; Russell 1983; Backman 1984) but surprisingly little consensus. Consequently, despite evidence from palaeoecological, historical and vegetational studies suggesting that many of the forests of central New England have been repeatedly affected by windstorms (Perley 1891; Stephens 1955; Flaccus 1959; Henry & Swan 1974; Reiners & Lang 1979), ice storms (Abbott 1952), pathogens (Baker & Cline 1936; Davis 1981, 1983), fire (Belknap 1813; Dwight 1969; Henry & Swan 1974), and short-term climate change (Davis, Spear & Shane 1980), other investigations have concluded that large areas can remain undisturbed for centuries (Egler 1940; Leak 1970; Forcier 1973; Fox 1977; Bormann & Likens 1979a). The result has been the formulation of divergent views of community organization in New England. One view stresses stochasticity, vegetation dynamics and the natural role of periodic, broad-scale disturbance (Raup 1957), whereas the other emphasizes community-level stability, steady-state ecosystem properties and endogenous gap formation (Bormann & Likens 1979b).

Much of this difference in perspective results from real differences among the forests investigated. A gradient of decreasing natural disturbance has been described latitudinally northward and inland from the coast in New England, that is interdependent with the zonation of forest vegetation. Historical sources and geographic patterns of vegetation, climate and aboriginal populations have led to the general view that fire (ignited by lightning and by humans) was historically important in coastal areas (Pitch Pine–Scrub Oak Forest) and in southern New England (central Hardwoods Forest; Fig. 1), decreasing through the region of transition and northern Hardwood Forest in central and northern New England (Bromley 1935; Day 1953; Cronon 1983). Although drastically altered by European settlement this pattern has been largely substantiated by modern studies (Egler 1940; Brown 1960; Niering, Goodwin & Taylor 1970; Lorimer 1977; Bormann & Likens 1979a; Fahey & Reiners 1981) and the few investigations of sedimentary charcoal and pollen (Patterson, Saunders & Horton 1983a, 1983b; Backman 1984).

The incursion of hurricanes into New England similarly exhibits a decreasing frequency inland and to the north (Smith 1946; Neuman *et al.* 1978). The most destructive hurricanes (1635, 1778, 1815 and 1938) extended through central New England; catastrophic wind has, therefore, come to be considered as the disturbance that most strongly affects the vegetation pattern in this region (Cline & Spurr 1942; Stephens 1955; Raup 1957; Bazzaz 1983). The geographical distribution of other natural disturbances (e.g. tornadoes, ice storms, disease, insect outbreak) either has yet to be studied on a regional scale, or is hopelessly obscured by anthropogenic activities.

The uncertainty concerning the disturbance history, organization and dynamics of New England forests suggests a need for further palaeoecological investigation and examination of those few forests that remain relatively undisturbed by anthropogenic activity. The present study, undertaken in remnants of the Pisgah old-growth forest in south-western New Hampshire, explores the structure and dynamics of the vegetation in relation to the disturbance regime.

The Pisgah forest has been the focus of study since 1905 when the first descriptions of the virgin forest were made by R. T. Fisher (Harvard Forest Archives, unpublished). Subsequent vegetation and historical analysis (Branch, Daley & Lotti 1930) were partially incorporated in a description of the factors controlling the structure and distribution of the major forest types (Cline & Spurr 1942). Detailed analysis of a 0·04 ha plot utilizing the forest-reconstruction methods of Stephens (1955) revealed a history of periodic disturbance by fire and windstorm that resulted in the formation of even-aged forests (Henry & Swan 1974). During these and other studies of the Pisgah forest, considerable unpublished data have been assembled in the archives of the Harvard Forest, which owns a portion of the forest. Analysis of these historical data, in conjunction with a new study of the forest, was undertaken to address the following questions: (i) With what frequency, intensity and scale have disturbance processes affected the old-growth forests? (ii) To what extent are the vegetational characteristics of old-growth forests controlled by these disturbances? (iii) What are the generalized patterns of landscape damage and stand

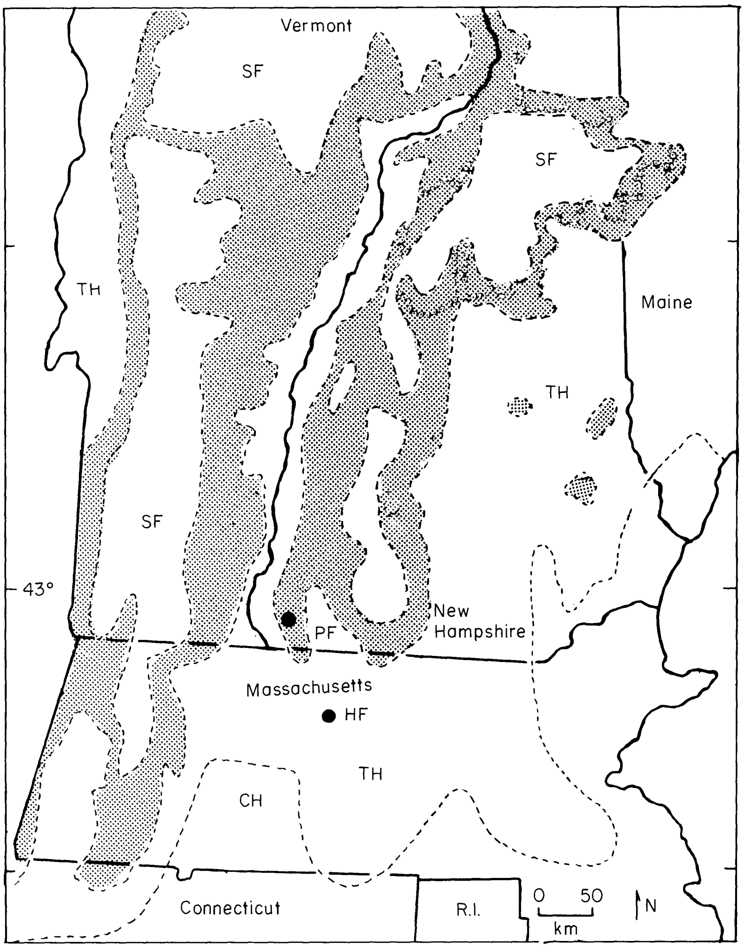

FIG. 1. Central New England, showing the location of sites mentioned in the text and the major vegetation zones, modified from Westveldt (1956). Sites are: HF, Harvard forest; and PF, Pisgah forest. Vegetation zones are: CH, central Hardwoods–Hemlock–White Pine; TH, transition Hardwoods–White Pine–Hemlock; shaded area, northern Hardwoods–Hemlock–White Pine; SF, Spruce Fir–northern Hardwoods.

development following modern disturbances (e.g. the 1938 hurricane), and do these provide adequate analogues for explaining historical information?

STUDY AREA

The study area occupies approximately 2000 ha of the 5300 ha Pisgah State Park in Winchester, south-western New Hampshire (42° 49′N, 72° 27′W) (Figs 1 & 2). Physiographically the area consists of north–south trending hills 200–400 m a.s.l. The bedrock is schist, granite and gneiss, with only shallow glacial deposits. The stony soils are podzolic with a thin leached layer (Simmons 1942). Approximately 100 cm of precipitation fall evenly through the year, and the growing season averages 120 days

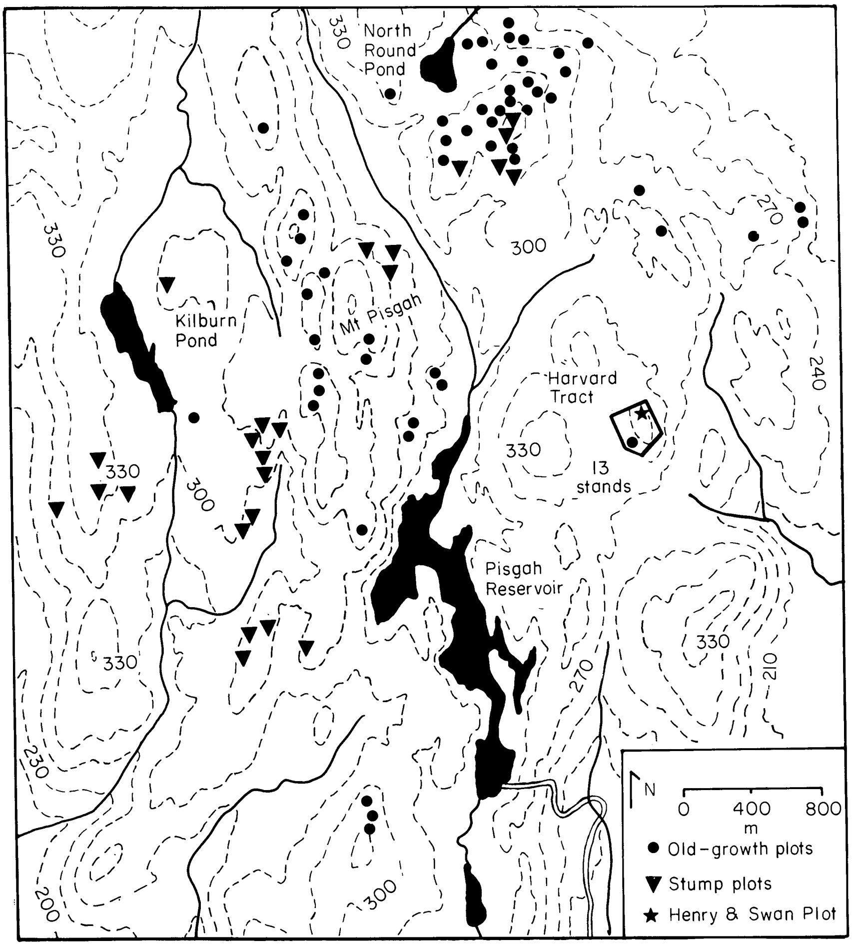

FIG. 2. Topography of the study area (30-m elevational contours) in central New England with locations of the old-growth plots and stump plots investigated in 1929–30, outline of the Harvard Tract and location of the Henry & Swan (1974) plot.

(U.S.D.A. 1941). The vegetation is the southern extension of the northern Hardwoods–Hemlock–White Pine Forest region (Westveldt 1956).

Cultural history of the Pisgah area

The town of Winchester was settled in 1751 and by the 1880s most of the forest was cut except for approximately 300 ha in the Pisgah area (Branch, Daley & Lotti 1930). The Harvard Tract, 10 ha of a large stand of old-growth conifers, was purchased for protection in 1927 (Fig. 2). Large stands of old-growth hardwood forest also survived south of North Round Pond as a consequence of low timber prices. The hurricane of 21 September 1938 severely damaged the Pisgah forest and much of southern and central New England (Fig. 3). In the late 1960s the state of New Hampshire established the Pisgah State Park, an undeveloped area that encompasses the study area.

FIG. 3. The Harvard Tract of the Pisgah forest in 1942, four years after the hurricane. Photograph by S. H. Spurr.

METHODS

Historical sources for the study

Data collected in 0·04-ha plots by R. T. Fisher from 1905 to 1915 provide the earliest information on the Pisgah forest (Harvard Forest Archives, unpublished). The bulk of the historical material for the present investigation comes from an intensive survey in 1929–30 (Branch, Daley & Lotti 1930). That study consisted of two major portions: the sampling of old-growth stands (Old-Growth Study) and a subsequent tree-ring analysis of clear-cut old-growth forests (Stump Plot Study).

In the Old-Growth Study, sixty-one 0·04-ha plots were sampled in the 2000-ha area (Fig. 2) in stands free from human activity. On each plot physiographic information was noted, a detailed soil description was made, and two to five of the largest trees were aged from increment cores. The cause and size of canopy openings were recorded, and approximate ages of disturbances such as windthrow, fire and disease were provided by ageing trees growing on windthrow mounds, dating changes in tree growth, and analysing fire scars on trees (Harvard Forest Archives 1930–1).

The tree cover was sampled by height class. The overstorey (dominant and codominant trees) and middlestorey (intermediate and suppressed trees) were tallied by species and diameter at breast height (dbh). Saplings (individuals 1–15 ft (0·3–4·6 m) tall) and seedlings (less than 1 ft (0·3 m) tall) were tallied by species. Dead or downed trees were tallied by species and dbh and shrubs and herbs were quantified as few, many, or plentiful.

In the Stump Plot Study, twenty-three 0·04-ha plots were sampled in old-growth stands within nine months of logging. Environmental and vegetation data were colleted as in the Old-Growth Study, with the exception that stump diameters were substituted for dbh.

Tree-ring chronologies (in ten-year growth increments) were obtained from 181 overstorey trees which were a minimum of 10 inches (25 cm) in diameter. The age of each tree was calculated using a species-specific adjustment for stump height.

Following the 1938 hurricane, vegetation surveys on the Harvard Tract include the analysis of one 0·04-ha plot (Harvard Forest Archives 1942–1) and a transect (2 m × 110 m) across the tract in which all trees were tallied by species, dbh and height (Harvard Forest Archives 1948–54). In 1968 the pre-hurricane vegetation was reconstructed from the woody litter in a permanently marked 0·04-ha plot and the standing trees were tallied by species and dbh (Henry & Swan 1974).

Analysis of the historical data

Data from the Old-Growth Study were analysed with the classification and ordination programs TWINSPAN and DECORANA (Hill 1979; Gauch 1982). The four height classes (overstorey, middlestorey, saplings, and seedlings) of each species were treated independently in the analyses. Five classes of relative abundance were assigned on the basis of basal area for the overstorey and middlestorey, density for saplings and seedlings, and abundance class for the shrubs and herbs.

Vegetation noda were defined from the TWINSPAN classification according to species, relative abundance and the identification of differential species (Mueller-Dombois & Ellenberg 1974). Based on this larger phytosociological study, the twenty-three stump plots (Stump-Plot Study) were subjectively assigned to noda. The age-structure and the establishment patterns of the 181 canopy trees were examined by species and by plot.

Changes in growth rate recorded in the 181 tree-ring chronologies were plotted as ring width versus time for each ten-year interval. As many similarities among the 181 chronologies were apparent, a simple scheme was used to examine the overall trends in growth based on periods of release or suppression of growth (Stephens 1955; Henry & Swan 1974). For each chronology, every period of growth at least double that of the preceding period was plotted on a time bar as a release for that tree. Conversely, every period of growth less than half that of preceding period was plotted as a suppression for that tree. The cumulative plot of the growth responses for each species from the 181 tree chronologies provides a graph of temporal changes in growth patterns by species.

The regional disturbance history was compiled from newspapers (*New Hampshire Recorder*, Keene, New Hampshire), local histories (Child 1885; Hurd 1886; Keene Historical Committee 1982), land deeds, and meteorological records (Channing 1939; Ludlum 1963; Neumann *et al.* 1978).

Analysis of the modern vegetation

In 1984 vegetation data were collected in 0·04-ha plots on the Harvard Tract (fourteen plots) and at North Round Pond (ten plots) (Fig. 2). Plots were placed subjectively in areas of apparent homogeneous vegetation and site conditions in order to cover the two sites evenly. Trees (>2·5 cm dbh) were tallied by dbh, saplings and seedlings were counted, and in four plots on the Harvard Tract all stems greater than 1·0 cm dbh were cored and aged at 10–15 cm from the ground. At the Harvard Tract the 0·04-ha plot sampled in 1968 by Henry & Swan (1974) was re-analysed.

The extent of damage from the 1938 hurricane was assessed by recording the volume, origin and orientation of all downed wood in each plot. Volumes were calculated for each stem according to Smalian's metric formula: $V = 3{\cdot}9 \times 10^{-5}\ (D0^2 + D1^2)\ L$, where V = volume, $D0$ and $D1$ are basal and top diameters and L = length (Wenger 1984). The 'preservation state' (Harmon *et al.* 1986) of each log was classified as: (i) solid, capable of supporting a person's weight; (ii) partially decomposed, but intact; (iii) decomposed, losing form and integrity (Rowlands 1941). The origin of each stem was classified as windthrown (uprooted), snapped, or unknown (Collins 1956) and the orientation was recorded to the nearest 15°.

To depict the spatial pattern of disturbance from the 1938 hurricane a topographic map was overlain with a map of damage as interpreted from 1939 aerial photographs (1:30 000; U.S. National Archives). Damage was estimated in three classes: (1) undamaged to slightly damaged, with few trees blown down; (ii) moderately damaged, with less than 50% of the trees blown down; (iii) extensively damaged, with more than 50% of the trees blown down and large continuous areas of complete destruction (Rowlands 1941). Windblown trees were mapped, as were agricultural lands and logged areas.

RESULTS

Phytosociology and site conditions of the old-growth vegetation

The sixty-one plots and seventy-six species-types are organized in a phytosociological table constructed by TWINSPAN (Table 1). Stands are arranged in noda (*sensu* Poore 1955) based on the relative abundance of the species (Fig. 4; Table 1).

The noda are arranged along a complex gradient of decreasing frequency and severity of disturbance and increasing soil depth and moisture as interpreted from the stand ordination and surveyors' notes (Figs 5 & 6; Harvard Forest Archives 1930–1). Site characteristics are largely governed by topographic position and exposure. Slope position decreases along the first ordination axis paralleled by a general increase in soil depth. The frequency and severity of disturbance, as indicated from the time of last disturbance, percentage of dead and downed overstorey trees and relative density of shade-intolerant species in the overstorey and middlestorey, decreases from high to low slope positions. Characteristics of the vegetation and sites are detailed below.

Old-growth vegetation types

Nodum I: Pinus–Betula–Tsuga *assemblage*

These stands had a discontinuous canopy of *Pinus strobus* (white pine) and a lower layer of *Betula papyrifera* (paper birch), *Acer rubrum* (red maple) and *Tsuga canadensis* (hemlock). Canopy gaps, created by lightning strikes and windstorms in 1898, 1904 and 1915 reached a maximum size of 30 m × 45 m and were oriented in an east–west or southeast–northwest direction (Harvard Forest Archives 1930–1). All stands were near the crests of north–south trending ridges (elevations 300–400 m), characterized by thin, dry soils. The prevalence of disturbance was indicated by the small diameter of the trees, the high percentage of dead and downed stems and by the presence of many light-demanding, pioneer species (*Betula papyrifera*, *Pinus strobus* and *Prunus pensylvanica*; Table 2).

Nodum II: Pinus–Tsuga–Quercus *assemblage*

The overstorey was composed of *Pinus strobus*, with either *Quercus borealis* and *Tsuga canadensis* or *Acer rubrum* and *Fagus grandifolia*. Many of the *Pinus* were windthrown from the 1898 and 1915 storms (Branch, Daley & Lotti 1930). In comparison with Nodum

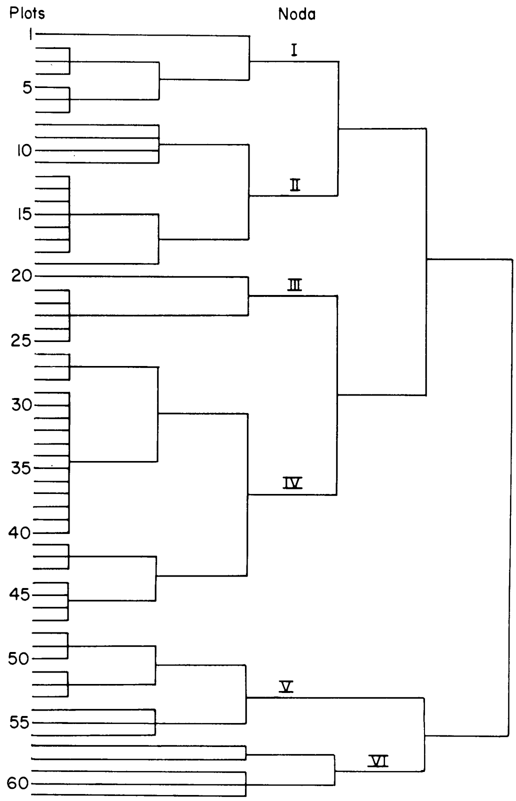

FIG. 4. Cluster diagram for the TWINSPAN output showing relationships between the old-growth plots and noda sampled in 1929 at the Pisgah forest.

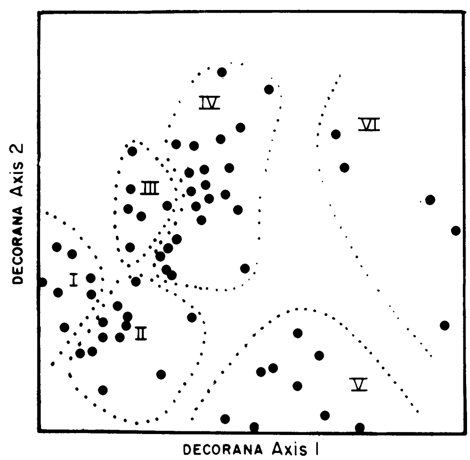

FIG. 5. Stand ordination of the old-growth data at the Pisgah forest on the first two DECORANA axes showing the relationships of the plots in the six noda defined in Table 1.

TABLE 1. Phytosociological table of the old-growth Pisgah forest. Vegetation analysis 1929–30. Each height category of the tree spec
to 5 for overstorey and middlestorey, based on basal area; from 1 to 5 for saplings and seedlings based, on density; and from 1 to 3 fo

[Nodum		I *Pinus–Betula–Tsuga*							II *Pinus–Tsuga–Quercus*												III *Pinus–T* *Hardw*		
Plot Number		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Aspect		W	—	N	W	—	W	W	SW	S	SE	—	W	N	S	—	S	W	—	S	—	NW	—
Species groups and species																							
I	*Betula papyrifera* 3	1	3	2	1	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Betula papyrifera 2	2	2	1	1	1	1	1	.	.	.	.	.	4	.	.	2	.	.	.	.	.	.
	Pinus strobus 2	.	1	2	.	1	3	2	.	3	.	.	.	.	.	.	.	3	3	.	.	.	.
	Pinus strobus 3	.	3	2	3	2	3	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Pteridium aquilinum	.	1	1	1	.	1	1	.	.	.	1	.	.	.	.	1	.	.	.	.	.	.
	Viburnum cassinoides	1	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
II	*Quercus borealis* 1	.	.	.	2	3	3	4	3	3	3	1	.	.	1	1	.	.	.	2	.	.	.
	Castanea dentata 2	2	.	.	.	.	.	.	.	.	.	2	.	.	.	3	1	.	1	.	.	.	1
	Vaccinium angustifolium	.	1	1	1	1	.	1	1	.	1	.	1	1	1	1	1	1	1	1	.	.	.
	Medeola virginiana	.	1	.	.	.	1	1	.	1	.	.	.	1	.	.	1	1	.	1	.	1	.
	Acer rubrum 2	.	1	1	1	1	.	1	1	1	1	.	1	.	1	2	2	2	4	1	.	2	3
	Epigaea repens	.	1	1	1	1	1	1	1	.	1	.	.	1	.	.	.	1	.	.	.	.	1
	Quercus borealis 2	.	.	1	1	.	.	.	.	4	2	.	3	3	2	3	2	4	.	1	.	.	.
	Pinus strobus 1	4	.	1	3	3	.	.	3	3	3	4	5	5	4	5	5	4	5	.	5	5	5
	Polypodium vulgare	.	1	.	1	.	.	.	.	1	1	1	1	.	2	1	1	1	1	.	.	1	.
	Pinus strobus 4	.	.	.	1	.	1	.	1	2	1	1	1	.	1	1	.	.	1	1	1	1	1
	Kalmia latifolia	.	1	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
III	*Picea rubens* 1	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.
	Prunus pensylvanica 2	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Picea rubens 2	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
	Tsuga canadensis 3	5	5	5	2	5	3	3	1	1	2	.	1	.	1	1	1	1	1	.	.	2	3
	Maianthemum canadense	.	1	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.
	Tsuga canadensis 2	1	.	1	1	1	1	2	4	3	4	5	4	5	5	5	4	5	4	1	5	5	5
	Acer rubrum 3	1	2	1	2	1	3	1	.	.	.	.	.	.	1	.	.	.	.	1	2	1	1
	Betula lutea 4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.
	Picea rubens 3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.
	Picea rubens 4	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	4	2	.
	Cornus canadensis	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Coptis groenlandicum	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.
	Betula lenta 3	.	.	1	1	1	1	1	.	.	.	.	.	.	.	.	.	.	.	2	3	3	.
	Gaultheria procumbens	.	1	1	1	1	1	.	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1
	Betula lutea 3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.
	Acer rubrum 4	.	.	.	.	.	1	3	.	.	.	.	1	1	1	.	1	1	.	1	4	4	5
	Betula lenta 4	.	.	.	.	.	.	1	.	.	.	.	2	1	2	1	.	.	.	.	4	4	5
	Tsuga canadensis 1	.	.	.	.	.	1	3	3	3	3	2	1	.	.	.	.	.	.	.	.	2	.
	Tsuga canadensis 4	2	1	2	.	.	.	.	1	2	2	1	1	.	1	2	1	1	1	1	3	4	5
	Viburnum alnifolium	.	1	.	.	.	.	1	.	.	.	.	1	.	.	.	1	.	.	.	.	1	1
	Dryopteris spinulosa	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Chimaphila maculata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
	Acer rubrum 1	.	.	.	.	.	.	.	.	1	.	1	.	.	1	.	.	.	.	1	.	.	.
	Betula lutea 2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
	Mitchella repens	.	1	.	.	.	1	1	.	.	1	.	.	1	1	1	1	1	1	1	.	1	1
	Lycopodium clavatum	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Aralia nudicaulis	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	1	1	1	1	.	.	.
IV	*Betula lenta* 1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	.	.
	Lonicera villosa	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Fagus grandifolia 1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.
	Acer pensylvanicum 5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Fagus grandifolia 2	1	.	.	.	.	.	1	.	.	.	.	1	1	.	2	2	1	1	2	1	1	2
	Fagus grandifolia 3	1	.	.	.	.	.	.	.	.	.	.	.	1	1	.	1	.	.	3	1	.	.
	Fagus grandifolia 4	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	1	.	1	3	.	.	1
	Castanea dentata 4	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
	Aster acuminatus	.	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.
	Castanea dentata 1	.	.	.	.	1	.	1	.	.	.	.	.	1	.	.	.	1	3	1	.	1	.
	Prunus pensylvanica 3	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.
	Acer pensylvanicum 3	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
	Acer pensylvanicum 1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Acer pensylvanicum 2	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.
	Betula lenta 2	3	.	1	1	.	1	1	1	.	.	2	.	1	.	1	.	.	.	.	.	.	1
	Quercus borealis 4	.	1	.	.	.	.	.	.	1	.	.	.	1	1	.	.	.	.	1	.	.	.
	Viburnum acerifolium	.	.	.	.	.	.	.	1	2	.	.	.	.	.	1	.	.	.	.	.	.	.
	Betula papyrifera 1	.	.	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.	.	3	.	.	.
	Acer saccharum 2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Acer saccharum 1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Fraxinus americana 1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Ostrya virginiana	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Acer saccharum 3	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
	Acer saccharum 4	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1	.	.
V	*Fraxinus americana* 3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.
	Tilia americana 3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Fraxinus americana 4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Tilia americana 4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Prunus serotina 4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Polystichum acrostichoides	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Viola rotundifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Additional species (plot no., relative-abundance value): *Acer spicatum* (20,1), *Betula lutea* (49,2; 50,1), *B. papyrifera* 4 (6,1; 7,1), *Castanea dentata* 3 (1,
L. obscurum (29,1; 38,1), *Nemopanthus mucronata* (21,2), *Populus tremuloides* 2 (2,1), *Prunus pensylvanica* 3 (62,1), *Quercus alba* 1 (9,2), *Q. boreal*

…tree species was treated as a separate species-type. The number after the name indicates: 1, overstorey; 2, middlestorey; 3, sapling; 4, see… 1 to 3 for shrubs and herbs, based on Branch, Daley and Lotti (1930) as: 1, few; 2, many; and 3, plentiful. Nomenclature of species f…

III *Pinus–Tsuga* Hardwood					IV *Tsuga*–Hardwood																						V *Castanea–B…*				
21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52
NW	—	W	W	W	—	W	E	W	E	—	E	—	NE	W	W	NW	NW	NW	N	N	N	N	N	N	N	N	NE	N	N	NW	N
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4	5	4	2	1	.	.	1	.	2	.	.	2	1	5	4	.	.	1	1	1	1	.	.	.	1	.	1	.	.	.	.
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…*tata* 3 (1,1; 5,1; 32,1), *Fraxinus americana* 2 (62,1; 71,1), *Goodyera pubescens* (49,1), *Hamamelis virginiana* (20,1; 26,1; 29,1), *Kalmia angustifolia* (57,1), *Ly…* *Q. borealis* 3 (2,1; 4,1), *Ribes* glandulosum (20,10), *Rubus hispidus* (3,1; 20,1; 31,1; 64,1), *Sambucus pubescens* (20,1), *Smilacina racemosa* (55,1), *Tax…* *americana* 2 (62,1).

sapling; 4, seedling. Relative abundance values range from 1
ure of species follows Fernald (1970).

V *Castanea–Betula*							VI Hardwood				
50	51	52	53	54	55	56	57	58	59	60	61
N	NW	N	—	N	N	—	NE	—	E	E	E
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4	3	4	4	3	3	2	3	3	3	3	2
3	3	2	3	3	3	3	3	4	3	1	2
2	1	2	1	3	2	1	3	3	3	1	2
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.	.	.	.	.	.	.	.	1	.	.	.

tifolia (57,1), *Lycopodium annotinum* (57,1), *L. lucidulum* (5,1; 53,1),
nosa (55,1), *Taxus canadensis* (953,1), *Tilia americana* 1 (66,1), *T.*

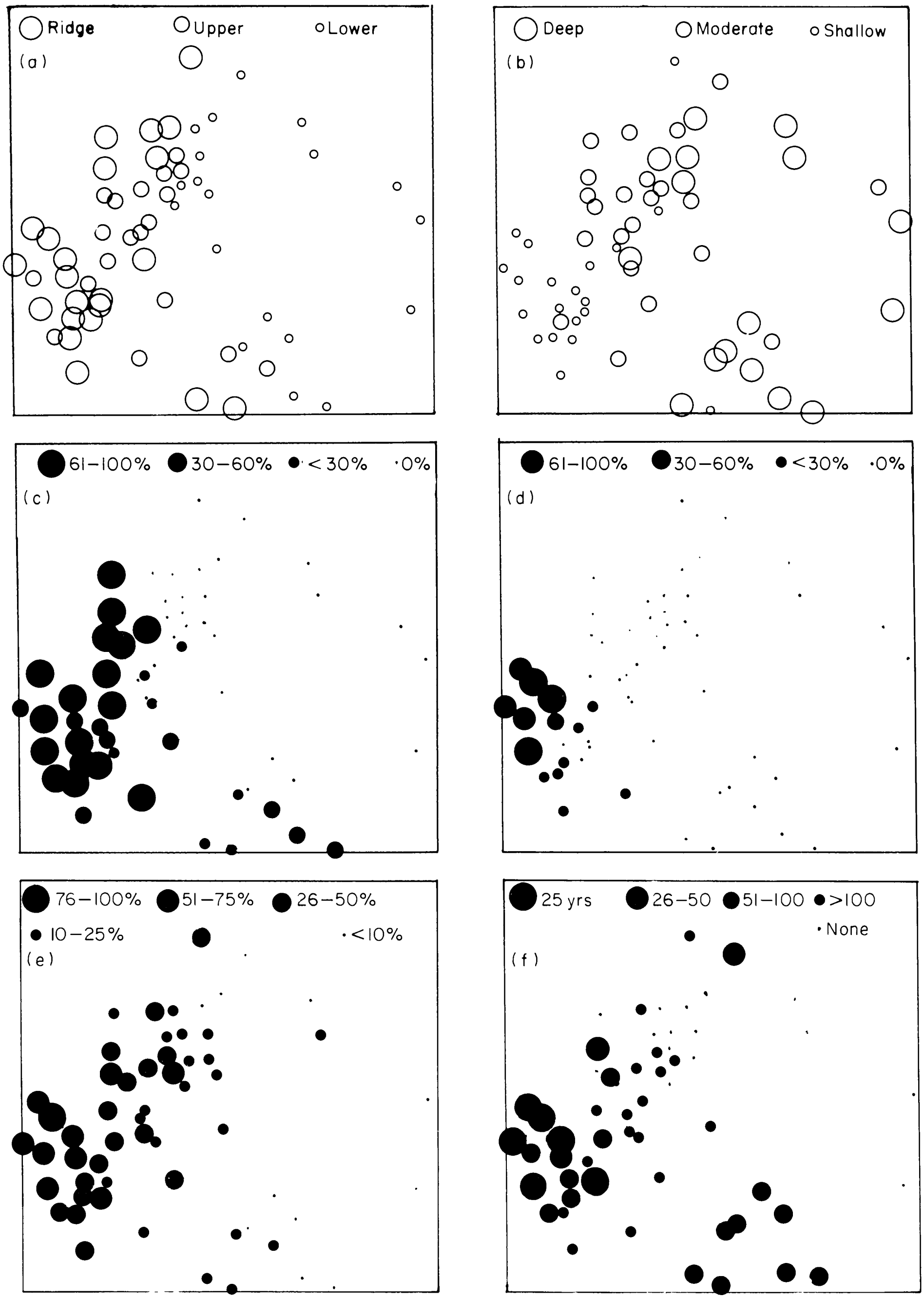

FIG. 6. Site, compositional and historical characteristics of the old-growth stands sampled in 1929 at the Pisgah forest plotted on the first two DECORANA axes. Stand positions correspond to Fig. 5. Plot characteristics: (a) slope position; (b) soil depth; (c) and (d) per cent of intolerant species (*Pinus strobus*, *Betula papyrifera*, *Prunus pensylvanica* and *Populus tremuloides*) in the overstorey (c) and understorey (d); (e) per cent of dead and downed stems of canopy-sized trees; (f) time since last disturbance as noted by Branch, Daley & Lotti (1930).

TABLE 2. Characteristics of the arboreal component in the old-growth stands sampled at the Pisgah forest in 1929.

Nodum	Relative density of dead and downed trees	Relative density of intolerant* tree species	
	Overstorey	Overstorey	Middlestorey
I	0·60 ± 0·21	0·70 ± 0·32	0·63 ± 0·12
II	0·37 ± 0·11	0·65 ± 0·29	0·10 ± 0·08
III	0·35 ± 0·13	0·89 ± 0·13	0
IV	0·25 ± 0·06	0	0
V	0·16 ± 0·07	0·30 ± 0·28	0
VI	0·11 ± 0·06	0	0

* Intolerant tree species: *Pinus strobus*, *Betula papyrifera*, *Prunus pensylvanica*, *Prunus serotina* and *Populus tremuloides*.

I these sites were more protected from prevailing winds, exhibited less evidence of recent disturbance and had fewer pioneer trees.

Nodum III: Pinus–Tsuga–Hardwood *assemblage*

Pinus strobus was the dominant in these stands with *Tsuga canadensis* and *Fagus grandifolia* in the middlestorey. The sites ranged from mid to upper protected slopes and consequently the depth to bedrock was moderate. The old *Pinus* canopy was opened by windstorms in 1915 to form small gaps that were filled by *Fagus, Tsuga* and *Acer rubrum* (Harvard Forest Archives 1930–1). Fire scars were noted in one site and mortality of overstorey trees by porcupine (*Erethizon dorsatum* (L.)) damage was observed in two stands.

Nodum IV: Tsuga–Hardwood *assemblage*

Tsuga canadensis was dominant in all strata of the vegetation and shade-intolerant species were absent (Table 2). *Betula lenta* and *Quercus borealis* occurred in the canopy with *Fagus grandifolia* in the understorey. This assemblage occupied slopes throughout the study area and was sampled in half the plots on the Harvard Tract. In the 1920s small to large gaps in the canopy were opened in six stands through shoe-string fungus (*Armillaria mellea* (Vahl: Fr.) Kummer) mortality of *Tsuga*.

Nodum V: Castanea–Betula *assemblage*

Dead *Castanea dentata* interspersed with *Betula papyrifera* formed a very broken overstorey above a lower canopy of *Fagus*, *Betula lenta*, and *Acer saccharum*. These stands were restricted to the region east and south of North Round Pond (Fig. 2), where they occupied lower to upper slopes with a northern exposure. Fire scars from a light surface fire in approximately 1830 were noted on *Castanea*, *Quercus* and *Fagus* in eight of nine plots. The fire, which resulted in decreased growth and presumably the mortality of many of the hardwoods, was probably responsible for the establishment of the *Acer pensylvanica* and *Betula papyrifera* (Harvard Forest Archives 1930–1).

Nodum VI: Fagus–Acer saccharum–Betula lenta *assemblage*

Betula lenta, *Fagus*, *Acer saccharum* and *Fraxinus americana* formed the canopy on lower slopes with deep soils and eastern or north-eastern exposure. The stands exhibited little evidence of recent disturbance and the hardwood canopy was continuous except for

TABLE 3. Arboreal composition of the old-growth stump plots sampled at the Pisgah forest in 1929. The number after the name indicates: 1, overstorey; 2, middlestorey. Relative abundance values range from 1 to 5 for overstorey and middlestorey, based on basal area.

Nodum		II					III				IV							V				VI		
	Plot	5	27	28	11	22	6	16	20	21	7	9	12	13	14	17	26	18	23	24	25	8	15	19
	Aspect	S	S	S	E	SW	S	SW	W	S	E	SE	SW	SW	W	W	SE	SW	SW	W	SE	SE	SW	SE
	Elevation*	h	r	r	r	r	h	m	h	r	h	m	l	m	m	h	m	r	l	h	h	l	h	m
I	*Betula papyrifera* 2	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
II	*Quercus borealis* 1	.	4	3	2	.	1	.	.	1	.	.	.	.	.	.	.	2	.	.	.	.	.	.
	Castanea dentata 2	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Acer rubrum 2	.	1	.	2	1	.	.	.	1	1	.	.	.	.	.	1	.	.	.	.	1	.	.
	Quercus borealis 2	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Pinus strobus 1	4	5	5	5	5	5	4	5	5	.	.	4	3	4	.	.	3	.	.	.	.	.	.
III	*Picea rubens* 1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.
	Tsuga canadensis 2	2	3	2	1	3	4	4	1	1	1	1	1	1	1	1	1	1	3	1	1	2	2	1
	Tsuga canadensis 1	3	.	.	1	2	.	2	.	.	5	4	5	5	5	5	5	3	.	.	.	.	.	.
	Acer rubrum 1	.	.	.	1	.	.	.	.	.	.	.	.	2	.	.	.	.	2	.	.	.	.	.
	Betula lutea 2	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	2	.
IV	*Betula lenta* 1	1	.	.	1	.	.	.	.	2	.	.	.	1	.	.	.	2	3	.	.	.	1	1
	Fagus grandifolia 1	3	.	.	1	1	1	2	1	4	.	3	.	.	1	.	.	.	1	1	1	4	1	4
	Fagus grandifolia 2	2	1	2	2	2	2	2	1	.	2	1	1	1	1	1	1	2	3	4	4	1	.	1
	Castanea dentata 1	.	.	.	4	.	.	2	.	3	.	.	.	.	.	.	.	5	4	4	5	.	.	3
	Acer pensylvanicum 2	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	1	1	.	1
	Betula lenta 2	2	1	.	1	.	3	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.
	Betula papyrifera 1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Acer saccharum 2	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	2
	Fraxinus americana 1	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.

* r, ridge; h, high slope; m, mid slope; l, low slope.

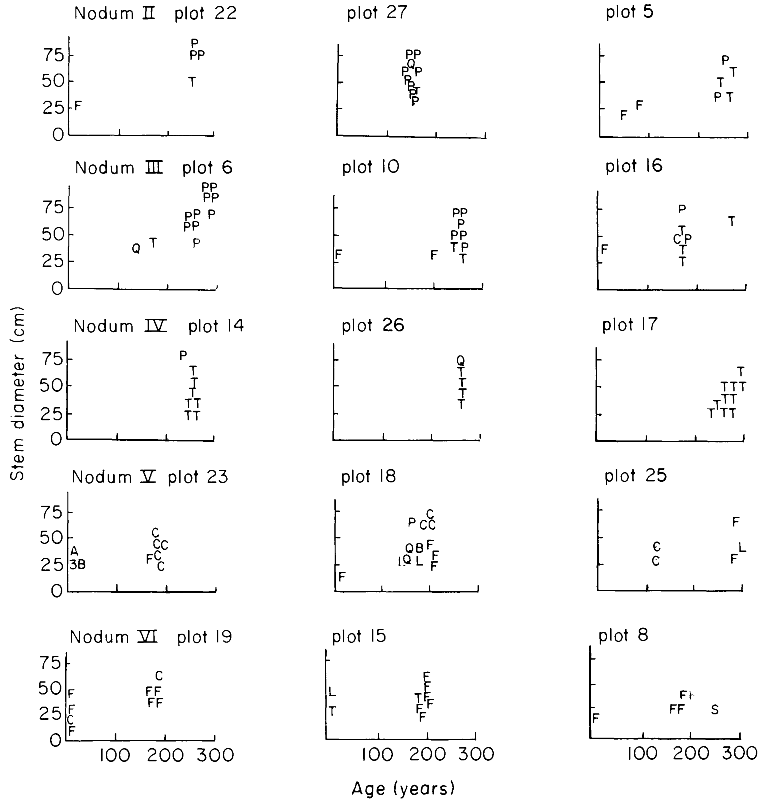

FIG. 7. Age–diameter graphs for trees on fifteen of the twenty-three stump plots sampled in 1929 on the Pisgah forest. Plots are organized by noda. Letters stand for species (T, *Tsuga canadensis*; P, *Pinus strobus*; Q, *Quercus borealis*; C, *Castanea dentata*; B, *Betula papyrifera*; S, *Acer saccharum*; F, *Fagus grandifolia*; A, *Fraxinus americana*; L, *Betula lenta*). Letters along the ordinate indicate the size of undated or poorly dated trees. Only trees which were living at the time of cutting are included.

small gaps. The absence of recent disturbance and the compositional similarity of the overstorey and lower storeys led Branch, Daley & Lotti (1930) to characterize the stands as climax vegetation.

Age structure of the old-growth forests

On the basis of the relative abundance of tree species, the twenty-three stump plots were subjectively assigned to the old-growth noda established from TWINSPAN output (Table 3). Age structure was analysed for a representative sample of fifteen of the stump plots (Fig. 7). Nodum I (*Pinus–Betula papyrifera*) was not sampled; this vegetation had been avoided by loggers due to the small size and poor quality of the timber and limited accessibility to the sites. The overstorey of Noda II–IV is even-aged or composed of two prominent age-classes. In Nodum V the overstorey of stand 18 has an age span of fifty-three years although the *Castanea* and *Fagus* in the other two stands are more tightly grouped in age. *Fagus* is the predominant overstorey in all stands in Nodum VI and is

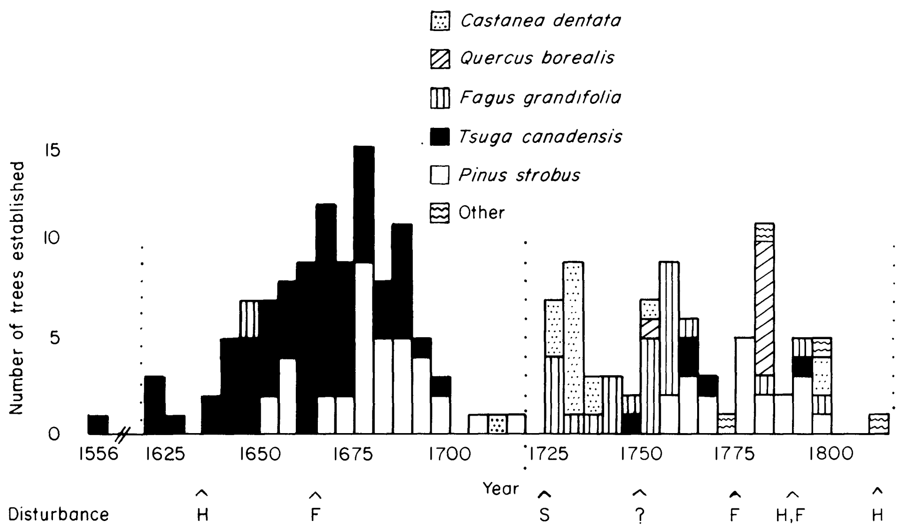

FIG. 8. Establishment patterns for the twenty-three stump plots sampled at the Pisgah forest in 1929. The disturbance history is indicated below the graph: H, hurricane; F, fire; S, windstorm; ?, unknown. The dotted line separates the graph into the two periods (1620–1720, 1720–1820) that are presented in Table 4.

TABLE 4. Overstorey species establishment on the stump plots at the Pisgah forest sampled in 1929. Values are given for the percentage of each species established in the periods 1620–1720 and 1720–1820 and for each species calculated as a percentage of all species established in these periods.

	Individual species		All species	
	1620–1719	1720–1819	1620–1719	1720–1819
Tsuga canadensis	93%	7%	61%	6%
Pinus strobus	65	35	36	25
Fagus grandifolia	7	93	2	33
Castanea dentata	6	94	1	20
Quercus borealis	0	100	0	10
Other	0	100	0	5

quite even-aged; the other species *Picea rubens*, *Acer saccharum* and *Betula lenta* exhibit a wider range of age.

Disturbance history

Disturbance events were identified from the temporal pattern of tree establishment and growth response, which are discussed below. The disturbance history is subsequently outlined in three historical periods.

The even-aged overstorey in many stands suggests that the temporal and geographical pattern of tree establishment may provide information on the disturbance history that may be cross-checked with other sources (Stephens 1955; Heinselman 1973). Pulses of tree

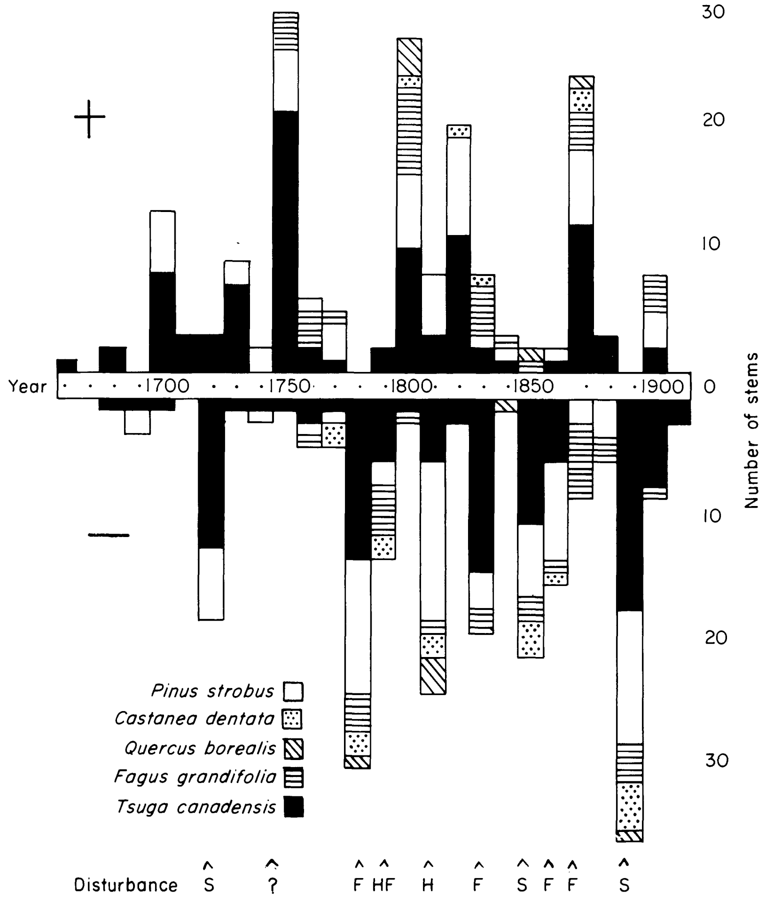

FIG. 9. Growth response of trees in the stump plots sampled at the Pisgah forest in 1929. Bars above the date line indicate the number and species of trees showing enhanced growth, whereas bars beneath the date line tabulate reduced growth rates. The dates of major disturbances are provided beneath the graph: S, windstorm; F, fire; H, hurricane; ?, unknown.

establishment occur in: 1645–1690, 1725–1735, 1750–1765, 1775–1785 and 1790–1800 (Fig. 8; Table 4).

Growth rates of overstorey trees, inferred from tree-ring chronologies may elucidate the disturbance history of the area. The growth–response data (1660 to 1910) temporally overlaps and complements the information on tree establishment. Growth responses were recorded for five species, with *Tsuga canadensis* and *Pinus strobus* more abundantly represented than the hardwoods. Distinct peaks of increased or decreased growth are recognized (Fig. 9). All periods of suppressed growth, with exception of 1840–50, are followed by peaks of increased growth. One explanation for this pattern of declining growth followed by a positive response is that disturbance damages the overstorey trees, slowing their growth; after a short interval of adjustment to the damage the trees begin to grow at normal or above normal rates in response to higher levels of light, water and nutrients in the naturally-thinned stands. The correlation between periods of sharply declining growth and known disturbances (windstorms and fire) supports this interpretation. In addition, analysis of overstorey *Pinus strobus* and *Tsuga canadensis* on the Harvard Forest following the 1938 hurricane, documents a 5–10 year post-hurricane period of slower growth followed by growth rates that exceed pre-hurricane levels (S. Mansour, personal communication).

Historical periods

The disturbance history of the study area may be separated into three periods—(i) establishment (1635–1790), (ii) growth, development and exploitation (1790–1910) and (iii) extensive disturbance (1910–1938)—distinguished by differences in the type of disturbance and the associated vegetation response. The periods and the primary sources of information are outlined below.

Period of establishment 1635–1790

The major establishment episode during the past 400 years occurred from 1635 to 1685. In stands across the area, 103 of 181 overstorey trees became established, primarily *Tsuga canadensis* and, especially after 1665, *Pinus strobus*. The absence of hardwood species dating from this period may be due to their shorter longevity than the conifers (Fowells 1965).

The major disturbance episodes from 1635 to 1685 include the hurricane of 1635 (Perley 1891; Stephens 1955) and a fire in approximately 1665 at the Harvard Tract (Henry & Swan 1974). The presence of charcoal layers at the corresponding stratigraphic interval in many swamps and forest hollows around the Harvard Tract suggests that the fire may have been extensive (P. K. Schoonmaker, personal communication).

From 1700 to 1740 *Fagus* and *Castanea* established in three stands on a ridge between Pisgah Reservoir and Kilburn Pond (Figs 8, 10b). Coincident with the tree establishment there occurs a decline in the rate of tree growth from 1720 to 1730 (Fig. 9). The peak represents eighteen stems from seven plots. Four plots (5, 6, 13 and 14) situated on exposed ridges contain two to five trees that declined in growth (Fig. 10b). The only known disturbance for this period is a windstorm in 1726 (Appendix 1; Ludlum 1963). A small positive growth response in 1730–40 includes five stems represented in the previous negative peak.

In the period 1750–1765, twenty-one trees of *Fagus*, *Pinus* and *Tsuga* established in six stands west of Pisgah Reservoir and south of Kilburn Pond (Figs 8 & 10c). The decade 1750–60 displays the only recorded peak in increased growth that is neither preceded nor followed by a sharp decline in growth (Fig. 9). Seven of the nine plots comprising the peak (plots 5, 6, 8, 14, 17, 20 and 26) contain more than one responding tree. The majority of the individuals are *Tsuga canadensis*.

No disturbance is noted for this period, although Branch, Daley & Lotti (1930) suggest that the increased growth of trees during this period was a response to canopy opening. One possibility is the windthrow of overstorey *Pinus strobus* by the hurricane of 18 October 1748 (Ludlum 1963), followed by a resurgence of understorey *Tsuga* (75% of the stems responding are *Tsuga*).

From 1775 to 1800 eleven stands contain two to four trees that exhibit decreased growth. The trend of decreasing growth is followed by a pronounced positive trend from 1800 to 1810 that includes all but one of the stands exhibiting a decrease. A total of twenty-eight *Quercus borealis*, *Pinus* and *Fagus* established in two stands south-east of North Round Pond and two stands west of Pisgah Reservoir during this period. The *New*

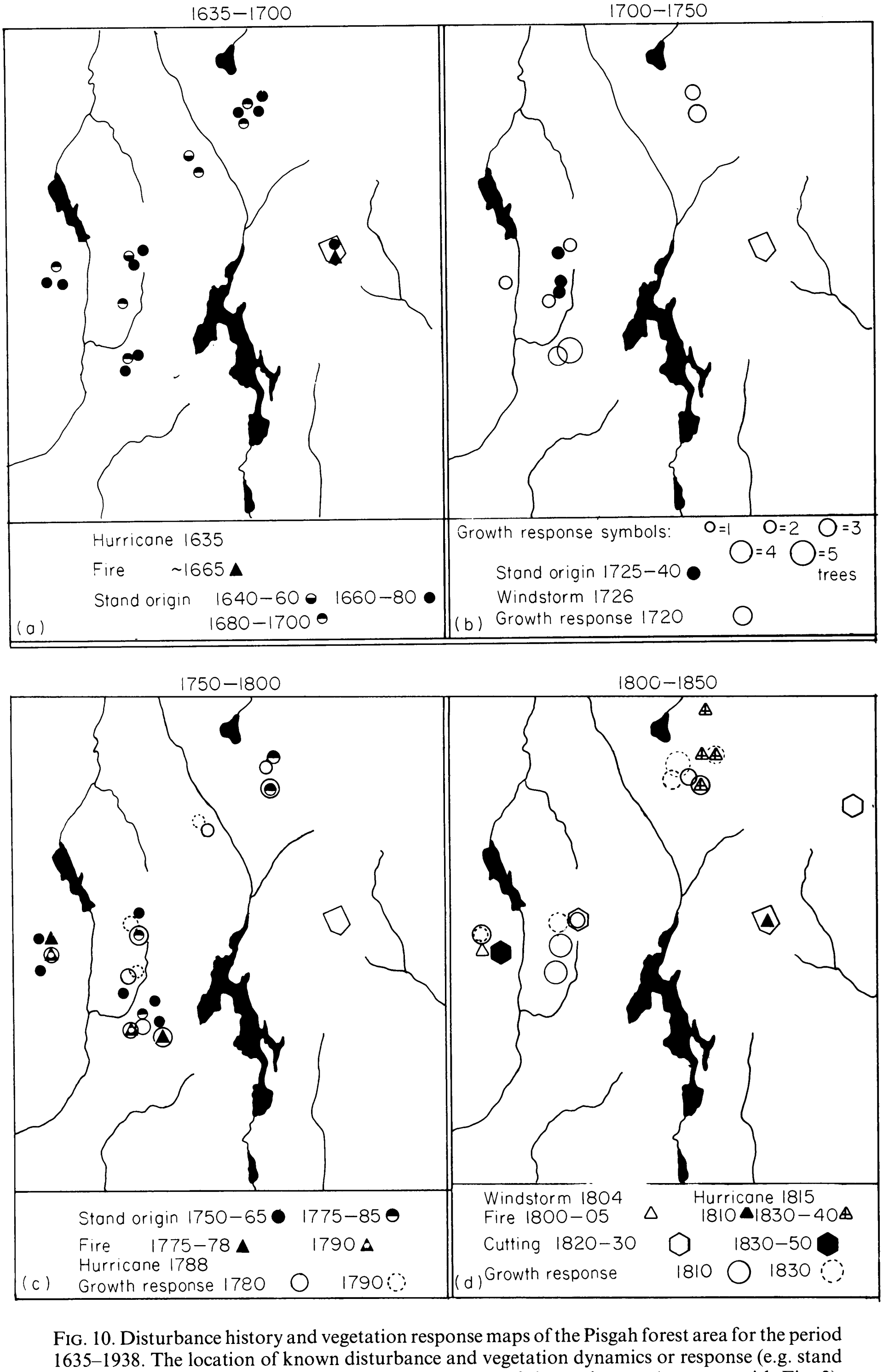

FIG. 10. Disturbance history and vegetation response maps of the Pisgah forest area for the period 1635–1938. The location of known disturbance and vegetation dynamics or response (e.g. stand origin, suppression, growth) are located on the maps of the study area (compare with Fig. 2). Stand origin is defined as a period when more than 33% of the trees in the overstorey established.

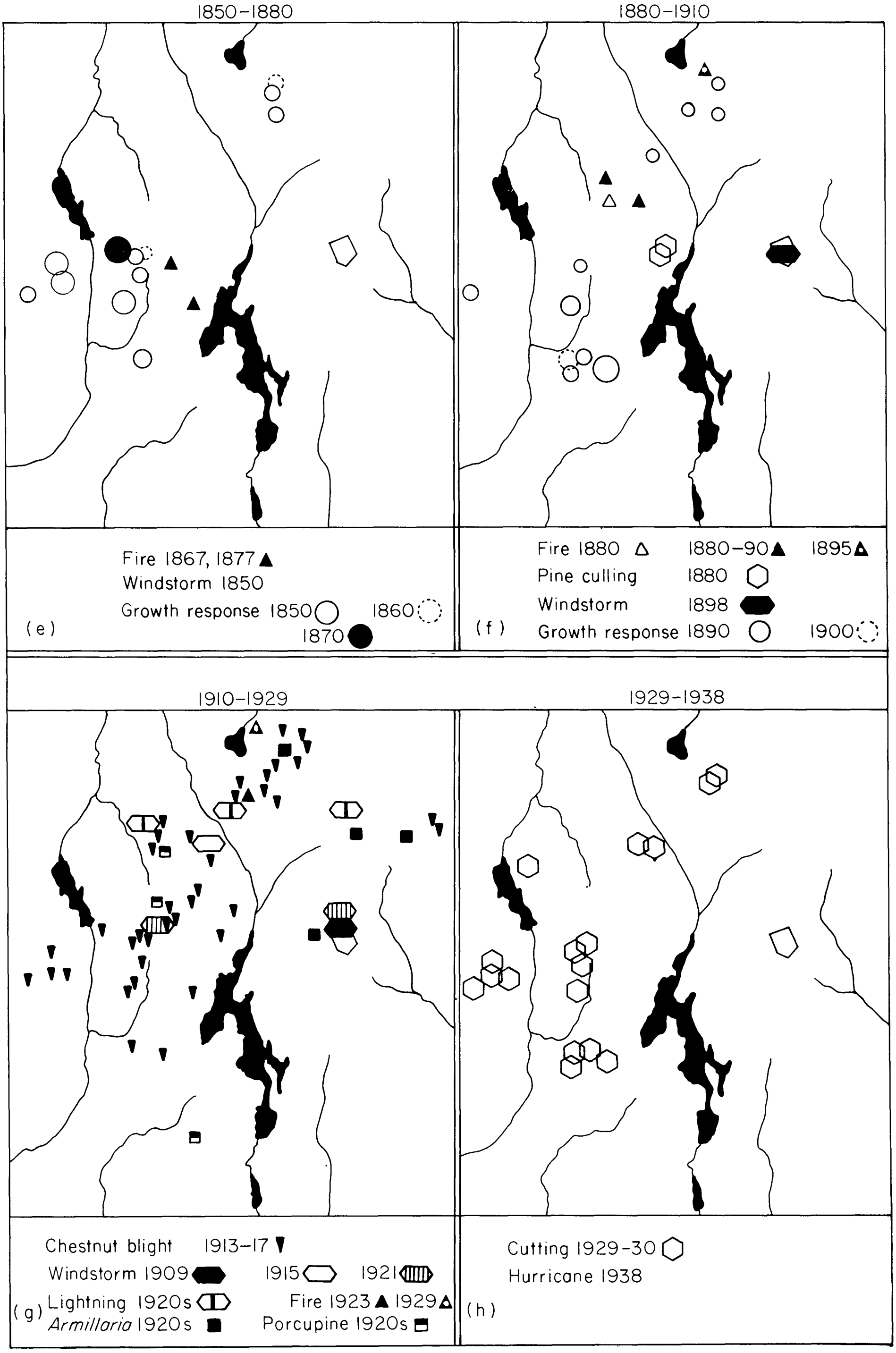

FIG. 10 (*cont.*)

Broad-scale disturbance such as windstorms and chestnut blight are merely listed. The size of the circle corresponding to negative growth response illustrates the number of individuals responding in that plot (see (b) for scale of circle size).

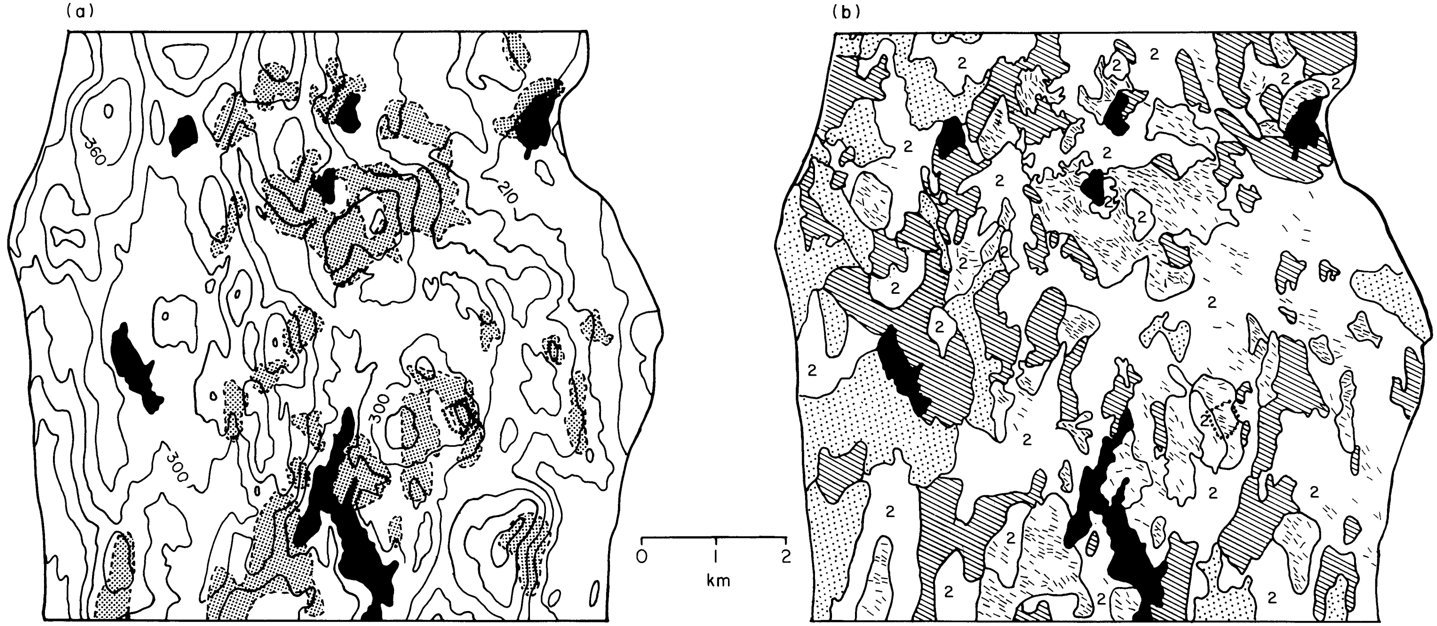

FIG. 11. Relationship between physiography and forest damage resulting from the 1938 hurricane in the Pisgah forest. Black areas are lakes or ponds. Topographic 30-m contours for the study area are depicted in (a) with severely damaged areas shaded. The short lines in the moderately to severely damaged classes in (b) represent individual windthrows visible on the aerial photograph. Hurricane damage in (b) is indicated as: ▒, severely damaged; [2], moderately damaged; ▨, undamaged; and □, logged or cultivated prior to the storm.

Hampshire Recorder published in Keene reported a 'Great Hurricane' on 9 September 1788 (also see Smith 1946; Ludlum 1963), which is considered the second most destructive storm in the area's history after the hurricane of 1938 (Keene Historical Committee 1982). Fires followed the hurricane south of Kilburn Pond and west of Pisgah Reservoir in 1790 (Fig. 10c; Appendix 1).

In summary, for this approximately 200-year period, 176 of 181 trees in the stump plots established; establishment peaks closely follow known disturbances (Fig. 8). Separation of the age-structure graph into two equal periods (1620–1719; 1720–1819) reveals that from 1620 to 1719 93% of the *Tsuga* overstorey and 65% of the *Pinus strobus* became established (Table 4). More than 90% of the stems of each of the hardwood species date to the period 1720–1819.

Period of growth, development and exploitation 1790–1910

By the beginning of this period the overstorey trees in the old-growth stands were established and the first documented cuttings in the area occurred. The period is characterized by changes in the growth of the overstorey stems attributable to known disturbances.

From 1810 to 1820 six stands contain two to five trees with decreasing growth. The known disturbances include a fire in 1800–05 of unknown size, south of Kilburn Pond, an 1810 fire near the Harvard Tract, and the hurricane of 1815. The storm is described as 'not as severe as the hurricane of 1788' but was locally quite destructive (Keene Historical Committee 1982). During the 1820s and 1830s, 83% of the trees showing decreasing growth in 1810–20 respond with positive growth. From 1830 to 1840 nineteen trees, primarily *Tsuga*, show declining growth. The majority of the stems are located in three plots on the hill south of North Round Pond. Fires in 1830 were detected in four stands in this area (Fig. 10d), suggesting that a single fire may have swept the entire area.

The twenty-year period from 1850 to 1870 involves a decrease in tree growth in twenty stands, of which eleven contain more than one individual. All major tree species are included, and the decline undoubtedly relates to the windstorm in 1850 (Keene Historical Committee 1982; Appendix 1). A windstorm in 1898 is responsible for the windthrow of several trees on the Harvard Tract (Henry & Swan 1974) and may be associated with decreasing growth in several trees on exposed ridges west of the Pisgah Reservoir and south of North Round Pond during the 1890s.

Period of extensive disturbance 1910–1938

This period is marked by frequent broad-scale disturbance from natural and anthropogenic factors. The blight on *Castanea* entered the area in 1913, and by 1915 mortality was extensive (Fig. 10g). Strong windstorms in 1909, 1915 and 1921 were responsible for uprooting individuals across the area (Fig. 10; Henry & Swan 1974). Lightning damage and associated fires in 1923 resulted in the formation of gaps ranging from 300 to 1200 m^2 (Harvard Forest Archives 1930–1). Additional disturbance during the 1920s included *Tsuga* mortality from *Armillaria mellea* and extensive porcupine damage, especially to *Fagus* and *Betula* spp. Openings greater than 800 m^2 were created by *Armillaria* with the worst damage occurring after fire or on shallow soils (Branch, Daley & Lotti 1930). From 1924 to 1930 the Pisgah forests were increasingly logged (Fig. 10h). On 21 September 1938 the area was devastated by the hurricane that followed 23 cm of rain in eight days (Foster 1988).

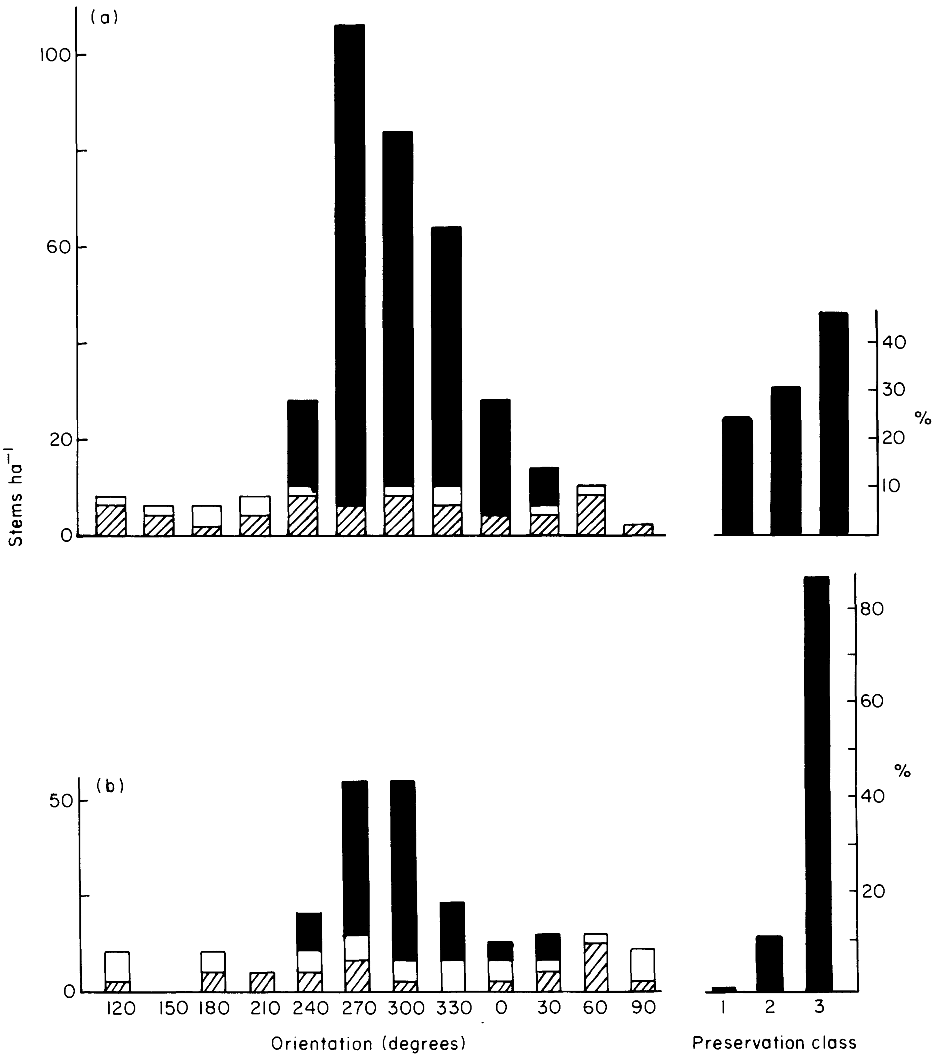

FIG. 12. Orientation, origin, and preservation state (class 1, well preserved; class 2, moderately preserved; class 3, poorly preserved) of trees blown down by the 1938 hurricane on (a) the Harvard Tract, (b) the North Round Pond stand. The origin of downed stems in indicated as: ■, windthrown; ▨, broken stems; and □, unknown.

Damage from the 1938 hurricane

Forest damage from the hurricane of 1938 provides an analogue for the structural damage resulting from the catastrophic winds that historically affected the old-growth forest (e.g. 1635, 1788, 1815) and, therefore, was examined in detail.

The hurricane created a structural mosaic of differential damage (Figs 3 & 11). Approximately half of the study area, across level and rolling terrain, suffered moderate damage. Equal area (approximately 25%) were undisturbed or severely disturbed. The size and shape of blow-down areas are highly irregular. Windblown trees occur in discrete

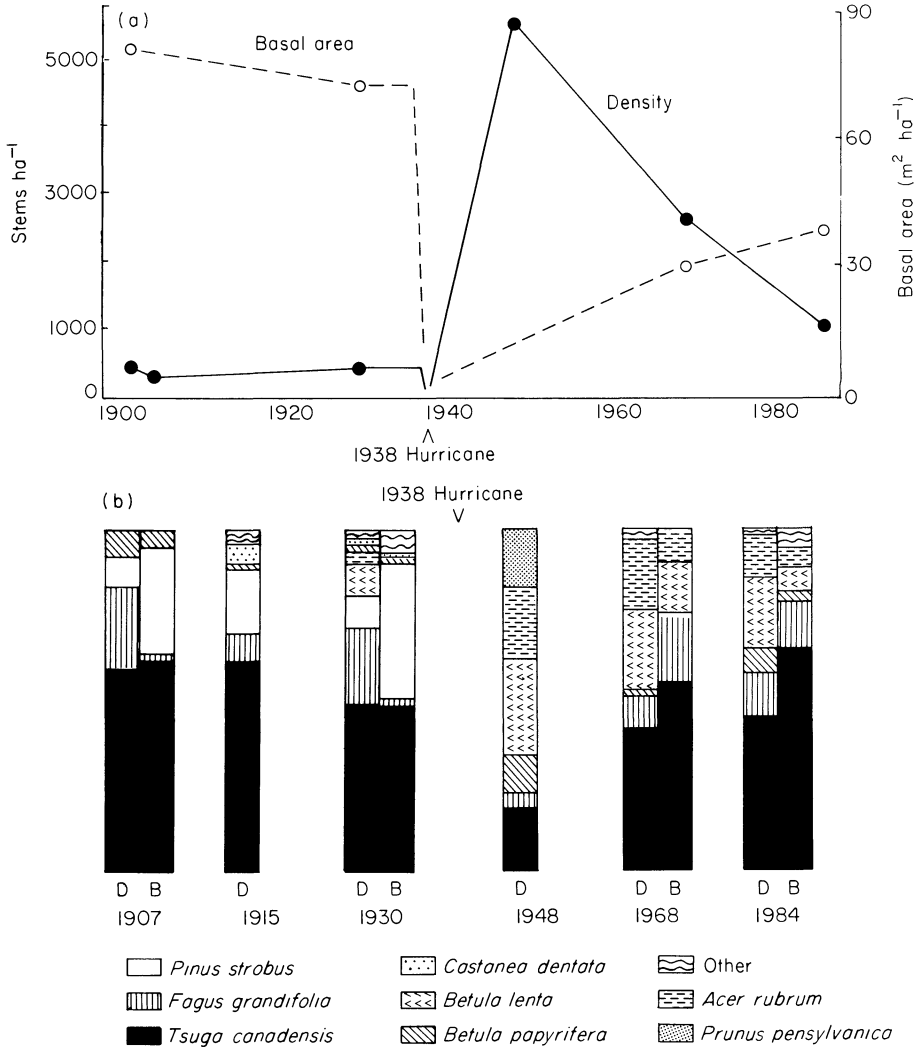

Fig. 13. Change in (a) basal area and density and (b) relative density (D) and relative basal area (B) from 1907 to 1984, on the Harvard Tract. (Data on basal area were not collected in 1915 or 1948.)

patches as small as 30 m^2; as mapped from aerial photographs, however, the areas of complete damage range from 0·03 to approximately 3·25 km^2.

The spatial pattern of wind damage was largely controlled by physiography and the structure of the pre-hurricane vegetation (Fig. 11). Logged and agricultural areas located along the perimeter of the study area supported herbaceous, shrubby or second-growth vegetation of low stature that was undisturbed by the wind. The extent of damage in mature forests was primarily determined by local topography. The strongest winds came from the south-east as shown by the 240° to 30° orientation of the windthrown trees (Figs 11 & 12). Severe damage characteristically occurred on south- to east-facing slopes and on

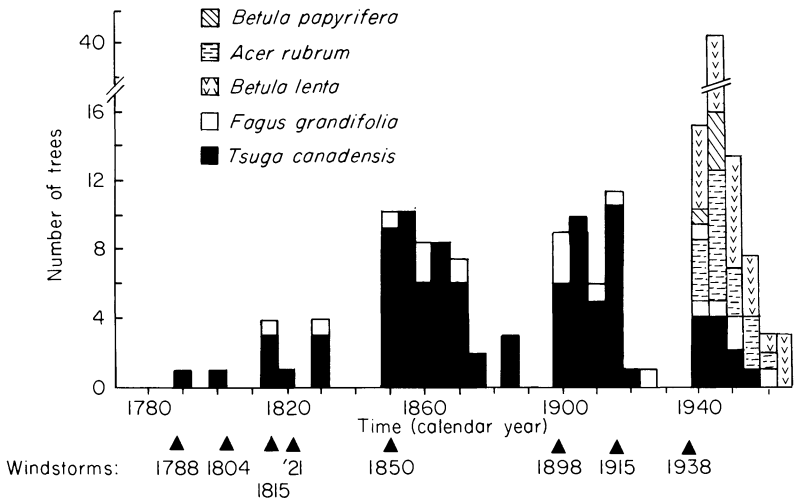

FIG. 14. Establishment dates of trees on four 20 m x 20 m plots on the Harvard Tract in 1984. The dates of known windstorms are provided beneath the graph.

the north-western shores of lakes. Little disturbance occurred to forests lying in the lee (north-west exposure) of broad hills, on the south-east and east shores of water bodies or in valleys.

In 1984 the forests bear clear evidence of the catastrophic storm. At the Harvard Tract where the overstorey was destroyed in 1938, only fifteen large *Pinus* and *Tsuga* remain today on the entire 10 ha, including ten dead standing snags 75–120-cm dbh and over 30 m tall. At both the Harvard Tract and North Round Pond, massive windthrown trees have a north-west (270–330°) orientation and provide a unique structural component to the young stand (Figs 3 & 12). Snapped trunks, i.e. fallen stems broken from an erect trunk, show no systematic orientation, which suggests that these have fallen randomly since the hurricane. Downed stems of uncertain origin (i.e. unrelatable to a stump or pit and mound) also exhibit no particular orientation, indicating that these were not blown down during the storm.

The volume and partitioning of coarse wood litter in various preservation classes varies sharply between North Round Pond Forest and the Harvard Tract (Fig. 12). At the Harvard Tract, 374 m^3 ha^{-1} of wood is contained in very large boles and is rather uniformly partitioned in the three preservation classes (24%, 31% and 45%, for classes 1 (solid), 2 (partially decomposed but intact) and 3 (decomposed and losing integrity), respectively). At North Round Pond approximately half this volume of downed wood occurs (180 m^3 ha^{-1}) with most well-decomposed (1%, 12% and 87%, for preservation classes 1, 2 and 3, respectively).

Post-hurricane vegetation recovery and development

The post-hurricane development of the forests on the Harvard Tract was examined in an attempt to understand the old-growth stands. The pre-hurricane forest had a density of 300–400 trees ha^{-1} and basal area was approximately 70–90 m^2 ha^{-1} (Fig. 13a). *Tsuga canadensis* comprised 50–60% of the stems and basal area, whereas a relatively small

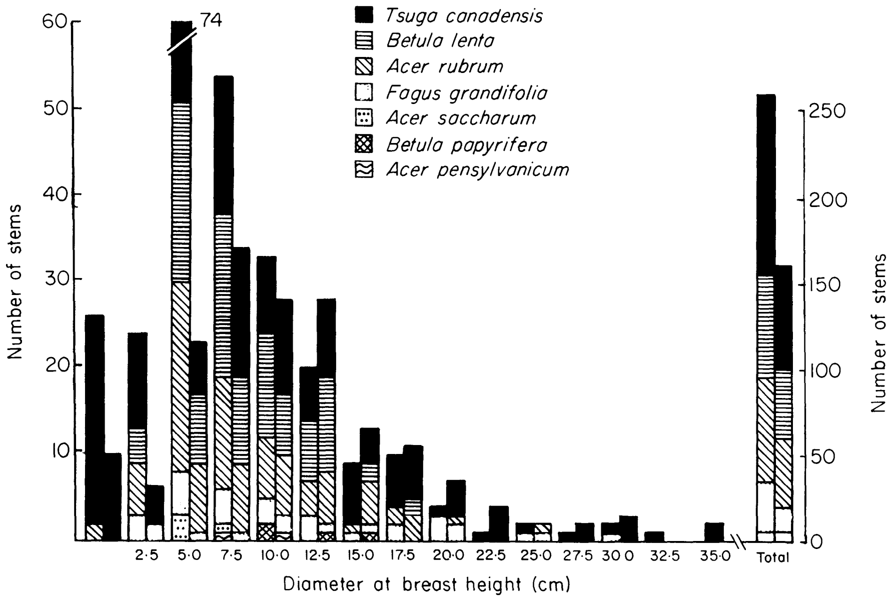

FIG. 15. Number of trees and their diameter distribution on the 0·04-ha Henry & Swan (1974) plot at the Harvard Tract. For each diameter class the left bar represents the 1968 survey (Henry & Swan 1974) and the right bar represents the 1984 survey. In the sixteen-year period the total density has declined while the average size has increased.

number of very large *Pinus strobus* formed 40% of the basal area (Fig. 13b). Other common species included *Betula lenta*, *Acer rubrum* and *Quercus borealis*.

Following the hurricane the basal area dropped to less than 5 m^2 ha^{-1} (1942) and has increased to approximately 35 m^2 ha^{-1} in 1984. Density exceeded 5000 stems ha^{-1} in 1948 and has decreased since, to less than 1100 stems ha^{-1} in 1984. Short-lived deciduous species including *Prunus pensylvanica*, *Betula lenta* and *Betula papyrifera* increased dramatically in relative density following the storm, whereas *Tsuga canadensis* decreased sharply and *Pinus strobus* disappeared almost completely from the 8 ha tract. *Tsuga* has been increasing relative to the deciduous species in the forty-five years since the hurricane, as a result of lower rates of mortality.

Age-structure data document differences in the reproductive responses of the species on the Harvard Tract. The majority of the hardwoods (*Betula lenta*, *B. papyrifera* and *Acer rubrum*), established (by resprouting or seed) within twenty-five years following the hurricane and grew rapidly into the canopy (Fig. 14). In contrast, all of the tree-size *Tsuga* and the majority of the tree-size *Fagus* showed advanced regeneration in the old-growth forest (establishment peaks: 1815–20, 1830, 1850–60, 1895–1915, coinciding with earlier disturbances) and rapidly grew to form the new canopy. The many *Tsuga* and *Fagus* that established in 1939–45, were overtopped by aggressive hardwoods and advanced regeneration.

DISCUSSION

Recent reviews of disturbance processes in temperate forests of eastern North America, document a return interval for canopy disturbance of 50–200 years, with geographical variation in the scale of individual disturbance events (Runkle 1984, 1985). For example, cove forests of the Appalachian mountains experience frequent local disturbance by glaze storms, lightning, wind and mortality, that opens small canopy gaps subsequently filled by advance regeneration of shade-tolerant species (Lorimer 1980; Barden 1981; Runkle 1982). In contrast, forests of the Allegheny plateau experience both local windthrow and more broad-scale disturbance by fire and large blowdown that creates large gaps, allowing the formation of even-aged stands of intolerant species (Lutz 1930; Hough & Forbes 1943; Runkle 1985). The size of historically-important gaps and the intensity of disturbance are, therefore, as important as the return interval, in characterizing the disturbance regime.

In the Pisgah forest the disturbance history includes frequent small-scale disturbance (treefall, lightning, windstorms, pathogens, fire), punctuated by infrequent broad-scale events (hurricane and fire) that open extensive gaps. On the forest sites examined, the age-structure and composition of the forests suggest that the broad-scale disturbances are most important in stand establishment and organization, whereas more local events are recorded in tree-growth response. Physiography is a very important determinant of local disturbance regime. It is useful to discuss the disturbance factors individually and then to consider general patterns of vegetation response to large-scale disturbance events.

Windstorms

Windstorms, especially hurricanes, have exerted the greatest impact on the vegetation. Patterns of growth response and tree establishment within the study area document the impact of twelve historically recorded storms in 1635, 1726, 1749, 1788, 1804, 1815, 1850, 1898, 1909, 1915, 1921 and 1938, and characterize a forest area continually readjusting to broad-scale wind damage of varying intensity.

Exposure to prevailing winds, which generally come from the west or north, results in frequent canopy damage and is apparently responsible for much of the structural differences in the forest from low to upper slopes. Tropical storms, which occur most commonly in September or October (Neumann *et al.* 1978) have been most important in overstorey removal and stand initiation. Approximately 5–10 hurricanes hit New England each century, with decreasing frequency inland, and it has been estimated (albeit based on four storms—1635, 1788, 1815 and 1938) that a major storm occurs in this region approximately every 70–100 years (Brooks 1939).

The damage from hurricanes creates a landscape mosaic that is controlled by physiography and the pre-hurricane vegetation (Foster 1988). In central New England, hurricane winds come from the south-west to east (Smith 1946) and, therefore, site susceptibility is controlled by the degree of exposure to those directions. Following the storm of 1938, exposed south-east slopes and north-western lakeshores suffered the greatest damage. Sharp discontinuities in the amount of damage are especially prevalent along natural physiographic breaks, such as ridges, hilltops, and lake shores.

The composition and physiognomy of the vegetation are the other major factors controlling susceptibility to wind damage (Rowlands 1941; Foster 1988). At the time of the 1938 hurricane the Harvard Tract, situated on an exposed hilltop and forested with old *Pinus strobus* and *Tsuga*, was exceptionally vulnerable to destruction.

In contrast, extensive anthropogenic alteration of the landscape during the last two centuries has reduced the susceptibility of most of New England to wind damage. Second-growth forest is younger, shorter and more uniform than old-growth forest (Rowlands 1941; Dunn, Guntgenspergen & Dorney 1983; Canham & Loucks 1984) making it more resistant to wind. However, logging and agriculture also create abrupt height and density differences among the vegetation patches, which cause damage along forest margins and to surviving old-growth stands projecting above the second-growth forest.

Hurricanes exert a long-lasting effect on site conditions (Lutz 1940; Hutnick 1952; Lyford & MacLean 1966). The micro-topography from 1938 windthrows has much greater relief than comparable features in second-growth forests. These tip-up mounds continue to erode with time and, therefore, provide an unstable site for the black and paper birch that establish on them.

Large snags, remnants of the old forest, continue to fall and create small canopy gaps. Most of the coarse woody material, however, was blown down in the storm and creates a unique structural component by the near-parallel 300° orientation of the massive logs (Fig. 3). The preservation of coarse wood depends on size and species, as demonstrated by the rapid decomposition of hardwood logs at North Round Pond and slower break down of larger conifer logs at the Harvard Tract. Woody debris will remain a major structural feature of these stands for at least 100 years following catastrophe (cf. Falinski 1978; Franklin & Hemstrom 1981).

Fire

Fire has been the second most frequent although less widespread disturbance in the study area, occurring in 1665 (approximately), 1778, 1790, 1804, 1810, 1830, 1868, 1880, 1923 and 1929. Soil charcoal in the old-growth stands indicates that most forests have burned at some time (Griffith, Hartwell & Shaw 1930). Sedimentary analysis of small hollows on the Harvard Tract documents two fires within the period 1000–300 years ago (P. K. Schoonmaker, personal communication).

Interpretation of the cause of ignition and the behaviour of the fires is conjectural. One fire (1665) occurred before settlement of the region (*c.* 1740) and, therefore, European man is an unlikely cause. Although it is reported that the Squakheag Indians burned the major river terraces for agriculture (Hurd 1886), the physiography of the Pisgah area is generally unsuited for aboriginal use (Harrington 1984). Lightning strikes have caused fires and sizeable forest gaps (Branch, Daley & Lotti 1930). Most of the detected fires occurred when ignition by European settlers was possible (1788–1870) or probable (1810–1890). Early logging practices generally involved slash reduction by fire, which often spread to the surrounding areas (Belknap 1813).

It is possible to get only a rough estimate of the size of historical fires. The 1665 fire is especially intriguing because of the large number of stands (nine of seventeen stump plots with sixty trees, mostly *Pinus strobus*) it apparently initiated. From this rather circumstantial information it appears possible that major portions of the study area may burn.

As a result of lush deciduous vegetation the fire season in central New England occurs in the spring, associated with dry frontal storms, and in the autumn, under the influence of stagnating high-pressure systems (Stickel 1932; Pyne 1982). Fuel accumulation following catastrophic windthrow may contribute to historically important fires (Stearns 1951; Brown 1958, Curtis 1971). This would be particularly true in conifer forests but of little consequence in hardwood forests because of differential flammability of the resulting litter (W. A. Patterson III, personal communication). In this study, seven fires occurred within twenty years of wind damage in the local area. The threat of fire following the 1938 hurricane prompted rapid salvage of timber throughout New England (N.E.T.S.A. 1943; Pyne 1982).

Pathogens

Although presettlement outbreaks of native pathogens occurred (Davis 1981, 1983), the known history of such damage is restricted to the present century and largely involves the introduction of exotic species. *Castanea dentata* was common throughout the park and locally comprised up to 40% of the basal area at North Round Pond before the *Castanea* blight. *Fagus grandifolia*, which was able to capitalize on the open conditions following the blight (Mackey & Sivec 1973), has been severely affected by a bark disease (scale insect *Cryptococcus fagisuga* Lindinger and fungus *Nectria coccinea* var. *faginata* Lohman, Watson & Ayes) since the 1960s (Shigo 1970). *Armillaria mellea* was noted as a local cause of mortality to *Tsuga* and *Pinus* (Branch, Daley & Lotti 1930). Small stands ranging to 0·2 ha in size were killed and damage was especially severe where the trees had been weakened previously.

Patterns of vegetation development following broad-scale disturbance

Analysis of the pattern of vegetation following the 1938 hurricane elucidates the structure of the old-growth forests that established after similar events. Stand development follows Oliver's (1981) model for even-aged forests. Immediately following disturbance, stand initiation commenced with the establishment of fast-growing species (*Betula lenta*, *B. papyrifera*, *Acer rubrum* and *Prunus pensylvanica*) that rapidly fill large openings. Slow-growing, shade-tolerant species, such as *Fagus grandifolia* and *Tsuga canadensis*, are represented by two cohorts: advanced growth that established following earlier windstorms and resurged from a suppressed condition after the hurricane and smaller saplings (< 8 cm dbh) that established soon after the hurricane. This latter group has been overtopped and will remain as suppressed until released by a subsequent disturbance or will suffer mortality (Oliver & Stephens 1977; Hibbs 1982, 1983). The presence of the shade-tolerant species is, therefore, much less a consequence of their ability to establish and grow up beneath a canopy than a function of initial establishment in openings, slow growth during suppression and more rapid growth following release.

The even-aged development of dense stands has precluded further establishment in the last twenty-five years, with the result that succession has largely become a thinning process (Fig. 15; Niering & Goodwin 1974; Peet & Christensen 1980). The increased prominence of *Tsuga canadensis* (Fig. 13b), is the result of higher mortality rate of *Prunus pensylvanica* and *Betula* spp. and emphasizes the competitive advantage conferred to *Tsuga* by its extreme shade tolerance and ability to respond from advanced regeneration.

The episodic nature of disturbance and the even-aged establishment pattern of trees can result in rapid and dramatic changes in forest composition, as mediated by such factors as the composition of the original forest, differential removal of the species by the disturbance, seedbed conditions and the relative availability of plant propagules. On the Harvard Tract, the old-growth forest of *Pinus*, *Tsuga* and hardwoods that persisted until 1938, developed immediately following the 1635 hurricane and subsequent fire. In sharp contrast, the forest that developed after the 1938 hurricane included no regeneration of *Pinus*, although over twenty seed trees remain. The absence of *Pinus* is probably the result of a qualitative difference in the disturbance (e.g. the absence of fire; cf. Maissourow 1935; Brake & Post 1941; Hawley & Clapp 1942; Hough & Forbes 1943; Fig. 13b). There is no evidence that the last 350 years have provided the stability or growth patterns expected in a steady-state forest.

CONCLUSION

The results of this study, based on virgin forest remnants in a 2000-ha area, strengthen the conclusions concerning the disturbance history of central New England derived from previous studies of much smaller stands (Stephens 1955; Henry 1968; Henry & Swan 1974). Most of the forests display population characteristics (e.g. age structure, growth rates) that have been greatly controlled by known disturbance; primarily windstorms, fire and pathogens. Disturbance acts selectively within the landscape and sites may be arranged along an exposure gradient. This differential exposure to disturbance, in concert with previous stand history and edaphic conditions, leads to the mosaic pattern of vegetation structure observed in the landscape. A generalized description of the geographic role of disturbance in New England will only emerge with additional field studies and palaeoecological investigations.

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APPENDIX

Disturbance history of the Pisgah forest, 1635–1938.

Date	Disturbance	Location	Scale	Source[a]
1635	Hurricane	Throughout	Broad	Channing 1939
~1665	Severe fire	Harvard Tract	?	Henry & Swan 1974
1726	Windstorm	Throughout	Broad	Cline & Spurr 1942
1775–8	Fire	Plot XXI[b]	?	SPD, fire scar
1788	Hurricane	Throughout	Broad	Keene, N.H. Recorder
1790	Fire	Plot X, XIV, XX	?	SPD, fire scar
1804	Windstorm	Throughout	Broad	Ludlum 1963; KHC 1982
1800–05	Fire	Plot XX	?	SPD, fire scar
~1810	Fire/windthrow	Harvard Tract	?	OPD
1815	Hurricane	Throughout	Broad	Keene, N.H. Recorder
1820–30[c]	Cutting	Near plot XVII	?	SPD, dated stumps
~1830	Pine culling	Near plot 52	Local	OPD
~1830	Fire	Plot 38, 11, 36	Local	OPD, fire scar
1830–40	Fire	Ridge E of NRP[d]	?	TL, fire scar
1840–50	Cutting	Scattered	?	WB
1850	Windstorm	Throughout	Broad	Ludlum 1963
1830–55[e]	Cutting	Near plot XX	Local	SPD, dated stumps
1867	Fire	Slope above NRP	Broad?	TL, fire scar
1877	Fire	Plot XXII	?	SPD, fire scar
1880	Fire	Plot 72	?	OPD, fire scar
1880	Cutting	Plot 61, 62	?	OPD
1880–90	Fire	Plot 71	?	OPD, fire scar
1880–90	Fire	Ridge E of NRP	Broad	TL, fire scar
1895	Fire	Plot 67	?	OPD, fire scar
1898	Windstorm	Harvard Tract	?	Henry & Swan 1974
1909	Windstorm	Harvard Tract	?	Henry & Swan 1974
1913–40	Chestnut blight	Throughout	Broad	U.S.D.A. 1941
1913–?	Chestnut salvage	Throughout	Broad	
1915	Windstorm	Plot 8	Local?	OPD
1920s	*Armillaria mellea*	Plots 19, 27, 50, 51	Patchy	OPD
1920s	Lightning	Plots 44, 49, 68	Local	OPD
1920s	Porcupine damage	Plots 8, 56, 57	Patchy	OPD
1921	Tornado/windstorm	Harvard Tract	?	Henry & Swan 1974
1921	Windthrow	Plot 55	70′ × 200′	OPD
1923[f]	Fire	Plot XXVI	?	SPD, fire scar
1927–30	Cutting	Throughout	Broad	SPD
1929	Fire	NE corner NRP	?	WB, fire scar
1938	Hurricane	Throughout	Broad	

[a] SPD, Stump Plot Data; OPD, Old-Growth Plot Data (Branch, Daley & Lotti 1930); TL, T. Lotti field notes; WB, W. Branch field notes; KHC, Keene Historical Committee 1982.
[b] Roman numerals stand for Stump Plot Data, cardinal numbers for Old-Growth Data.
[c] Evidence is two pine stumps 150 years old in the 260-year-old stand.
[d] NRP, North Round Pond.
[e] Decayed pine stumps approximately that old.
[f] Fire scars suggestive of light fire before 1924 culling.