

**Species and Stand Response to Catastrophic Wind in Central New England,
U.S.A.**



David R. Foster

Journal of Ecology, Volume 76, Issue 1 (Mar., 1988), 135-151.

Stable URL:

<http://links.jstor.org/sici?sici=0022-0477%28198803%2976%3A1%3C135%3ASASRTC%3E2.0.CO%3B2-F>

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

Journal of Ecology is published by British Ecological Society. Please contact the publisher for further permissions regarding the use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/briteco.html>.

Journal of Ecology

©1988 British Ecological Society

JSTOR and the JSTOR logo are trademarks of JSTOR, and are Registered in the U.S. Patent and Trademark Office. For more information on JSTOR contact jstor-info@umich.edu.

©2003 JSTOR

SPECIES AND STAND RESPONSE TO CATASTROPHIC WIND IN CENTRAL NEW ENGLAND, U.S.A.

DAVID R. FOSTER

Harvard Forest, Harvard University, Petersham, Massachusetts 01366, U.S.A.

SUMMARY

(1) The effect of catastrophic hurricane wind on forest vegetation in central New England was examined at the species and stand level.

(2) Species susceptibility to wind is largely explained by canopy position: fast-growing, pioneer species that form overstorey dominants (*Pinus strobus*, *P. resinosa*, *Populus* spp. and *Betula papyrifera*) suffered much greater damage than slower growing, or tolerant species occurring primarily in codominant, intermediate and suppressed canopy positions (*Carya* spp., *Acer rubrum*, *Quercus alba*, *Q. velutina* and *Tsuga canadensis*). Uprooting was much more important than breakage as the primary form of damage. This result, which contrasts with the findings of most studies of wind damage, may perhaps be explained by the very high levels of precipitation that accompanied the storm, saturating the soil and loosening the roots.

(3) Damage to forest stands exhibits a positive, linear relationship with stand age and height and negative relationship with density. Conifer forests are significantly more susceptible than hardwood forests. *Pinus strobus* and *P. resinosa* stands are susceptible to wind at 15 years of age and are completely destroyed at 30 years; hardwood stands exhibit increasing damage from age 20 years, but are not completely blown down until age 80–100 years.

(4) Within stands, damage shifts progressively from the dominant trees in young stands to include trees in the codominant, intermediate and suppressed layers in older forests. Parallel changes with age in the type of damage include a decline in the number of leaning trees and increase in uprooting.

(5) Damage to species and stands from a catastrophic windstorm occurs quite predictably and specifically within the forests studied. This discriminating impact of wind has profound consequences on the vegetation at a range of spatial scales and is largely mediated by historical factors and structural and compositional aspects of the vegetation mosaic.

INTRODUCTION

Under stable conditions and in the absence of exogenous disturbance, vegetation may be expected to assume an equilibrium condition in which species abundance and distribution are controlled by interspecific interactions, niche differentiation and the mosaic of site characteristics. However, considerable investigation of vegetation history has documented that such equilibria seldom exist (Wright & Heinzelman 1973; White 1979). Rather, the organization of most plant communities is significantly affected by disturbance (Raup 1964; Pickett 1980). In many temperate and most boreal forests, for example, disturbance has initiated the existing old-growth stands, and subsequent disturbance has shaped their composition and structure over time (Wright & Heinzelman 1973).

Studies in central New England suggest that catastrophic wind damage from hurricanes has generated much of the recent structural pattern and dynamics of the

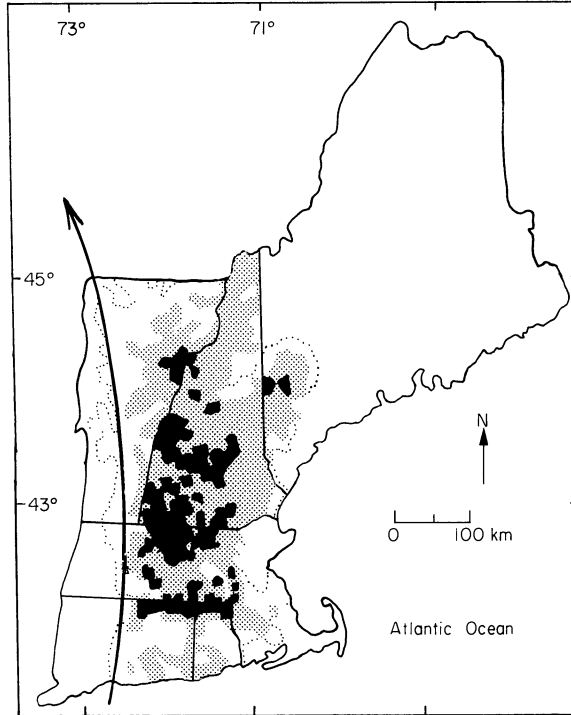


FIG. 1. Track of the eye of 1938 hurricane (arrow) through central New England showing the distribution of forest damage: black = extensive damage; shaded = moderate damage; white, within dotted line = slight damage. The Harvard Forest is located in north-central Massachusetts within the area of extensive damage.

upland forests (Cline & Spurr 1942; Smith 1946; Stephens 1956; Henry & Swan 1974; Foster 1988). From meteorological records and forest reconstructions it has been estimated that hurricanes strike southern and central New England every 20–40 years, while catastrophic storms like those of 1635, 1788, 1815, and 1938 occur approximately every 100–150 years (Brooks 1939; Smith 1946; Neumann *et al.* 1978).

The hurricane of 1938 was accompanied by 15–35 cm of rain and winds in excess of 200 km h⁻¹ (Brooks 1939). The tropical storm destroyed over 6×10^9 board feet* of timber along a 100-km wide path as it travelled northward through New England along a general pressure gradient (Fig. 1; NETSA 1943). The most destructive winds occurred in the vortex near its eastern inner margin where the rotary velocity (anti-clockwise) and forward movement produced the greatest wind speed. Lower wind velocities to the west of the eye resulted in reduced damage there. Occasional gusts of extraordinary velocity, resulting from the penetration of projectiles of freely moving air from considerable heights, augmented the local velocity and destructiveness of the winds (Brooks 1939).

At the Harvard Forest approximately 70% of the standing volume of timber was windthrown; the storm thereby exerted the major impact on the forest in its eighty-year management history (Fig. 2). In the century preceding the hurricane, open agricultural land was gradually reverting to forests dominated by white pine. The storm and

* Board foot, a common unit of timber volume measurement in the United States, is equivalent to a board 12 inches long by 12 inches wide by 1 inch thick (c. $30 \times 30 \times 2.5$ cm³).

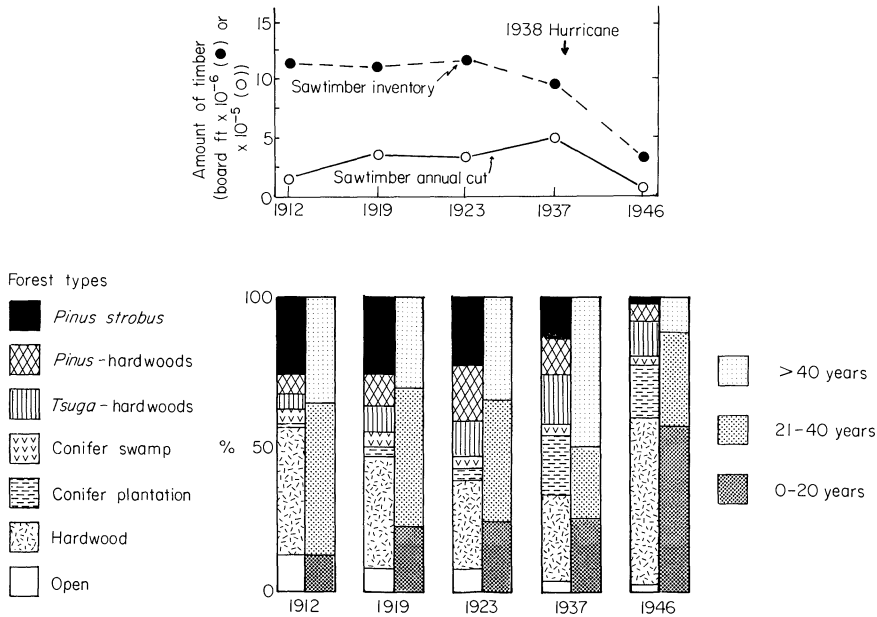


FIG. 2. Merchantable timber, average annual timber harvest and vegetation structure and composition on the Harvard Forest for the period preceding and subsequent to the 1938 hurricane (from Spurr 1956; Gould 1960).

subsequent vegetation dynamics converted the white pine–hardwood forest to hardwood forest and increased the percentage of young forest in the region (Brake & Post 1941).

Despite considerable attention to post-hurricane vegetation dynamics (Brake & Post 1941; Spurr 1956; Hibbs 1983), the actual patterns of damage and their implications in terms of landscape processes and long-term vegetation change have been little studied. The present study seeks to understand vegetation change by assessing wind damage at the species, stand and landscape scale. This information is being used to interpret the present compositional, structural and spatial characteristics of the Harvard Forest, to explain historical changes in these features, and to generate techniques for the simulation of the effect of catastrophic wind on forest vegetation for use in ecological and applied studies.

Specific objectives of the present paper are: (i) to examine species differences in susceptibility to wind damage; (ii) to investigate the differential susceptibility of the major forest types as controlled by composition, age, height and density; (iii) to examine damage by strata within stands of different age and structural differentiation; and (iv) to use this information to explain historical changes in vegetation structure and composition.

STUDY AREA

The study was conducted in and adjacent to the Harvard Forest in Petersham, Massachusetts (42°30'N, 72°10'W). The forest cover is characteristic of the Transition Hardwood–White Pine–Hemlock vegetation zone (Westveld 1956). The principal tree species include *Quercus borealis* (red oak), *Fraxinus americana* (white ash), *Acer rubrum* (red maple), *Betula lenta* (black birch), *Tsuga canadensis* (hemlock) and *Fagus grandifolia*

(beech).^{*} Other species that are widely distributed and locally important include *Betula papyrifera* (white birch), *Betula lutea* (yellow birch), *Quercus alba* (white oak), *Betula populifolia* (grey birch), *Pinus strobus* (white pine), *Carya ovata* and *C. cordiformis* (hickory) and *Quercus velutina* (black oak) on the uplands, and *Picea mariana* (black spruce), *Picea rubens* (red spruce) and *Larix laricina* (tamarack) on the wetlands. *Pinus resinosa* (red pine), *Picea abies* (Norway spruce) and *Picea glauca* (white spruce) are commonly planted in this region. At the time of the hurricane (21 September 1938) approximately ninety years had passed since the peak of agricultural activity in the region (Raup & Carlson 1941); the second-growth forests, which covered 65% of the landscape, were generally even-aged and in various stages of vegetation development (Gould 1960). The soils are formed on thin glacial till and outwash of variable thickness, and the bedrock is composed of gneisses, schist and granite. The mean annual precipitation of 105 cm is evenly distributed throughout the year.

METHODS

Following the hurricane, detailed descriptions and maps of damage were made in 1938–39 by W. Rowlands for each of the approximately 900 stands on the 1200-ha Harvard Forest (Harvard Forest Archives, unpublished). Quantitative information was collected to analyse differences in forest-type and species susceptibility to wind (Rowlands 1941). To minimize any confounding effects of topography and complex forest history only even-aged stands, fully exposed to the wind on level to gently rolling uplands and on moderate- to well-drained soils were sampled. Stand histories were well known, and pre-hurricane vegetational data from an intensive study in 1937 included stand age, composition, canopy height and stratification, density and basal area, and such soil characteristics as type, depth, drainage and stoniness (Harvard Forest Archives, unpublished).

A total of 115 plots (0.04–0.10 ha) were sampled by W. Rowlands, 65% on the Harvard Forest and the rest in adjacent Petersham. Hardwood forests comprised 55% of the stands, and 45% were conifer stands. Trees were tallied in each plot by species, height, canopy position (dominant, co-dominant, intermediate and suppressed) and damage class (standing, leaning, uprooted and broken; Rowlands 1941). Stand damage was computed as the percentage of dominant and codominant trees (trees forming the forest canopy) that were leaning, uprooted, or broken.

In the present study susceptibility to damage is analysed by species, forest type and stratal position as influenced by age, density and height using statistical procedures available on SYSTAT (Wilkinson 1986). Forest types were identified using detrended correspondence analysis (DECORANA; Hill 1979) based on species relative density for trees exceeding 5-cm diameter at breast height (dbh).

RESULTS

Vegetation types

Five major vegetation types occurred in the study plots sampled by Rowlands: *Pinus resinosa*, *Pinus strobus*, *Quercus–Carya–Pinus strobus*, *Acer rubrum–Quercus borealis* and

^{*} Species names follow Fernald (1970).

Northern Hardwood–*Tsuga* forests (Fig. 3). Relative density of species exhibits clear patterns of distribution on the stand ordination (Fig. 3). Axis 1 separates the plots by stand history: *Pinus resinosa* stands are entirely of anthropogenic origin and contain few native species, *Pinus strobus* stands include 20% plantations and 80% natural stands (old-field succession), and the other forests are of natural, second-growth origins.

Pinus resinosa (82%) and *Picea glauca* (14%) dominated the *Pinus resinosa* forests with *Picea abies* and *Pinus strobus* comprising the remainder of the stems (Table 1). These plantations dated to the establishment of the Harvard Forest in 1907 and ranged from 10 to 29 years of age. In *Pinus strobus* forests *Pinus strobus* was the dominant with numerous other species contributing 1–2%. Stands ranged to 100 years in age (Fig. 2). This forest type was prominent on abandoned agricultural sites and therefore formed a major component of the Petersham landscape in 1937.

Quercus–Carya–Pinus strobus forest occupied well-drained and infertile sites and was dominated by *Carya* species, *Pinus strobus*, *Quercus velutina*, *Q. alba* and *Acer rubrum*. On finer-textured soils *Acer rubrum* and *Quercus borealis* increased, and with *Pinus strobus*, *Quercus alba* and *Betula papyrifera* formed the *Acer rubrum–Quercus borealis* forest. Northern hardwoods, including *Fraxinus americana*, *Betula lutea* and *B. papyrifera* were found with *Tsuga canadensis* on moist fine-textured soils. This classification parallels other descriptions of the vegetation of this region and includes the major upland forest types (Raup & Carlson 1941; Spurr 1956).

Stand damage

The strong south-east winds resulted in a north-western orientation of the windblown trees (Fig. 4). In all forest types damage exhibits a positive linear relationship with stand age (Figs 5, 6 & 7) and height, and negative relationship with stand density (Table 2). Regressions using each variable are all significant ($P < 0.001$ – 0.05) with the exception of

TABLE 1. Relative density of tree species in the five forest types sampled in the study area in 1937.

	<i>Pinus resinosa</i>	<i>Pinus strobus</i>	<i>Quercus–Carya–Pinus strobus</i>	<i>Acer rubrum–Quercus borealis</i>	Northern Hardwoods– <i>Tsuga</i>
<i>Picea abies</i>	0.03				
<i>Picea glauca</i>	0.14				
<i>Pinus resinosa</i>	0.82	0.02			
<i>Prunus pensylvanica</i>		0.01		0.01	
<i>Betula populifolia</i>		0.01	0.01	0.03	
<i>Pinus strobus</i>	0.01	0.90	0.17	0.08	0.02
<i>Carya</i> spp.			0.21	0.03	
<i>Quercus velutina</i>			0.23	0.05	
<i>Populus tremuloides</i>			0.03	0.02	
<i>Fraxinus americana</i>			0.01	0.07	0.20
<i>Quercus alba</i>		0.01	0.20	0.09	0.03
<i>Acer rubrum</i>		0.02	0.08	0.16	0.11
<i>Quercus borealis</i>		0.01	0.06	0.23	0.12
<i>Betula lenta</i>		0.01		0.04	0.11
<i>Betula papyrifera</i>		0.01		0.07	0.13
<i>Betula lutea</i>				0.04	0.15
<i>Acer saccharum</i>				0.03	0.01
<i>Tsuga canadensis</i>				0.02	0.10

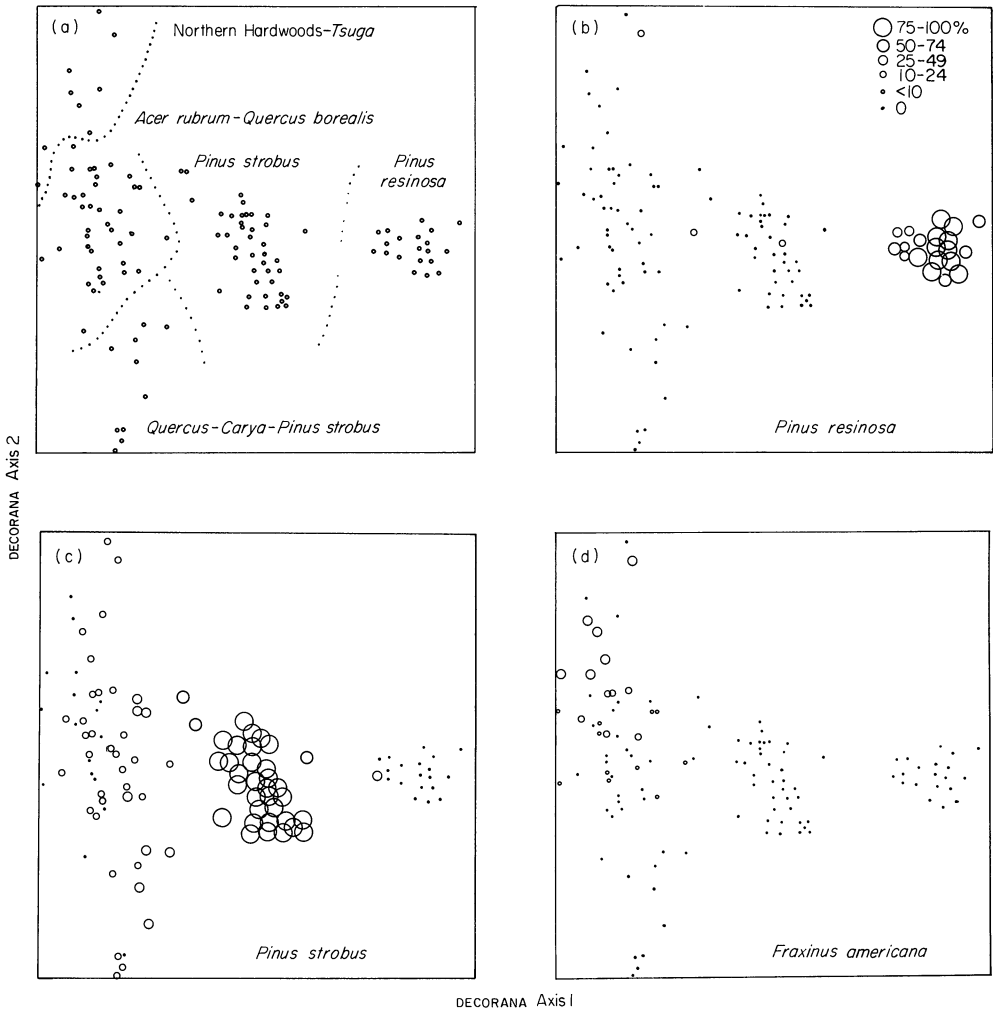


FIG. 3. Ordination of the 115 plots sampled in the study on the first two DECORANA axes (a) and relative density of the major species in those plots (b-h). Scale for relative density symbols provided in (b).

density for *Pinus resinosa* stands. The *Pinus resinosa* stands were planted and thinned to prescribed densities by silvicultural techniques rather than by natural establishment and self-thinning (Gould 1960); therefore, density was highly variable, weakly related to age (Table 3), and poorly explains the variation in damage.

The relationship between wind damage and age is quite different for conifer stands and hardwood stands (Fig. 5). From approximately 15 years of age conifers increase sharply in susceptibility. By 30 years of age conifer stands were completely destroyed by the storm. In contrast, hardwood forests show a more gradual increase in damage with age. Complete damage occurred only in stands exceeding 70 years of age. Some variation in susceptibility to wind damage is apparent among the hardwood forest types. *Quercus*-

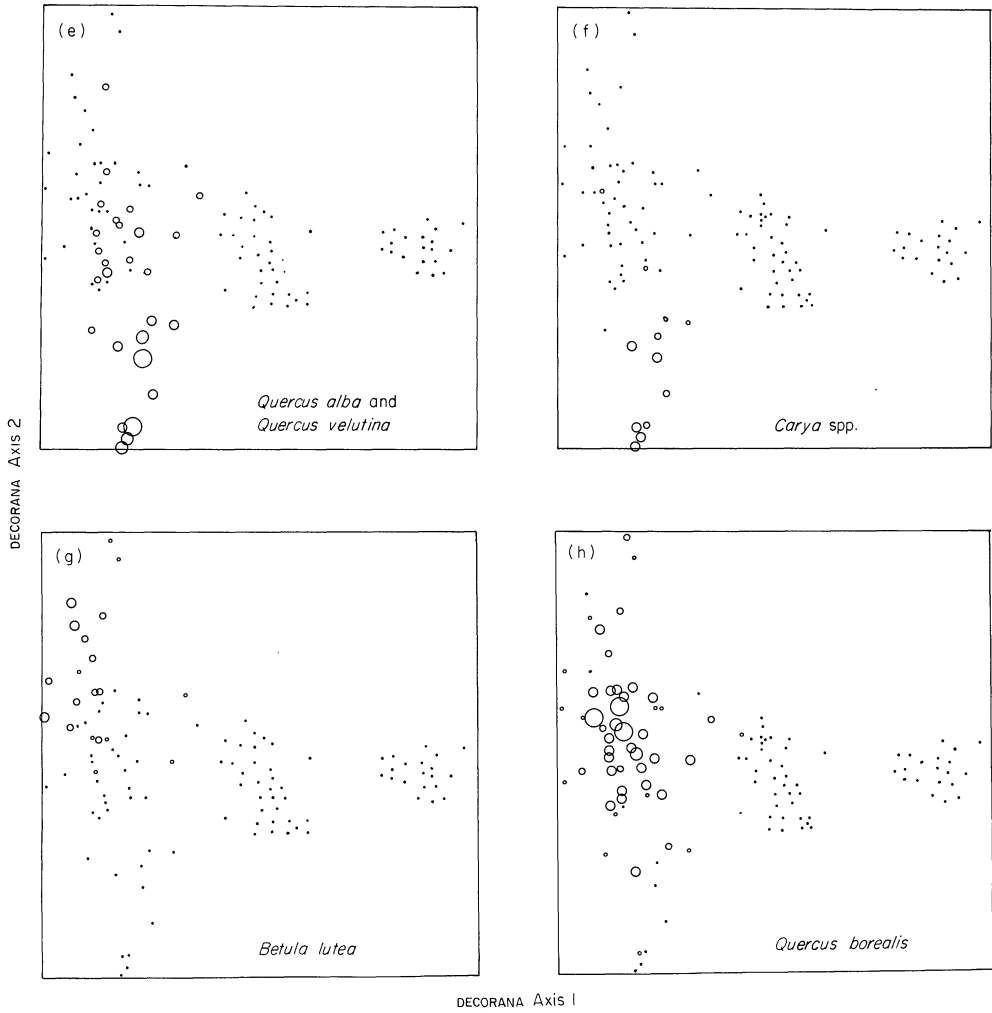


FIG. 3 (continued)

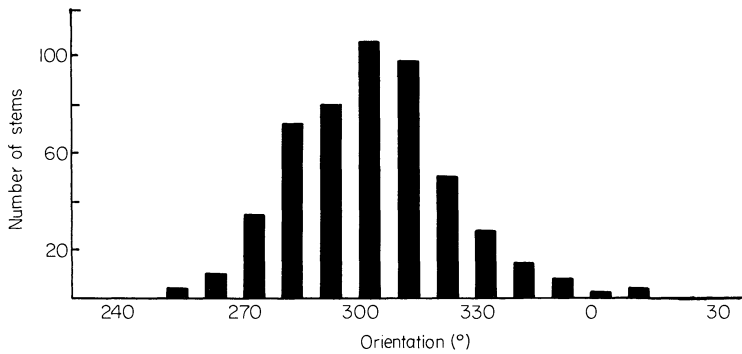


FIG. 4. Orientation of downed stems in the sample plots. The hurricane came from the south with strongest winds from east of south-east.

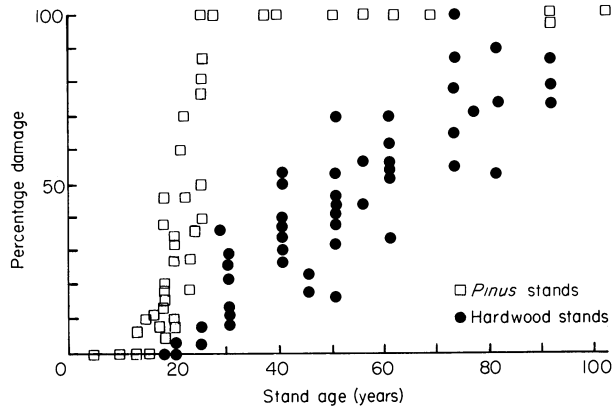


FIG. 5. Relationship between hurricane damage and stand age for conifer stands (*Pinus strobus* and *Pinus resinosa* forests; open squares) and hardwood stands (*Quercus-Carya-Pinus strobus*, *Acer rubrum-Quercus borealis* and Northern Hardwoods-*Tsuga* forests; filled circles).

Carya-Pinus strobus appeared somewhat more susceptible than the other stands, largely as a consequence of selective damage to *Pinus strobus*, which forms an emergent canopy over the hardwoods.

Type of damage

The vertical distribution of damage type among the forest strata was examined for the two most abundant forest types, the *Acer rubrum-Quercus borealis* and the *Pinus strobus* forests. In *Pinus strobus* stands, damage was approximately equally distributed among the strata at different ages (Fig. 6). Leaning, which is the prevalent type of damage in young stands, gave way to breakage and uprooting in older stands. Breakage was slightly more

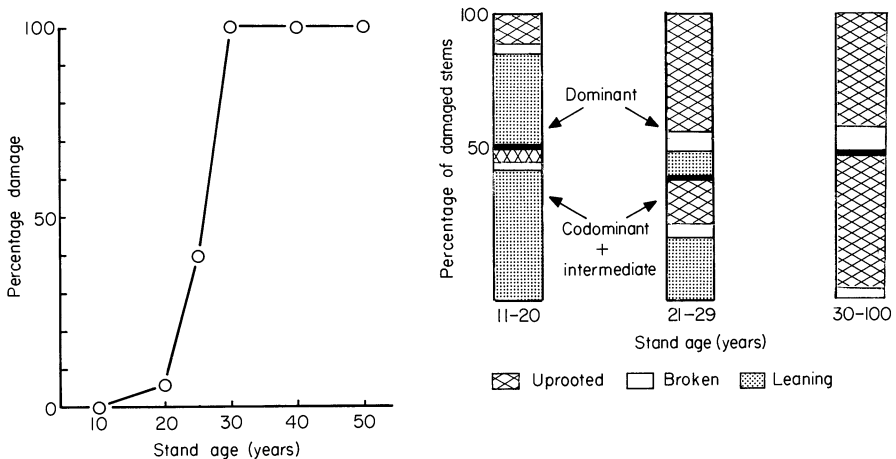


FIG. 6. Relationship between average stand damage and age for *Pinus strobus* stands and changes in the stratal distribution and type of damage following the 1938 hurricane at the Harvard Forest. Heavy bar separates dominant from codominant and intermediate strata of the vegetation.

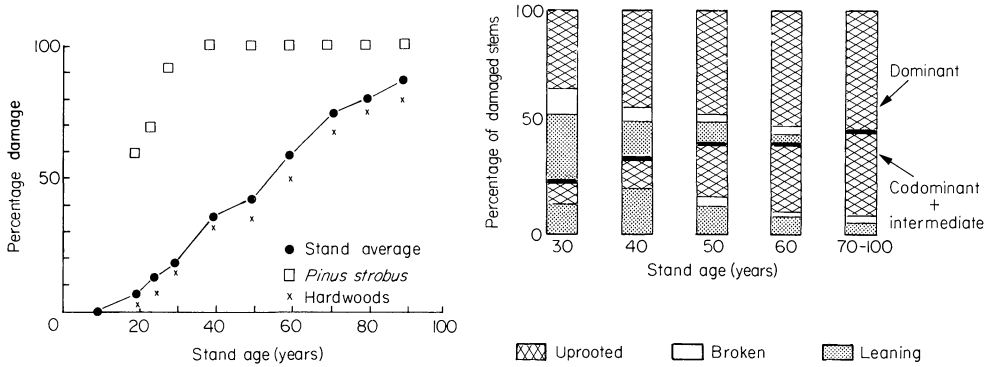


FIG. 7. Relationship between average stand damage and age for hardwood stands (*Acer rubrum-Quercus borealis* forest) and changes in the stratal distribution and type of damage following the 1938 hurricane at the Harvard Forest. Heavy bar separates dominant from codominant and intermediate strata of the vegetation. Average damage to *Pinus* trees and hardwoods for each stand age are indicated by separate symbols.

TABLE 2. Coefficients of determination of damage on stand age, height and density for the major vegetation types sampled in the study area in 1938. The highest r^2 is underlined. Significance values are given as: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Forest type (number of stands)	Age	Height	Density
<i>Pinus resinosa</i> (20)	0.46***	0.43**	0.002
<i>Pinus strobus</i> (41)	0.66***	0.63***	0.48***
<i>Quercus-Carya-Pinus strobus</i> (10)	<u>0.71**</u>	0.43*	0.65**
<i>Acer rubrum-Quercus borealis</i> (35)	0.44***	0.43***	0.27*
Northern Hardwoods- <i>Tsuga</i> (9)	0.56*	0.54*	0.44*
Hardwoods stands (54)	<u>0.60***</u>	0.46**	0.41*
Conifer stands (61)	<u>0.61***</u>	0.58***	0.05

TABLE 3. Coefficients of determination for stand age on stand height and density for the major vegetation types sampled in the study area in 1938. The highest r^2 value is underlined. Significance values are given as: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Forest type (number of stands)	Height	Density
<i>Pinus resinosa</i> (20)	0.68***	0.07
<i>Pinus strobus</i> (41)	<u>0.82***</u>	0.51***
<i>Quercus-Carya-Pinus strobus</i> (10)	0.61***	0.48**
<i>Acer rubrum-Quercus borealis</i> (35)	<u>0.82***</u>	0.51***
Northern Hardwoods (9)	<u>0.91***</u>	0.62**

TABLE 4. Type of windthrow damage suffered by the major forest types in the Harvard Forest in 1938.

Forest type	Damage (%)		
	Uprooted	Broken	Uprooted:broken
<i>Pinus resinosa</i>	93	7	13.3
<i>Pinus strobus</i>	91	9	10.1
<i>Quercus-Carya-Pinus strobus</i>	89	11	8.1
<i>Acer rubrum-Quercus borealis</i>	88	12	7.3
Northern Hardwoods- <i>Tsuga</i>	95	5	19.0

Catastrophic wind damage to New England forests

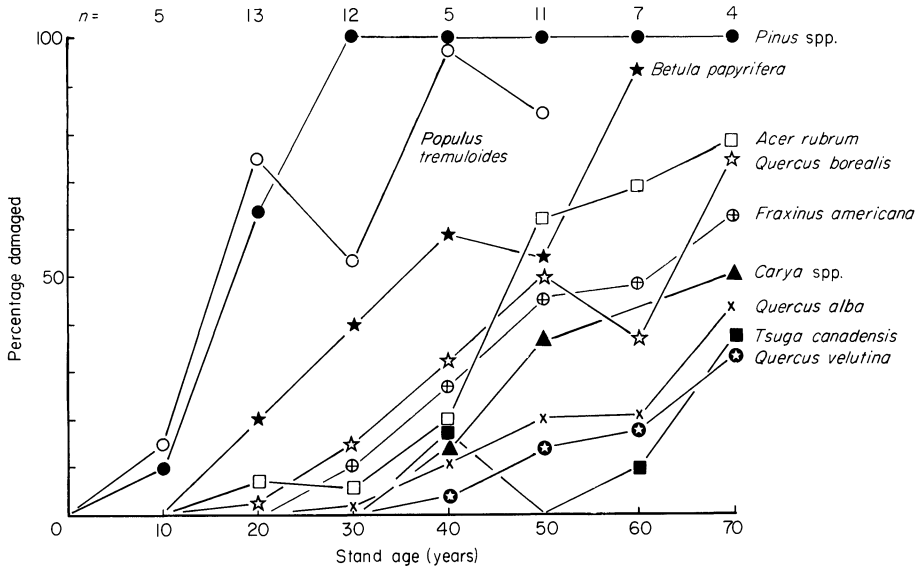


FIG. 8. Relationship between age and average percentage damage of the important tree species in all the plots following the 1938 hurricane at the Harvard Forest.

important in older conifer than hardwood stands, comprising 6–14% of the stems and generally occurring 1–5 m from the ground. Although breakage was highly conspicuous in the landscape after the 1938 storm, it was actually a much less important form of damage than uprooting (Table 4).

In the *Acer rubrum*–*Quercus borealis* forest the vertical distribution of damage shifted from the dominant trees in younger stands to include codominant and intermediate trees in older stands (Fig. 7). A decline in the proportion of leaning trees and corresponding increase in uprooted trees paralleled the general increase in severity of damage with age. Breakage was relatively unimportant, comprising 5–12% of total stems across all stand ages and strata.

Species damage

The relationship between age and damage was examined for all species with an average relative density exceeding 2% (Fig. 8). Each species exhibits a general trend of increasing damage with age, but the slope of this relationship varies. Ranking by decreasing susceptibility to wind shows: *Pinus* spp. > *Populus* > *Betula papyrifera* > *Acer rubrum* > *Quercus borealis* and *Fraxinus americana* > *Carya* spp., *Quercus alba*, *Q. velutina* and *Tsuga canadensis*.

DISCUSSION

Species level response

Differences in species susceptibility to wind damage are generally explained by shoot and root structure as they influence the turning moment, strength of compression of the

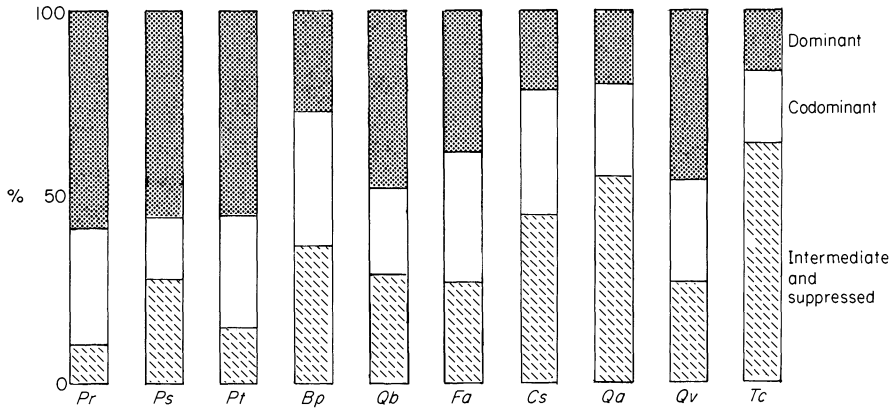


FIG. 9. Vertical stratification of the major tree species in the 115 plots sampled in 1938. Dark shading = dominant; white = codominant; hatched = intermediate and suppressed. Species abbreviations: Pr, *Pinus resinosa*; Ps, *Pinus strobus*; Pt, *Populus tremuloides*; Bp, *Betula papyrifera*; Qb, *Quercus borealis*; Fa, *Fraxinus americana*; Cs, *Carya* spp.; Qa, *Quercus alba*; Qv, *Quercus velutina*; Tc, *Tsuga canadensis*. Species are arranged by approximate susceptibility to wind damage (see Fig. 8).

wood, and anchorage (Mergen 1954; McMahon 1975; Savill 1983). In the present study there is close agreement between susceptibility and canopy position at the time of the 1938 hurricane. In the Harvard Forest in 1938, rapidly growing, shade-intolerant species (*Pinus strobus* and *P. resinosa*, *Populus*, *Betula papyrifera*) tended to occupy dominant positions in the canopy (Fig. 9) where they were exposed to the highest wind velocities (Harvard Forest Archives, unpublished). Slower growing, more shade-tolerant species (*Acer rubrum*, *Carya* spp., *Quercus alba* and *Tsuga canadensis*) generally occupied a subordinate canopy position in the forests in which they occurred and consequently were protected from the wind (Fig. 8).

Quercus velutina in particular does not fit the pattern described above; it has approximately the same relative canopy position in *Quercus*–*Carya*–*Pinus* forest as *Q. borealis* in *Acer rubrum*–*Quercus borealis* forest (Fig. 9) and yet suffered much less damage (Fig. 8). Structural differences between the root systems of these species may explain this differential response. *Quercus velutina*, like *Q. alba* and the *Carya* spp., has deep spreading lateral roots and a central tap root, whereas *Q. borealis* has a much more superficial root system that affords much less stability (Fowells 1965).

The relationship between crown position and damage emphasizes the critical role that autecology plays in controlling forest dynamics, and is well illustrated by the comparison of *Pinus strobus* and *Tsuga canadensis*. Both conifers are extremely susceptible to windthrow because of their full crowns and shallow root systems (Raymer 1962), although *Tsuga* may be less susceptible as a result of the great vertical extent of the crown, flexible branches and tapering shape. In pure stands or stands in which it dominates the canopy, *Tsuga* is noted to be as prone to uprooting as *Pinus strobus* (Harvard Forest Archives, unpublished; Pinchot & Graves 1896; Collins 1956). In central New England, however, *Tsuga canadensis* often forms a suppressed understorey beneath *Pinus* or hardwoods, whereas *Pinus strobus* forms the upperstorey or a supercanopy above hardwoods and *Tsuga*. These differences in canopy placement and attendant structural differences result in *Pinus strobus* being the most susceptible and *Tsuga canadensis* the

least susceptible trees in the study. The result at the stand level is that *Pinus* is frequently eliminated from the stand by catastrophic wind, whereas *Tsuga* may actually increase through the release of suppressed saplings (Marshall 1927; Henry & Swan 1974).

Intraspecific variation in susceptibility may be explained by shoot and root form, local soil conditions, historical factors and chance. On shallow or very wet soils restricted root development enhanced susceptibility (Harvard Forest Archives, unpublished). Shoot form, e.g. shape and length of crown, controls the turning moment (distance perpendicular to the vector resulting from the wind force: Curtis 1943; Wilson & Archer 1979), and as a consequence there is considerable difference in response for open-grown trees with broad, long crowns and densely-packed trees with tall narrow stems and compact crowns. Many stands of dense, young *Pinus* spp. were destroyed leaving scattered, older trees that had established in old fields and subsequently provided the seed source for the dense stand (Rowlands 1941). In addition to having a long crown that distributes the wind force down the trunk, open-grown trees develop a sturdier root system in response to wind pressure during growth (Zimmermann & Brown 1979).

Trees in recently thinned plots were much more vulnerable than in adjacent unmanaged stands (Harvard Forest Archives, unpublished), but edge trees that were continually exposed to wind were more resistant. Despite the generally uniform action of the wind in the landscape, local gusts and turbulence produced some inexplicable patterns of damage and survival.

Stand level response

Stand differences in response to wind appear to be adequately explained by an understanding of species susceptibilities and their relative density in the various forest types. For example, *Pinus strobus*, the most susceptible species, exhibits a similar damage curve in pure stands, mixed *Pinus strobus*–*Pinus resinosa* stands, and also in the hardwood stands, in which it ranges from rare to plentiful (Figs 6 & 7). As a consequence, although the *Quercus*–*Carya*–*Pinus strobus* forest is largely composed of wind-resistant species (*Carya* spp., *Quercus alba* and *Q. velutina*), it exhibited fairly high susceptibility because of the complete destruction of the *Pinus* that accounted for 17% of the stems. This consistent susceptibility of *Pinus strobus* occurred because it had a dominant canopy position in all of the forest types; presumably if the vertical position of a species changes in different forests its response to wind would be much more variable.

Over the age and structural characteristics covered in this study, damage exhibited an approximately linear response with stand age (Table 2), an observation generally corroborated in other studies (Curtis 1943; Andersen 1953). The general trend of increasing wind susceptibility with age is explained by progressive changes that occur in tree structure and architecture. As the canopy increases in height, the length of the turning moment increases. This, together with the general increase in canopy size with age and greater wind speed at taller heights, induces greater susceptibility (Curtis 1943; Wilson & Archer 1979). In addition, as the canopy of even-aged stands stratifies and differentiates vertically with age, the increase in canopy surface roughness (Oliver 1975; Kelty 1984) augments wind turbulence and allows greater incursion of air to accelerate blowdown (Savill 1983).

The vertical distribution and quality of damage parallels the extent of damage. Within hardwood and conifer stands, as the percentage of damage increases, i.e. at increasing age and height, the lower strata suffer increasing damage and windthrow increases relative to

leaning. When stand damage is slight, injury to subordinate trees occurs primarily through crushing and therefore depends on their placement relative to the windthrown overstorey trees. As overstorey damage and gap size increase the probability of direct damage to subordinates by wind increases. Under severe canopy damage extensive exposure of the understorey to the direct force of the wind produces widespread understorey windthrow.

Qualitative aspects of damage

Many investigations of forest disturbance processes and subsequent vegetation dynamics concentrate on gap dimensions, especially as these control the light regime and the role of tree encroachment, advanced regeneration or pioneer establishment (e.g. Denslow 1980; Runkle 1985; White, Mackenzie & Busing 1985; Canham & Marks 1985). With some exceptions (e.g. Naka 1982; Putz *et al.* 1983; Harmon *et al.* 1986; Franklin *et al.* 1987) little attention has been directed towards qualitative differences in tree mortality and their attendant impact on vegetation development.

A survey of the limited mortality data from various tropical and temperate forests suggests some surprising, yet consistent results. In most forests single or small multiple-tree gaps result more frequently from tree-snap than uprooting. Occasionally, standing dead comprise a greater proportion of the mortality, as in some Dipterocarp forests in Borneo (P. Ashton, personal communication) and Malaysia (Putz *et al.* 1983). Similarly, under dry conditions in most forests, breakage far exceeds uprooting following strong windstorms (Naka 1982; Kanzaki & Yoda 1986). The major exceptions, in which uprooting is reported to predominate over snapping, include the edges of clear-cuts (Boe 1965; Alexander 1964), plantations (e.g. Day 1950; Holtam 1971), moist tropical forest (Hartshorn 1980; Uhl 1982), forested swamps (Stoeckler & Arbogast 1955) and damage from the 1938 hurricane in New England (Curtis 1943; Brake & Post 1941). In the latter cases, uprooting comprised 87–100% of the damage in all forest types, as was documented in the present study (Table 4).

In forests not subject to high winds, trees die standing or may break, frequently at some point of injury or decay (Andersen 1953; Alexander 1964; Putz *et al.* 1983). As trees are increasingly subjected to strong horizontal forces, rooting firmness joins stem structure in determining the proportion of uprooting to snapping (Mergen 1954). On shallow soils and on water-saturated sites (e.g. *Thuja* swamps—Eyre & Longwood 1951) or sites that restrict root penetration (e.g. clay soils—Brewer & Merritt 1978) uprooting may occur before breakage is reached. This pattern will naturally be dependent on the rooting characteristics of the species involved. During the 1938 hurricane 15–35 cm of precipitation preceded the strongest winds. Thus, the soil was saturated and loosened, rooting strength was reduced, and uprooting was the predominant source of damage (Rowlands 1941). Breakage was important only on very well drained soils or on rock outcrops where the trees were firmly anchored in crevices (Harvard Forest Archives, unpublished).

Smith (1946) and Brooks (1939) state that the meteorology of tropical storms is such that those of catastrophic magnitude reaching New England will produce sufficient precipitation to saturate the soil fully before the strongest winds develop. The damage from the 1938 hurricane may therefore be qualitatively representative of any equally powerful hurricane. Windthrow mounds have been dated and ascribed to hurricanes in 1635, 1815, and 1938 in central New England (Stephens 1956; Henry 1967; Harvard Forest Archives, unpublished). This episodic formation of mound and pit micro-

topography may be due not only to the fact that hurricanes represent the major disturbance factor in the area, but that this microtopography is differentially created by tropical storms, in comparison with other wind disturbances or normal mortality processes.

The type of damage has strong implications concerning site conditions and subsequent vegetation development; therefore, the observation that hurricane damage may differ in quality as well as quantity from other wind damage, general mortality processes, or silvicultural harvesting is important. Uprooting mixes the upper soil layers, impedes soil development, exposes a broad surface of mineral soil, creates considerable microtopographic and microenvironmental variation, and locally removes or exposes buried seed pools (Stephens 1956; Beke & McKeague 1984; Putz *et al.* 1983). The exposed soil favours the establishment of small-seeded and pioneer species such as *Betula* spp., *Pinus strobus* and *Tsuga canadensis* that require moist seedbeds (Beatty 1984), whereas the micro-differences in seedbed drainage, chemistry and substrate may accommodate a wider diversity of species than in a comparable stand that suffered only breakage or human harvesting (Lyford & MacLean 1966).

Forest damage and landscape processes

The major conclusion of studies on wind damage is that hurricane-force winds operate quite specifically in the forested landscape with a discriminating effect that has profound consequences on the vegetation over a range of spatial scales (Collins 1956). As shown elsewhere, wind damage occurs differentially within landscapes, largely controlled by topographic position and aspect (Fetherston 1987). Because hurricane winds in central New England are confined to a rather small range in overall direction (i.e. east to south west: Smith 1946) it should be quite possible to determine where individual sites lie on a continuum of probable susceptibility.

At a finer scale, at the stand level, forest types respond to wind with significantly different, yet predictable, patterns of damage depending on age. The consequences of this differential response for vegetation change are manifold. The response of vegetation to catastrophic wind will be determined by physiography and by the structural (age, height, density) and compositional characteristics of the vegetational mosaic. The extent of damage for a given landscape position and storm will therefore be determined largely by historical factors, e.g. time since last storm, the previous regime of human clearing and agriculture, the direction and extent of secondary vegetation development. For example, the landscape of central New England in the 1930s, dominated by 30–100-year-old *Pinus strobus* forests on abandoned agricultural land, was prone to catastrophe because of the extreme susceptibility of pine to wind. A similar storm in 1815, at the height of the agricultural period in central Massachusetts when nearly 70% of the Petersham landscape was cleared, left much less forest damage, despite extensive cultural destruction (Coolidge 1948). Similarly, a storm in today's landscape of even-aged hardwood forest would generate an entirely different landscape mosaic.

Within stands the selective removal of tree species in 1938 produced significant compositional changes. The widespread conversion of *Pinus strobus* and *Pinus*–hardwood forests to hardwood and hardwood–*Tsuga* was produced by three factors: (i) selective removal of *Pinus* in mixed stands; (ii) differential destruction of conifer versus hardwood stands; and (iii) the greater ability of hardwoods to revegetate sites through vegetative reproduction, resurgence of advanced growth, and rapid growth rates (Brake & Post 1941).

CONCLUSION

In general there exists a tendency to place disturbances and their effects on a gradient related to gap size: e.g. individual treefalls produce confined gaps whereas catastrophic windstorms blow down large areas of forest to favour pioneer species (Canham & Loucks 1984). Small gaps are thought to favour shade-tolerant species, whereas large gaps favour shade-intolerant species (Runkle 1985). The present study suggests that the issue may be much more complex. Even for a storm that devastates large areas there is a continuum of effect and consequence that is controlled by site and vegetational factors. On protected sites, in young stands or in many hardwood forests the 1938 hurricane produced individual or small group blowdowns in similar fashion to the 1985 hurricane in southern New England (D. R. Foster, personal observation). In older forests, in conifer stands, or on more exposed sites the wind created progressively more damage. This heterogeneous, though specific action, coupled with qualitative differences in the resulting microenvironments and patterns of recovery helped to produce the diverse forest landscape of the present.

ACKNOWLEDGMENTS

This paper is based on unpublished data largely collected by W. Rowlands; thanks are given to him for the use of the material and for helpful suggestions. Acknowledgment is given to H. Raup and E. Gould for enlightening discussions on the disturbance history of the Harvard Forest; to J. Franklin, J. Ogden, P. Schoonmaker, T. Sipe and G. Whitney for valuable comments; and to B. Flye for secretarial assistance.

REFERENCES

- Alexander, R. R. (1964). Minimizing windfall around clear cuttings in Spruce-Fir forests. *Forest Science*, **10**, 130-142.
- Andersen, K. F. (1953). Gales and gale damage to forests, with special reference to the effects of the storm of 31st January 1953, in the north-east of Scotland. *Forestry*, **27**, 97-121.
- Beatty, S. W. (1984). Influence of microtopography and canopy species on spatial patterns of forest understory plants. *Ecology*, **65**, 1406-1419.
- Beke, G. J. & McKeague, J. A. (1984). Influence of tree wind throw on the properties and classification of selected forest soils from Nova Scotia. *Canadian Journal of Soil Science*, **64**, 195-207.
- Boe, K. N. (1965). Windfall after experimental cuttings in old-growth redwoods. *Proceedings of the Society of American Foresters*, **1965**, 59-63.
- Brake, R. W. & Post, H. A. (1941). *Natural restocking following hurricane damaged 'old field' white pine areas in north central Massachusetts*. M.F.S. thesis, Harvard University.
- Brewer, R. & Merritt, P. G. (1978). Wind throw and tree replacement in a climax beech-maple forest. *Oikos*, **30**, 149-152.
- Brooks, C. F. (1939). Hurricanes into New England: meteorology of the storm of September 21, 1938. *Smithsonian Institution Report*, **3563**, 241-251.
- Canham, C. D. & Loucks, O. L. (1984). Catastrophic windthrow in the presettlement forests of Wisconsin. *Ecology*, **65**, 803-809.
- Canham, C. D. & Marks, P. L. (1985). The response of woody plants to disturbance: patterns of establishment and growth. *The Ecology of Natural Disturbance and Patch Dynamics* (Ed by S. T. A. Pickett & P. S. White), pp. 197-216. Academic Press, New York.
- Cline, A. C. & Spurr, S. H. (1942). The virgin upland forest of central New England. *Harvard Forest Bulletin*, **21**, 1-58.
- Collins, S. (1956). *The biotic communities of Greenbrook Sanctuary*. Ph.D. Thesis, Rutgers University.
- Coolidge, M. C. (1948). *The History of Petersham, Massachusetts*. Powell Press, Hudson, Massachusetts.
- Curtis, J. D. (1943). Some observations on wind damage. *Journal of Forestry*, **41**, 877-882.
- Day, W. R. (1950). Soil conditions which determine windthrow in forests. *Forestry*, **23**, 90-95.
- Denslow, J. S. (1980). Gap partitioning among tropical rainforest trees. *Biotropica*, **12** (Supplement), 47-55.

- Eyre, F. H. & Longwood, F. R. (1951). Reducing mortality in old-growth northern hardwoods through partial cutting. *USDA Forest Service Lake States Forest Experiment Station Paper*, **25**, 1–32.
- Fernald, M. L. (1970). *Gray's Manual of Botany*. D. Van Nostrand & Company, New York.
- Fetherston, K. (1987). *A computer cartographic analysis of a forested landscape's response to hurricane force wind in central New England*. M.F.S. thesis, Harvard University.
- Foster, D. R. (1988). Disturbance history, community organization, and vegetation dynamics of the old-growth Pisgah forest, south-western New Hampshire, U.S.A. *Journal of Ecology*, **76**, 105–134.
- Fowells, H. A. (1965). Silvics of forest trees of the United States. *USDA Agricultural Handbook*, **271**.
- Franklin, J. F., Klopsch, M., Luchessa, K. J. & Harmon, M. E. (1987). Tree mortality in some mature and old-growth forests in the Cascade Range of Oregon and Washington. *Canadian Journal of Forest Research*, **17** (in press).
- Gould, E. M., Jr (1960). Fifty years of management at the Harvard Forest. *Harvard Forest Bulletin*, **29**, 1–30.
- Harmon, M. E., Franklin, J. F., Swanson, F. J., Sollins, P., Lattin, J. D., Anderson, N. H., Gregory, S. V., Cline, S. P., Aumen, N. G., Sedell, J. R., Cromack, K. and Cummins, K. W. (1986). Role of coarse woody debris in temperate ecosystems. *Advances in Ecological Research*, **37**, 1–214.
- Hartshorn, G. S. (1980). Neotropical forest dynamics. *Biotropica*, **12**, 23–30.
- Henry, J. D. (1967). *The Pisgah forest: 300 years of change*. M.F.S. Thesis, Harvard University.
- Henry, J. D. & Swan, J. M. A. (1974). Reconstructing forest history from live and dead plant material—an approach to the study of forest succession in S.W. New Hampshire. *Ecology*, **55**, 772–783.
- Hibbs, D. E. (1983). Forty years of forest succession in central New England. *Ecology*, **64**, 1394–1401.
- Hill, M. O. (1979). *DECORANA—A FORTRAN Program for Detrended Correspondence Analysis and Reciprocal Averaging*. Cornell University, Ithaca, New York.
- Holtam, B. W. (1971). Windblow of Scottish forests in January 1968. *Forestry Commission Bulletin*, **45**.
- Kanzaki, M. & K. Yoda. (1986). Regeneration in subalpine coniferous forests. II. Mortality and pattern of death of canopy trees. *Botanical Magazine, Tokyo*, **99**, 37–51.
- Kelty, M. J. (1984). *The development and productivity of hemlock-hardwood forests in southern New England*. Ph.D. Thesis, Yale University.
- Lyford, W. H. & MacLean, D. W. (1966). Mound and pit microrelief in relation to soil disturbance and tree distribution in New Brunswick, Canada. *Harvard Forest Paper*, **15**, 1–18.
- Marshall, R. (1927). The growth of hemlock before and after release from suppression. *Harvard Forest Bulletin*, **11**, 1–43.
- McMahon, T. (1975). The mechanical design of trees. *Scientific American*, **233** (1), 92–102.
- Mergen, F. (1954). Mechanical aspects of wind-breakage and windfirmness. *Journal of Forestry*, **52**, 119–125.
- Naka, K. (1982). Community dynamics of evergreen broadleaf forests in southwestern Japan. I. Wind damaged trees and canopy gaps in an evergreen oak forest. *Botanical Magazine, Tokyo*, **95**, 385–399.
- NETSA (1943). *Report of the U.S. Forest Service Programs resulting from the New England Hurricane of September 21, 1938*. Northeastern Timber Salvage Administration, Boston, Massachusetts.
- Neumann, C. J., Cry, G. W., Caso, E. L. & Jarvinen, B. R. (1978). *Tropical cyclones of the North Atlantic Ocean 1871–1980*. National Oceanic and Atmospheric Administration, National Weather Service Washington, D.C.
- Oliver, C. D. (1975). The development of northern red oak in mixed stands in central New England. *Yale University, School of Forestry and Environmental Studies Bulletin*, **91**, 1–63.
- Pickett, S. T. A. (1980). Non-equilibrium coexistence of plants. *Bulletin of the Torrey Botanical Club*, **107**, 238–248.
- Pinchot, G. & Graves, H. S. (1896). *The White Pine*. Century Company, New York.
- Putz, F. E., Coley, D. D., Lu, K., Montalvo, A. & Aiello, A. (1983). Uprooting and snapping of trees: structural determinants and ecological consequences. *Canadian Journal of Forest Research*, **13**, 1011–1020.
- Raup, H. M. (1964). Some problems in ecological theory and their relation to conservation. *Journal of Ecology*, **52** (Supplement), 19–28.
- Raup, H. M. & Carlson, R. E. (1941). The history of land use in the Harvard Forest. *Harvard Forest Bulletin*, **20**, 1–64.
- Raymer, W. G. (1962). Wind resistance of conifers. *National Physical Laboratory Aerodynamics Division, UK, Report*, **1008**.
- Rowlands, W. (1941). *Damage to even-aged stands in Petersham, Massachusetts by the 1938 hurricane as influenced by stand condition*. M.F.S. thesis, Harvard University.
- Runkle, J. R. (1985). Disturbance regimes in temperate forest. *The Ecology of Natural Disturbance and Patch Dynamics* (Ed by S. T. A. Pickett & P. S. White), pp. 17–34. Academic Press, New York.
- Savill, P. S. (1983). Silviculture in windy climates. *Forestry Abstracts*, **44**, 473–488.
- Smith, D. M. (1946). *Storm damage in New England forests*. M.F. Thesis, Yale University.
- Spurr, S. H. (1956). *Stand composition in the Harvard Forest*. Ph.D. Thesis, Yale University.
- Stephens, E. P. (1956). The uprooting of trees: a forest process. *Proceedings of the Soil Science Society of America*, **20**, 113–116.

- Stoekler, J. H. & Arbogast, C. (1955).** Forest management lessons from a 1949 windstorm in northern Wisconsin and upper Michigan. *USDA Forest Service Lake States Forest Experiment Station Paper*, **34**.
- Uhl, C. (1982).** Tree dynamics in a species rich tierra firme forest in Amazonia, Venezuela. *Acta Cientifica Venezolana*, **33**, 72–77.
- Westveld, M. S. (1956).** Natural forest vegetation zones of New England. *Journal of Forestry*, **54**, 332–338.
- White, P. S. (1979).** Pattern, process, and natural disturbance in vegetation. *Botanical Review*, **45**, 229–299.
- White, P. S., MacKenzie, M. D. & Busing, R. T. (1985).** Natural disturbance and gap phase dynamics in southern Appalachian spruce-fir forests. *Canadian Journal of Forest Research*, **15**, 233–240.
- Wilkinson, L. (1986).** *SYSTAT: The System for Statistics*. SYSTAT Inc., Evanston, Illinois.
- Wilson, B. F. & Archer, R. R. (1979).** Tree design: some biological solutions to mechanical problems. *Bioscience*, **29**, 293–298.
- Wright, H. E. & Heinselman, M. L. (1973).** The ecological role of fire in natural conifer forests of western and northern North America. *Quaternary Research*, **3**, 319–328.
- Zimmermann, M. H. & Brown, C. L. (1979).** *Trees—Structure and Function*. Springer-Verlag, New York.

(Received 15 January 1987)