Heterogeneity in Forest Structure, Composition, and Dynamics Following Catastrophic Wind Disturbance, Pisgah Forest, Southwestern New Hampshire

A thesis presented

by

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to

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ABSTRACT

(1) This study examines the influences of physiography and forest structure on the immediate and long-term effects of the 1938 hurricane within the 10-ha Harvard tract, located in the Pisgah region of southwestern New Hampshire. The study site has never been logged. Data on the present characteristics and past growth of all trees (stems ≥1 cm dbh) within 11 0.01-ha plots were collected and analyzed, and results from previous studies of other sites within the Harvard tract were reviewed.

(2) Tree ring data from the present study and demographic data from early post-hurricane surveys indicate that hurricane damage, though universally severe, differed with slope position across the tract.

(3) Growth and establishment data from the present study and demographic data from a 1929 survey of the tract indicate that the pre-hurricane forest was quite heterogeneous in structure and composition, resulting in heterogeneity of hurricane damage and post-hurricane vegetation.

(4) Physiographically mediated patchiness in hurricane damage caused plots of different slope position to differ considerably in their post-hurricane development and present characteristics. Stems which were 4.00-7.99 cm in diameter at the time of the hurricane grew faster and attained the overstory more frequently in ridgetop plots than in lower plots. Ridgetop plots contain more stems which post-date the hurricane than do lower plots. Ridgetop plots have higher densities and lower basal areas than do lower plots.

(5) Partly because of differences in pre-hurricane and -- consequently -- post-hurricane stand structure, plots of similar slope position differ somewhat in their post-hurricane development and current characteristics.

(6) Although previous studies have demonstrated that hurricane damage is highly heterogeneous on a landscape scale, these results reveal that important heterogeneity, leading to significant long-term differences, also exists within relatively small areas of relatively homogeneous damage.

INTRODUCTION

Natural disturbance generates forest patchiness in two ways: (1) it recurs, creating patches of different age and successional status; (2) it differs in its effects from disturbance to disturbance and (in the case of widespread disturbance) from site to site. Under gap-disturbance and other milder disturbance regimes, these two mechanisms interact to determine the patterns of disturbance-induced patchiness. Catastrophic ("large-scale," Oliver 1981) disturbance, however, synchronizes this patchiness over large areas, generating forest heterogeneity solely through its differing effects across the landscape.

Catastrophes can produce considerable heterogeneity. Although severe catastrophic disturbances such as erosion, glacial scouring, and lava flows can cause universal destruction, damage from milder catastrophic disturbances such as hurricanes varies across the landscape (Oliver & Larson 1990). Hurricane damage varies with physiography and with stand structure, composition, and density, resulting in a diverse mosaic of surviving vegetation (Foster 1988a, 1988b; Foster & Boose 1992). Additionally, the composition, structure, and density of surviving vegetation can vary across a particular patch of the damage mosaic because of pre-disturbance patchiness.

Forest patchiness following catastrophic disturbance can have profound and lasting consequences. Patches with larger and denser advance regeneration contain less available growing space, resulting in lower growth and survival rates of seedlings, sprouts, and smaller advance growth, and in greater dominance of stems which predate the disturbance (Oliver & Stephens 1977; Peet & Christensen 1980). Even within areas of total canopy destruction, differences in the height and densities of surviving stems can produce dramatic long-term differences in forest dynamics and physiognomy (Marquis 1981). Yet, few attempts have been made to describe the varying structure, development, and effects of advance growth following catastrophic disturbance.

The great hurricane of 1938 left a mosaic of forest damage across southern and central New England (Spurr 1956; Foster 1988b, Foster & Boose 1992). Among the areas most heavily damaged by the hurricane was the Pisgah region of southwestern New Hampshire (Foster 1988a), site of Harvard University's 10-ha old-growth tract. Almost the entire overstory of the tract was destroyed (Fig. 1; Harvard Forest Archives; Foster 1988a; Schoonmaker 1992). In this study of the Harvard tract, the characteristics and growth of trees extant in 1990 are analyzed to address the following questions about the immediate and long-term effects of the hurricane: (i) Did hurricane damage differ with physiography across the tract,

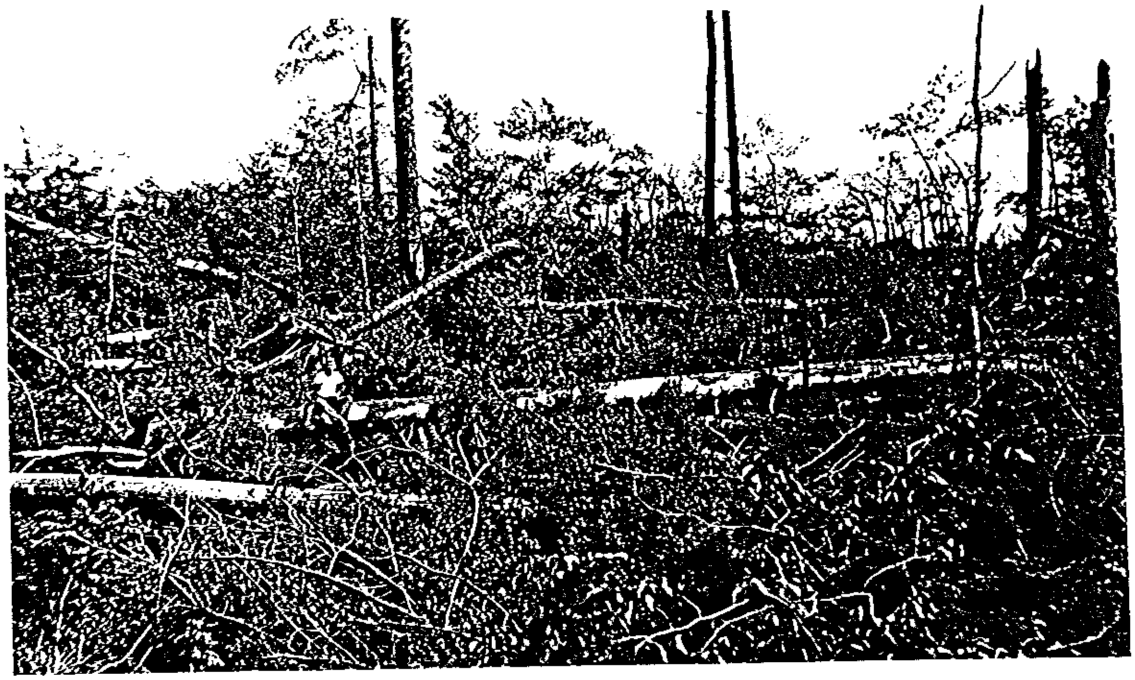


Figure 1. The Harvard tract in 1942, four years after the hurricane. The general impression resulting from such depictions of catastrophic wind disturbance is of relatively homogenous post-disturbance conditions and vegetation.

producing post-hurricane patchiness? (ii) Did pre-hurricane patchiness in forest structure and composition result in post-hurricane patchiness of advance regeneration within physiographically similar areas? (iii) How and why do patches generated by the hurricane differ in their post-hurricane dynamics and present vegetational characteristics?

STUDY AREA

Physical Characteristics

One of central New England's few remaining areas of virgin forest, the Harvard tract is located in Winchester, New Hampshire (42° 49'N, 72° 27'W), and surrounded by Pisgah State Park, 5,300 ha of protected, undeveloped land (Fig. 2). The tract's main physiographic features are a series of north-south ridges and valleys which form a patchwork of exposed and relatively protected sites approximately 300-350 m a.s.l. Slopes range from flat to gentle (<12%) over much of the tract's western portion and from flat to steep (>33%) along the tract's easternmost and largest ridge. The bedrock is schist, granite, and gneiss, with shallow glacial deposits (Foster 1988a). The stony soils, which are shallow throughout the tract, are spodozols with a thin leached layer (Simmons 1942). Approximately 100 cm of precipitation falls evenly through the year, and the growing season averages 120 days (U.S.D.A. 1941). Prevailing wind directions are northwest and southwest, with strongest hurricane winds from the south and east (Foster & Boose 1992).

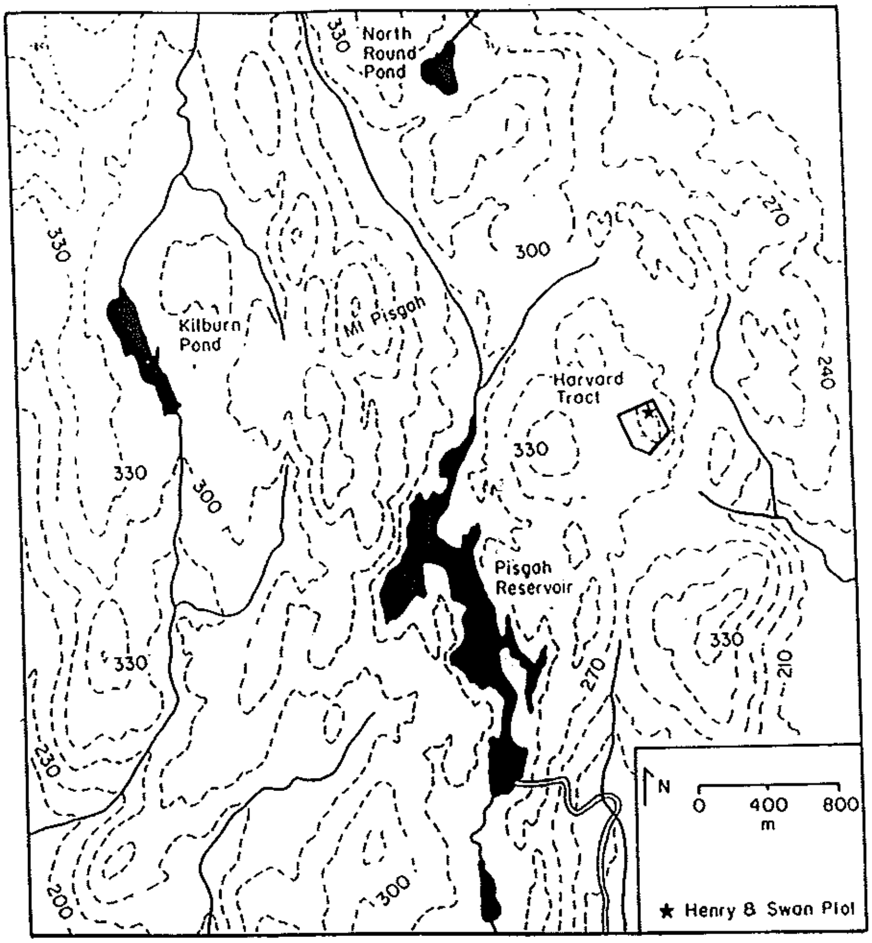


Figure 2. Elevational map of the Pisgah region of southwestern New Hampshire, showing the location of the Harvard tract.

Vegetational Characteristics

The Pisgah region's vegetation is characteristic of the southern extension of the northern Hardwoods-Hemlock-White Pine Forest region (Westveld 1956). An intensive survey of the region in 1929 found approximately 300 ha of old growth (Branch, Daley, & Lotti 1930; Cline & Spurr 1942). Re-analysis of the 1929 survey data classified this old growth into six species assemblages, each associated with a particular physiographically mediated disturbance regime, soil depth, and soil moisture level (Foster 1988a). The re-analysis classified 7 of the 13 stands surveyed on the Harvard tract as *Pinus - Tsuga* -Hardwood, 3 as *Tsuga*-Hardwood, and 2 as *Pinus-Tsuga -Quercus* (Foster 1988a; one 1929 study plot was not re-analyzed because it differed in size from the others). Stand reconstructions have revealed that a two-tiered overstory of *Pinus strobus* and *Tsuga canadensis* dominated the Harvard tract forest from the late 17th century to 1938 (Henry & Swan 1974; Schoonmaker 1992).

The hurricane of September 21, 1938, dramatically altered the forest's vegetational characteristics. The density of stems taller than 0.3 m increased from approximately 550-3300 ha^{-1} to greater than 10,000 ha^{-1} and basal area decreased from approximately 25-90 m^2 ha^{-1} to approximately 0.5-10 m^2 ha^{-1}. Fast-growing hardwoods such as *Acer rubrum*, *Betula lenta*, *Betula papyrifera*, and *Prunus pensylvanica* gained numerical and canopy dominance over much of the tract, replacing *Pinus strobus* and *Tsuga canadensis* (Branch, Daley, & Lotti 1930; Harvard Forest Archives).

The current forest on the Harvard tract differs considerably from both the pre-hurricane and early post-hurricane forest. Density in 1991 averaged approximately 2200 stems ha^{-1} and basal area 37 m^2 ha^{-1} (A. Lezberg, personal communication). *Tsuga canadensis* has gained numerical and basal area dominance by outsurviving the many hardwoods that established following the storm (Foster 1988a). In 1991, *Tsuga canadensis* constituted approximately 50 percent of the basal area compared to 10-15 percent each for *Acer rubrum*, *Betula lenta*, and *Fagus grandifolia* (A. Lezberg, personal communication). Other tree species found on the tract include *Acer pensylvanicum*, *A. saccharum*, *Betula alleghaniensis*, *B. papyrifera*, *Fraxinus americana*, *Picea rubens*, *Pinus strobus*, and *Quercus rubra*.

Disturbance History

The Pisgah forest experiences frequent gap disturbance punctuated by occasional catastrophic disturbance, with disturbance frequency and intensity at a particular site dependent largely on slope position and aspect (Foster 1988a). Agents of gap disturbance include tropical storms, front-associated windstorms, fire, lightning, ice storms, pathogens, and insects (Branch, Daley, & Lotti 1930; Henry & Swan 1974; Foster 1988a). Gap disturbances initiated numerous localized episodes of establishment and accelerated growth between 1665 and 1938 (Foster 1988a; Schoonmaker 1992).

Major pre-1938 disturbances in the Pisgah region included a hurricane in 1635 and a widespread fire in 1665 (Henry & Swan 1974; Foster 1988a; Schoonmaker 1992). Much of the overstory destroyed by the 1938 hurricane originated shortly after the 1665 fire (Henry & Swan 1974; Foster 1988a). Although most of the Pisgah region was logged within 140 years of Winchester's settlement in 1751, the Harvard tract escaped logging.

The 1635, 1665, and 1938 disturbances caused severe damage throughout the Harvard tract. Study plots across the tract contain evidence of extensive damage and regeneration resulting from the 1635 hurricane and 1665 fire (Henry & Swan 1974; Foster 1988a; Schoonmaker 1992). Aerial photographs from 1939 reveal that the 1938 hurricane's estimated 175-km hr $^{-1}$ peak sustained winds (E. Boose, personal communication) destroyed the overstory across all but the western edge of the tract (Foster 1988a). Surveys of six discrete plots in 1942 and 1948 recorded abundant hardwood regeneration and no stems taller than 5 m (Harvard Forest Archives). Tip-up mounds, windthrown stems, and standing snags dating from the 1938 hurricane occur throughout the tract (Foster 1988a; Schoonmaker 1992).

On a finer scale, however, the 1938 hurricane (and, almost certainly, the 1635 and 1665 disturbances) generated considerable heterogeneity. The 1942 survey found that surviving advance growth was denser and taller on lower than on upper slopes (Harvard Forest Archives), perhaps because of physiographically controlled differences in hurricane wind intensity. Additionally, stands with similar physiographic characteristics often differ noticeably in their current vegetational characteristics (Harvard Forest Archives), suggesting that these differences result from differences in pre-1938 structure and composition rather than from differences in hurricane wind intensity.

Post-1938 disturbance has been exclusively narrow-scale (Foster 1988a; Schoonmaker 1992) because of the immature forest's low wind susceptibility and because of the lack of major fires or windstorms.

METHODS

Data Collection

Data for the study were collected in November and December 1990 and April 1991 from 11 0.01-ha plots (Fig. 3). Each plot occupies a randomly chosen quadrant of one of the 13 permanent 0.04-ha plots established in 1984 to study historical patterns of disturbance and forest response in the Pisgah region (Foster 1988a). The 0.04-ha plots were originally selected to represent the forest's current physiognomic diversity. Because of time limitations, two of the permanent plots were not sampled for this study.

The sample plots were sited within the permanent plots for two reasons. First, the permanent plots are physiographically diverse, allowing an examination of the hypothesis that the hurricane's immediate and long-term effects differed with physiography. Four sample plots (Nos. 1-4) occupy exposed postions atop the tract's dominant ridge; seven (Nos. 5-11) occupy lower slopes. Additionally, it was anticipated that the data from the present study and from the permanent plot surveys would complement and illuminate each other.

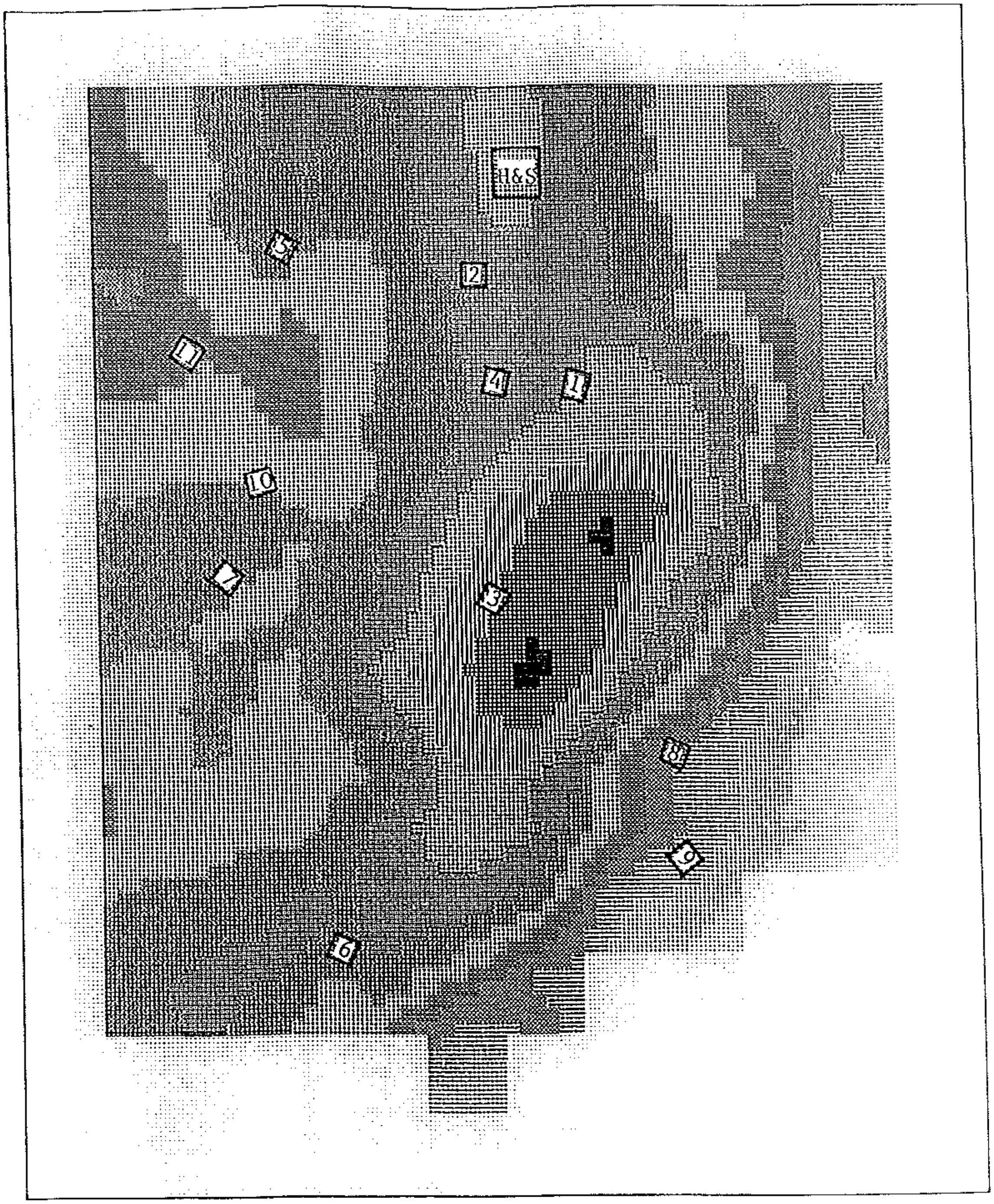


Figure 3. Elevational map of the Harvard tract (contour interval 5 m), showing the locations of the 11 sample plots and of the Henry & Swan plot. Sample plots are 0.01 ha (100 m^2); north is 21 degrees east of vertical. The darkest shade represents the greatest altitude (350 m a.s.l.). The exact sites of the 1929, 1942, and 1948 surveys mentioned in the text are unknown.

Within 10 plots, all trees greater than 1 cm in diameter at breast height (dbh) were numbered, counted, identified by species and crown class (overstory or understory), cored at 15 to 30 cm above the root collar, and measured for dbh. In one plot (plot 3), only hemlocks and even-numbered hardwoods were cored because of the high number of stems and because the hardwoods appear to post-date the hurricane.

One core per tree was sanded four times with progressively finer paper, ending with 400 grade. Cores were examined under a dissecting microscope to determine growth rates (mm/5 yr, measured backward from 1990), 1938 and 1990 end-of-growing-season diameters, post-hurricane increments (i.e., the difference between the 1990 and 1938 diameters), and 5-yr periods of establishment. All growth and diameter data are expressed in terms of inside diameter at approximately 20 cm height, corrected for core height and shrinkage and for stem asymmetry. The 1938 diameters of trees with indecipherable cores (i.e, with missing or unreadable segments) were estimated through regression analysis of 1938 *versus* 1990 diameter (for all such regressions, $r^2 > 0.45$; $p < 0.05$). Indecipherable cores were excluded from all growth rate analyses. The percentage of indecipherable stems was less than 20 percent for all but one plot (plot 2), which consequently was excluded from all establishment and growth release analysis and from by-plot growth-rate analysis.

Establishment dates incorporate the estimated number of growth rings omitted because the core was taken above the root collar or missed the pith. Because these numbers total 10 or less for most stems and because this study seeks to identify general patterns rather than exact dates of establishment, errors in establishment estimates are considered to be inconsequential. Although indecipherable stems could not be dated, almost all could be identified as predating or post-dating the hurricane through examination of general growth ring patterns.

Preliminary Data Analysis

The hypothesis that hurricane damage differed with physiography across the tract was tentatively accepted based on the 1942 survey's finding that surviving advance growth was larger on lower slopes. To test this hypothesis, the 1938 diameter data were compared among plots through dissimilarity and cluster analysis to see whether they differed according to slope position (Appendix A). This analysis further supported the hypothesis, separating the plots into three clusters (Fig. 4 & 5; Table 1): (i) the ridgetop plots (Nos. 1-4), which contain two extant stems that were larger than 8 cm in diameter in 1938 (and none that were larger than 9 cm in diameter); (ii) six lower (henceforth referred to as "mid-slope") plots (Nos. 5-10), which contain an average of 467 stems ha^{-1} that were larger than 8 cm in diameter in 1938; and (iii) the most sheltered (i.e., lowest west- or north-facing) plot (No. 11), which contains 9 stems (900 ha^{-1}) that were larger than 8 cm in diameter in 1938, and which is apparently the only plot to occupy the area of moderate damage identified by Foster (1988a) from 1939 photographs. Plots of similar slope position also showed dissimilarities, but of a lesser magnitude.

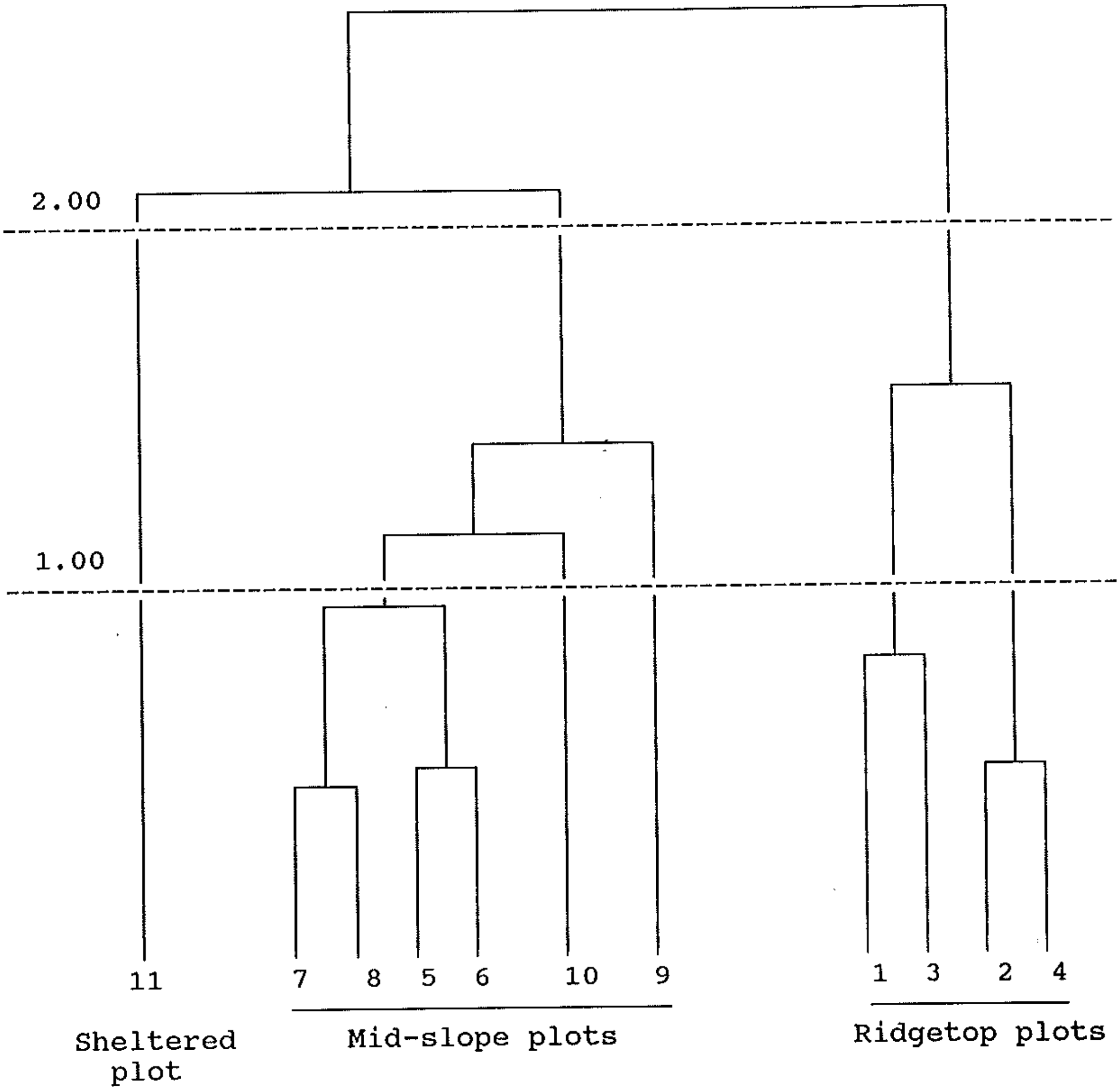


Figure 4. Dendrogram showing the relative dissimilarities of the 1938-diameter distributions of the sample plots.

Figure 5. 1938-diameter distributions of extant stems by species by sample plot. Slope postions of the plots are: ridgetop, plots 1-4; mid-slope, plots 5-10; and sheltered, plot 11.

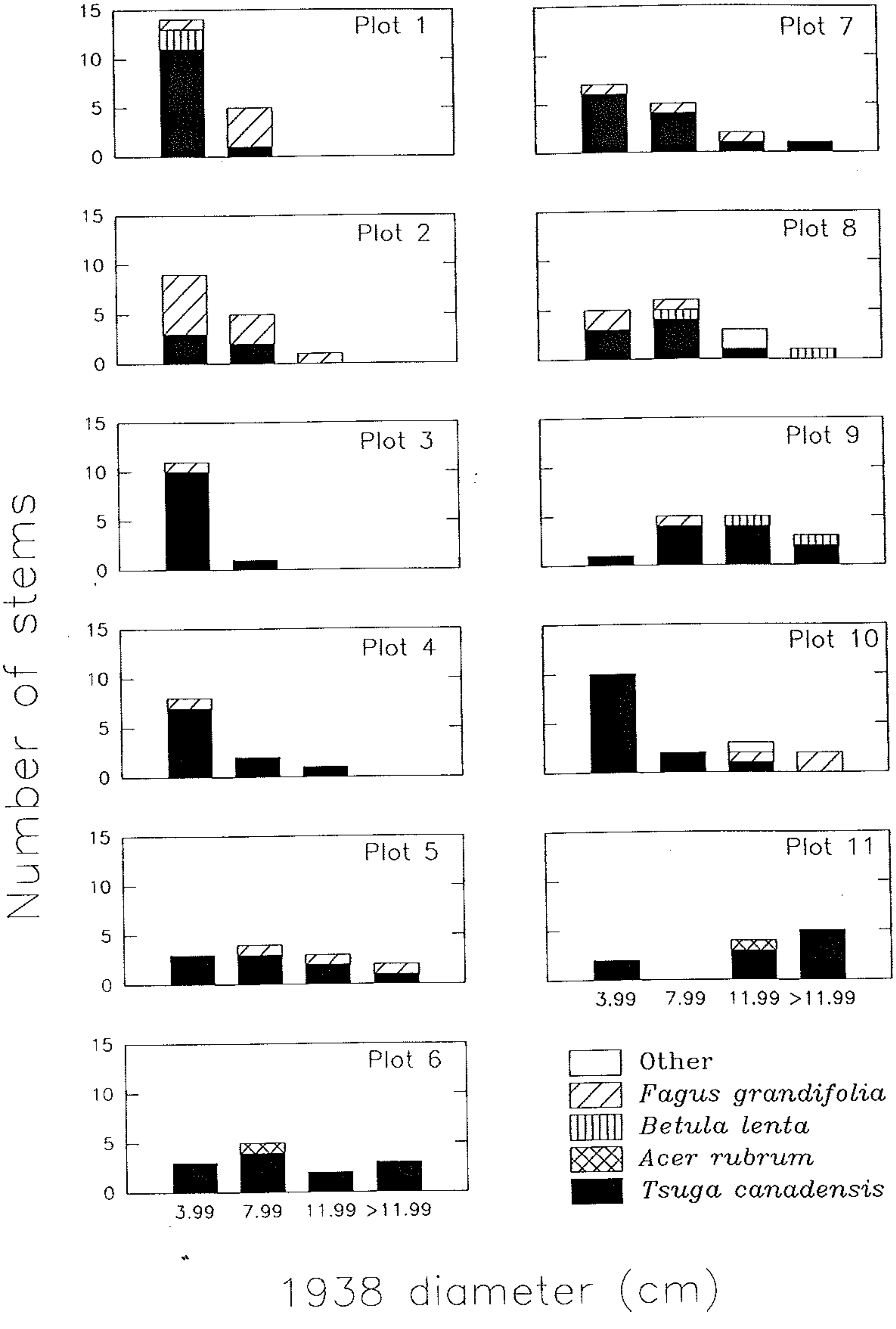

Plot 1
Plot 2
Plot 3
Plot 4
Plot 5
Plot 6
Plot 7
Plot 8
Plot 9
Plot 10
Plot 11
0
5
10
15
Number of stems
3.99
7.99
11.99
>11.99
1938 diameter (cm)
Other
Fagus grandifolia
Betula lenta
Acer rubrum
Tsuga canadensis

Table 1. Average densities (with standard errors) of extant pre-hurricane stems within ridgetop and mid-slope sample plots, and the density of such stems within the sheltered sample plot, categorized by 1938-diameter class. Significant differences (p<.05) within rows are indicated by asterisks.

	1990 density (stems/ha)		
1938 diameter (cm)	Ridgetop (4 plots)	Mid-slope (6 plots)	Sheltered (1 plot)
0.01-3.99	1050±132*	483±133*	200
4.00-7.99	325±103	450± 56	—
8.00-11.99	50± 29*	300± 45*	400
>11.99	—	200± 37	500

Thus, it was concluded that the hurricane's immediate effects differed primarily with slope position and other physiographic factors and secondarily according to patchiness in pre-hurricane physiognomy.

Data Analysis

The data from the sample plots were examined to see whether the differences in hurricane damage among slope positions led to differences in post-hurricane growth and establishment and in current physiognomy. The growth data were analyzed to determine whether trees which were of similar diameter at the time of the hurricane differ in their post-hurricane increments according to slope position. Pre-hurricane stems (i.e., stems which predate the hurricane) were categorized by the three slope positions described above, by species (hemlock or hardwood), and by the four 1938-diameter classes (0.01-3.99 cm, 4.00-7.99 cm, 8.00-11.99 cm, and >11.99 cm) used in the preliminary cluster analysis (diameter-class parameters were subjectively chosen based on preliminary inspection of the data). Post-hurricane increments were then compared between identical 1938-diameter classes and species types between slope positions through Mann-Whitney nonparametric analysis (nonhomogeneity of variance necessitated that most statistical tests employed in this study be nonparametric). Additionally, hemlock and hardwood post-hurricane increments were compared (when statistically feasible) within each 1938-diameter class within each slope position to determine whether growth rates differed with species type. All these procedures were repeated for post-hurricane stems (i.e., stems which post-date the hurricane).

Some possible comparisons were omitted because of insufficient data.

The relationship between slope position and the post-hurricane recruitment and survival of seedlings and small advance regeneration was examined. The densities within ridgetop plots of post-hurricane stems were compared to those within mid-slope plots through Mann-Whitney analysis. Densities of extant pre-hurricane stems which were less than 4.00 cm in diameter in 1938 were compared between these two slope positions through a two-sample t-test. The moderately damaged area could not be included in tests involving plot characteristics because only one plot occured within it.

The plots' current characteristics were compared among slope positions to determine whether differences in the hurricane's effect persist. The overall densities and basal areas of ridgetop plots were compared to those of mid-slope plots through Mann-Whitney and t-test analysis. The basal area comparison was repeated for each of the four 1938-diameter classes of pre-hurricane stems and for post-hurricane stems. The relative frequencies of hemlock and hardwoods were compared among slope positions through Fisher Exact Test contingency table analysis. To determine whether among-slope differences in the growth rates of stems which were of similar size in 1938 resulted in differences in their current crown positions, the relative frequencies of overstory and understory stems were compared between identical 1938-diameter classes and species types among slope positions through Fisher Exact Test analysis. The crown class frequencies of hemlocks within each 1938-diameter class within each slope position were compared to those of hardwoods through Fisher Exact Test analysis.

The data were also examined to assess whether plots of similar slope position (excluding plot 2) differ in their post-hurricane dynamics and current physiognomy. Post-hurricane increments, densities of post-hurricane stems, and basal areas were subjectively compared among plots (statistical comparisons of growth rates were impossible because of insufficient data).

To explore the relationship between early post-hurricane size structure and the densities of post-hurricane stems, plots' densities of these stems were regressed against their densities of (i) pre-hurricane stems and (ii) stems which were larger than 3.99 cm in diameter in 1938. The relationship between the densities of pre-hurricane stems which were smaller than 4.00 cm in diameter in 1938 and of stems which were larger than 3.99 cm in diameter in 1938 was similarly analyzed. Post-hurricane increments were subjectively compared among plots to see whether they vary according to the density of pre-hurricane stems.

Growth releases and establishments typically occur in temporally discrete, disturbance-initiated pulses (Oliver & Stephens 1977; Payette, Filion, & Delwaide 1990; Spies, Franklin, & Klopsch 1990; Frelich & Lorimer 1991). To elucidate patterns of pre-hurricane and post-hurricane disturbance and their role in producing post-hurricane patchiness, the numbers of growth releases and establishments per plot per 5-yr period (excluding plot 2) were counted and compared. A release was defined as a doubling of the growth rate from one 5-yr period to the next. This criterion has been used in several previous studies including the historical study of disturbance in the Pisgah region (Foster 1988a; Taylor & Halpern 1992). Releases and establishments were also compared by slope position to see whether patterns of narrow-scale disturbance might explain among-slope differences in the hurricane's effects.

RESULTS

The data provide further evidence of the catastrophic impact of the 1938 hurricane across the Harvard tract. Of the 250 trees within the sample plots, only four were larger than 20 cm in diameter (at 20 cm height) in 1938, and none was larger than 31 cm in diameter. The average 1941 to 1950 growth rate of surviving stems is 1.7 times that of any previous 10-year period (Fig. 6). The number of stems released from 1936 to 1945 nearly quadruples that of any other 10-year period (Fig. 7). In all but one plot (No. 8), releases peak during this period (Appendix B). The number of stems establishing from 1936 to 1940 nearly triples that of any other 5-year period (Fig. 7). An estimated 96 trees post-date the hurricane, including 89 individuals of the relatively shade-intolerant species *Acer rubrum*, *Betula lenta*, *B. papyrifera*, and *Quercus rubra* . Approximately 30 *Tsuga canadensis* saplings (<1 cm dbh), which likely post-date the hurricane (Henry & Swan 1974; Foster 1988a; Schoonmaker 1992), also occur within the plots.

Nevertheless, the data also provide evidence that the hurricane's effects have varied across the tract, primarily with physiographic factors. For example, hemlocks (but not hardwoods) of similar size at the time of the hurricane differ in their post-hurricane increments depending on slope position (Table 2; Fig. 8). Hemlocks which were 4.00-7.99 cm in diameter in 1938 grew significantly faster in

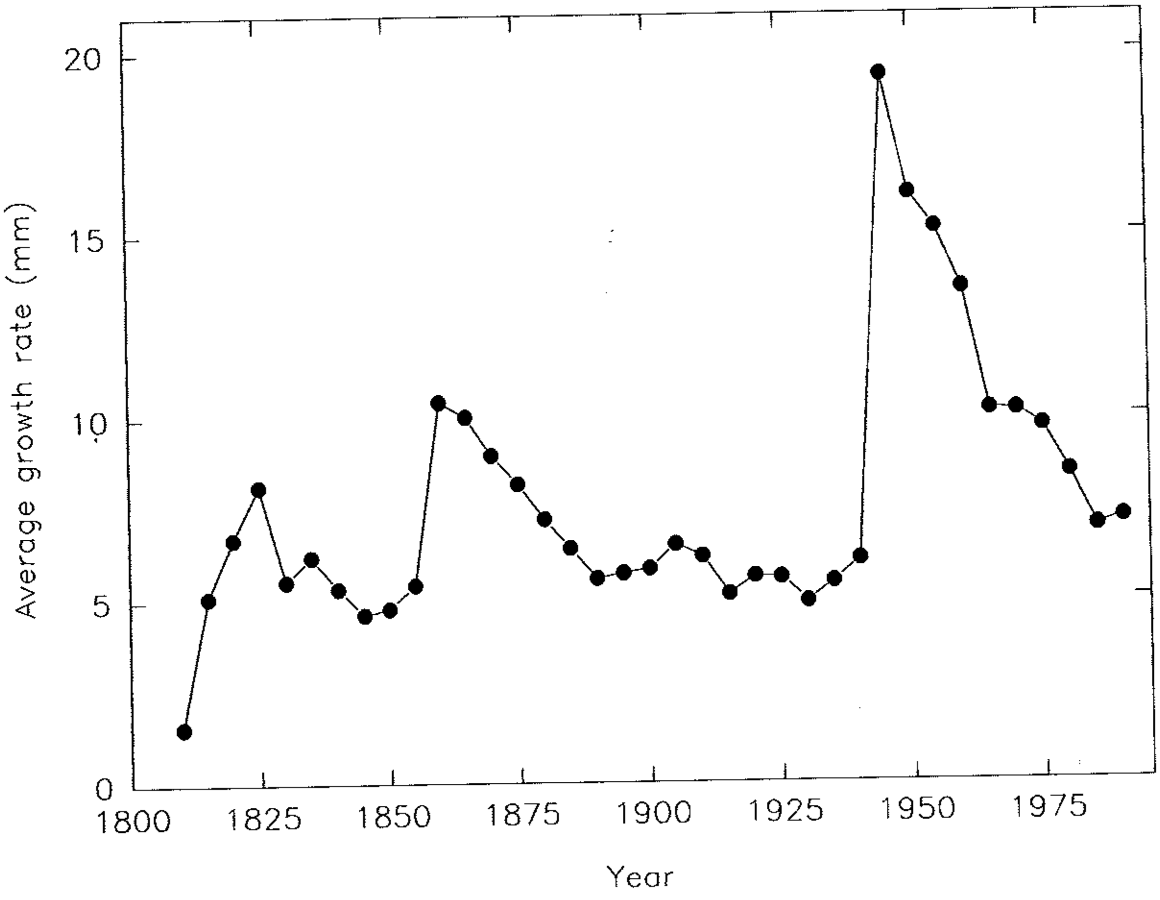


Figure 6. Average diametric growth rate of extant trees within the sample plots. The number of individuals represented ranges from 2 in 1810 to 81 in 1900 and 173 in 1990. Trees with indecipherable cores (i.e., with missing segments or imperceptible lines) were excluded from this analysis. Growth rates were not determined for plot 2 because of its high percentage of indecipherable cores.

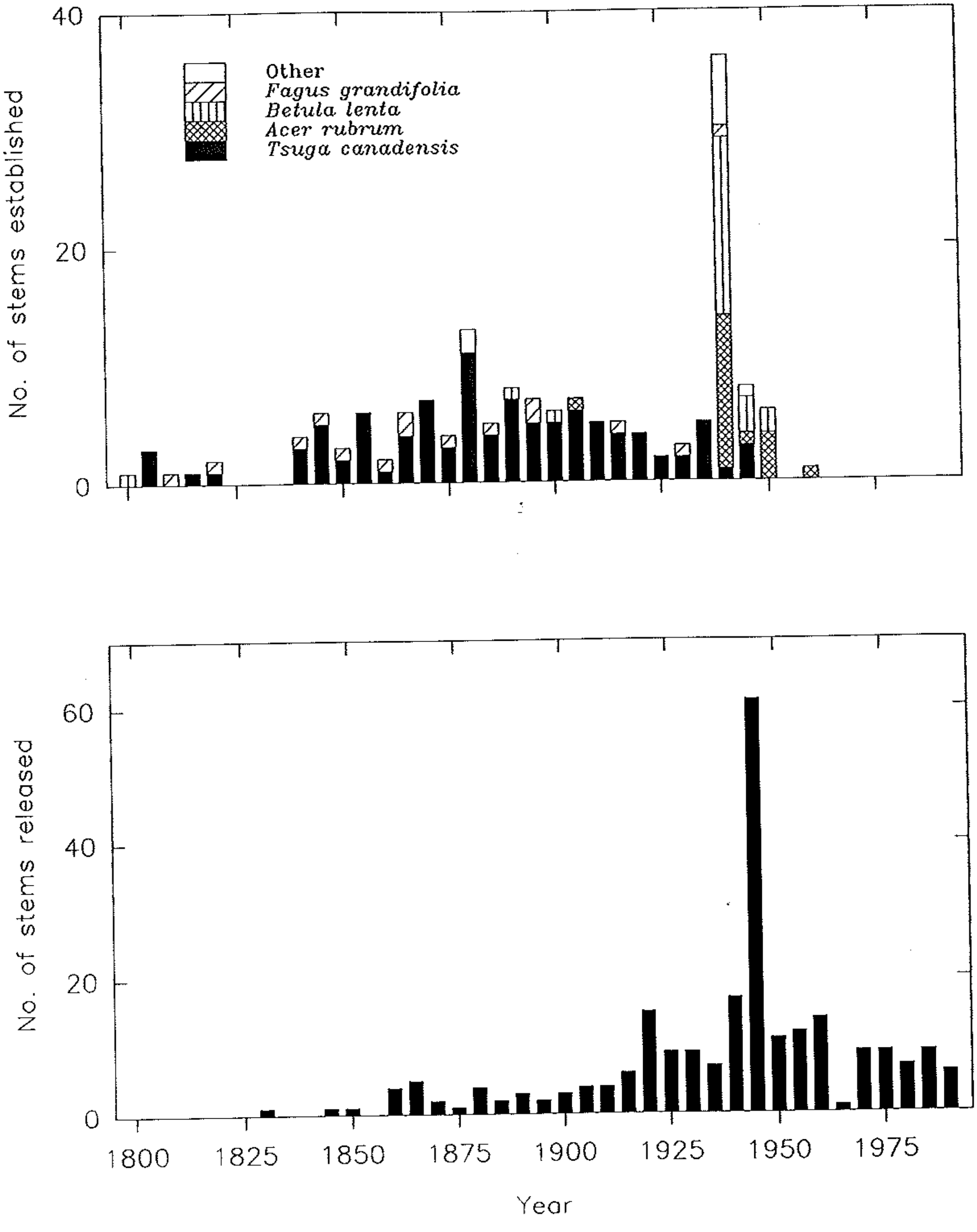
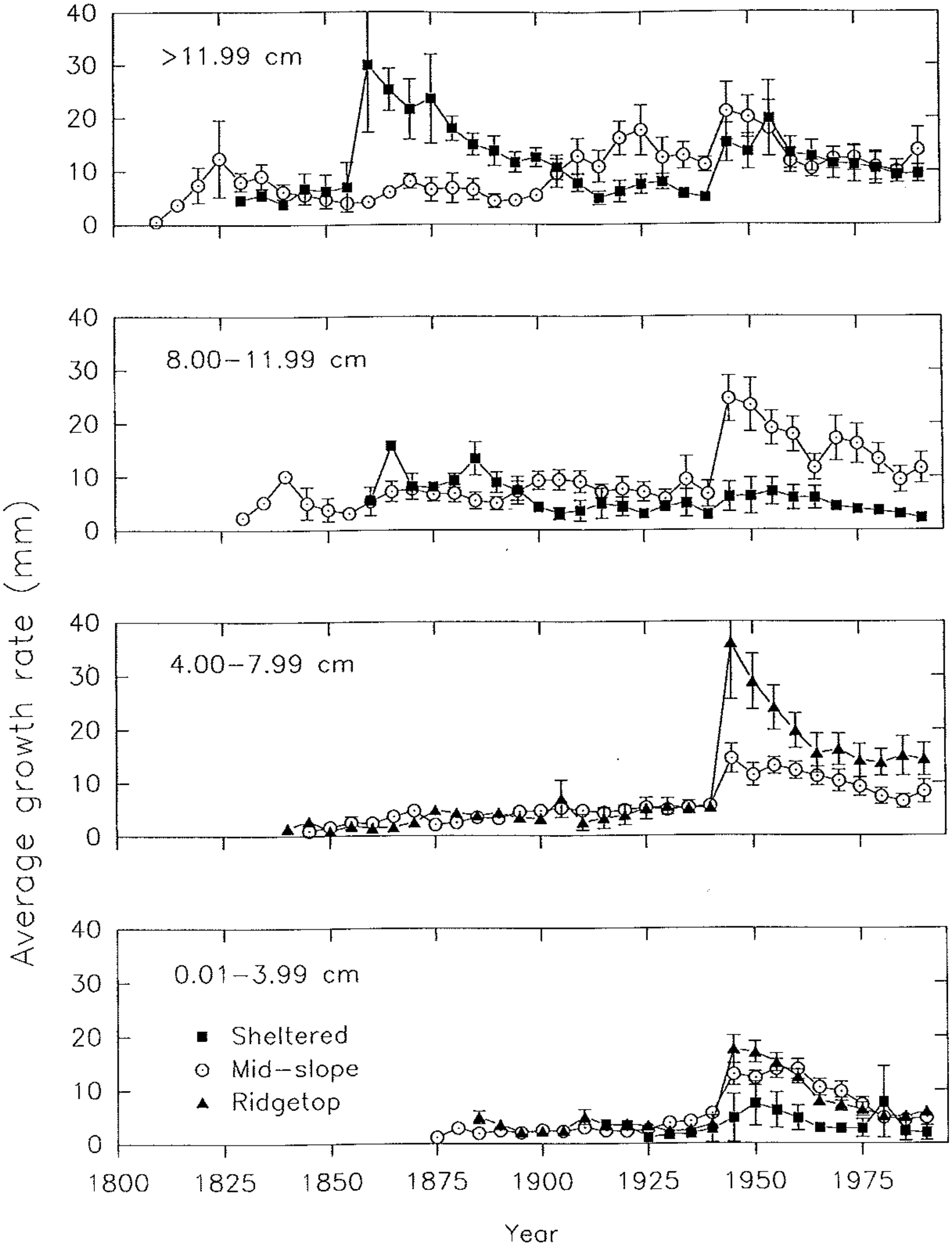


Figure 7. Total numbers of establishments (by species) and growth releases of extant stems within the sample plots by 5-yr period. Indecipherable stems and stems from plot 2 were excluded from this analysis.

Table 2. Average post-hurricane increments (with standard errors) of extant pre-hurricane hemlocks (excluding stems with indecipherable cores) within ridgetop, mid-slope, and sheltered sample plots, categorized by 1938-diameter class. The number of stems in each category is shown in parentheses. Significant differences (p<.05) within rows are indicated by asterisks.

	Average post-hurricane increment (cm)		
1938 diameter (cm)	Ridgetop (4 plots)	Mid-slope (6 plots)	Sheltered (1 plot)
0.01-3.99	10.3±1.1 (29)	9.7±0.9 (25)	4.4±2.3 (2)
4.00-7.99	19.3±3.1* (6)	10.6±1.1*(17)	——
8.00-11.99	——	16.8±2.3*(10)	5.0±1.1*(3)
>11.99	——	14.5±2.5 (4)	12.8±2.6 (4)

Figure 8. Comparative average diametric growth rates of pre-hurricane hemlocks of identical 1938-diameter class but of different slope position. The heading within each graph identifies the 1938-diameter class being compared.


>11.99 cm
8.00–11.99 cm
4.00–7.99 cm
0.01–3.99 cm
■ Sheltered
○ Mid–slope
▲ Ridgetop
Average growth rate (mm)
Year
0
10
20
30
40
1800
1825
1850
1875
1900
1925
1950
1975

ridgetop than in mid-slope plots. Hemlocks which were 8.00-11.99 cm in diameter in 1938 grew significantly faster in mid-slope plots than in the sheltered plot (No. 11). Conversely, stems which were less than 4.00 cm or greater than 11.99 cm in diameter in 1938 or which post-date the hurricane grew at similar rates in all slope positions (although no stems which were greater than 9 cm in diameter survive in ridgetop plots).

As these data suggest, ridgetop hardwoods which were less than 4.00 cm in diameter in 1938 have tended to grow faster (although not significantly so) following the hurricane than have hemlocks of similar size and slope position (13.4 cm ±2.5 *v.* 10.3 cm ±1.1). Interestingly, this relationship is reversed for ridgetop stems which were 4.00 to 7.99 cm in diameter in 1938 (13.5 cm ±3.5 *v.* 19.3 cm ±3.6). In other slope positions, pre-hurricane hemlocks and hardwoods differ little in their post-hurricane growth rates. Statistical comparisons of post-hurricane stems by species type were impossible because of the low number of post-hurricane hemlocks larger than 1 cm dbh. Nevertheless, the absence of such hemlocks and the abundance of overstory post-hurricane hardwoods indicate that the hardwoods have grown much faster.

Recruitment and survival of post-hurricane and of smaller pre-hurricane stems has also differed with slope position (Tables 1 & 3). Ridgetop plots significantly exceed mid-slope plots in their densities of post-hurricane stems. The density of post-hurricane stems within the sheltered plot is similar to those of mid-slope plots. Densities of pre-hurricane stems which were smaller than 4.00 cm in diameter in

Table 3. Average densities (with standard errors) of extant pre-hurricane and post-hurricane trees within ridgetop and mid-slope sample plots and the densities of such stems within the sheltered sample plot. Significant differences ($p<.05$) within rows are indicated by asterisks.

	1990 density (stems/ha)		
Establishment class	Ridgetop (4 plots)	Mid-slope (6 plots)	Sheltered (1 plot)
Pre-hurricane	1425±180	1433± 71	1100
Post-hurricane	1825±780*	333±133*	300
Total	3250±703*	1766±174*	1400

1938 are also significantly higher in ridgetop plots than in mid-slope plots. The density of such stems within the sheltered plot is 200 ha^{-1}.

Differences in the hurricane's immediate and long-term effects have led to differences in plots' current characteristics (Fig. 9). Because of their greater numbers of post-hurricane stems (most of them hardwoods; Table 3), ridgetop plots have significantly more stems than do mid-slope plots, as well as a significantly higher percentage of hardwoods (Table 4). Conversely, mid-slope plots have significantly higher basal areas than do ridgetop plots (Table 5), largely because they have 10 times as many stems which were greater than 7.99 cm in diameter in 1938 (Table 1). The additive contribution of these stems more than offsets the significantly higher basal areas within ridgetop plots of post-hurricane stems and of stems which were less than 4.00 cm in diameter in 1938. The sheltered plot is similar to mid-slope plots in density and basal area (Tables 3 & 5).

Differences in post-hurricane growth rates are also reflected in 1990 crown class data. Hemlocks which were 4.00-7.99 cm in diameter in 1938 occupy the overstory significantly more frequently in ridgetop plots than in mid-slope plots (Table 6). Additionally, ridgetop hardwoods which were less than 4.00 cm in diameter in 1938 occupy the overstory significantly more frequently (8 of 11 stems; $p=.001$) than do ridgetop hemlocks which were of similar size (4 of 31 stems).

Although plots differ in their post-hurricane development and current vegetation primarily according to slope position, plots of similar slope position also exhibit some differences:

Figure 9. Diameter distributions in 1990 of extant stems by species by sample plot.

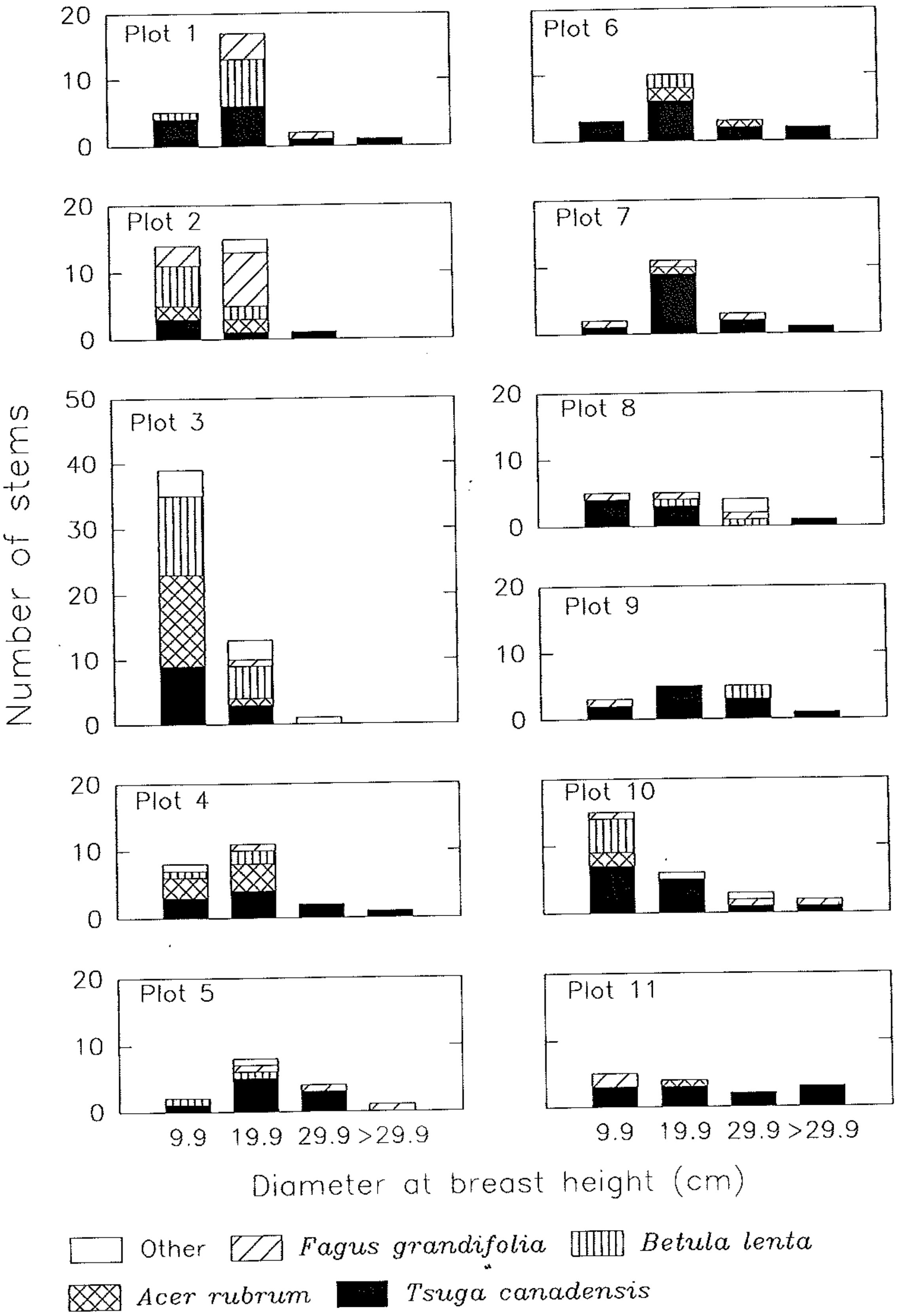

Number of stems
Plot 1
Plot 2
Plot 3
Plot 4
Plot 5
Plot 6
Plot 7
Plot 8
Plot 9
Plot 10
Plot 11
0
10
20
30
40
50
9.9
19.9
29.9
>29.9
Diameter at breast height (cm)
Other
Fagus grandifolia
Betula lenta
Acer rubrum
Tsuga canadensis

Table 4. Current total numbers of hemlocks and hardwoods within ridgetop and mid-slope plots.

	Number of stems (1990)	
Species	Ridgetop (4 plots)	Mid-slope (6 plots)
Hemlock	39	68
Hardwood	91	38

Table 5. Average basal areas (with standard errors) of extant pre-hurricane stems (categorized by 1938-diameter class) and post-hurricane stems within ridgetop and mid-slope sample plots, and the basal areas of such stems within the sheltered sample plot. Significant differences ($p<.05$) within rows are indicated by asterisks.

	1990 basal area (m^2/ha)		
Establishment/ size class (cm)	Ridgetop (4 plots)	Mid-slope (6 plots)	Sheltered (1 plot)
Pre-hurricane			
0.01-3.99	13.3±1.9*	5.0±1.7*	0.4
4.00-7.99	10.5±2.8	8.9±1.1	—
8.00-11.99	1.0±0.6	14.7±2.6	6.4
>11.99	—	14.2±2.9	41.2
Post-hurricane	12.0±2.3*	2.4±0.8*	0.8
Total	36.8±2.3*	45.1±1.4*	48.7

Table 6. Current crown class distributions of extant hemlocks which were approximately 4.00 to 7.99 cm in diameter in 1938 within ridgetop and mid-slope plots.

	Number of stems (1990)	
Crown class	Ridgetop (4 plots)	Mid-slope (6 plots)
Overstory	5	4
Understory	1	17

1. Plots 8 and 9 differed markedly from other mid-slope plots 5, 7, and 10 in their average post-hurricane increments of hemlocks which were 4.00 to 7.99 cm in diameter in 1938 (9.5 and 7.3 cm *v.* 14.3, 13.4, and 15.6 cm, respectively). These are by far the greatest such disparities for any 1938 size class within any slope position.

2. The density of post-hurricane stems varies from 600 ha^{-1} (plot 1) to 4100 ha^{-1} (plot 3) among ridgetop plots, and from 0 (plot 8) to 1100 ha^{-1} (plot 10) among mid-slope plots.

3. Basal areas range from 32.3 m^2 ha^{-1} (plot 3) to 41.2 m^2 ha^{-1} (plot 4) among ridgetop plots, and from 40.3 m^2 ha^{-1} (plot 8) to 49.9 m^2 ha^{-1} (plot 6) among mid-slope plots.

Regression analysis of plot density of post-hurricane stems *versus* density of pre-hurricane stems provides an explanation for among-slope-position and among-plot differences in post-hurricane-stem densities. Densities of post-hurricane stems exhibit a strong negative-exponential relationship with the densities of stems which were greater than 3.99 cm in diameter in 1938 [$y = e^{(-0.353x + 3.998)}$; r^2=.861]. Because ridgetop plots have fewer such pre-hurricane stems, they also have more post-hurricane stems. The densities of pre-hurricane stems which were smaller than 4.00 cm in diameter in 1938 also show a strong negative correlation with the densities of stems which were greater than 3.99 cm in diameter in 1938 ($y=-.97x+13.8$, r^2=.63, p=.003). In contrast, the densities of post-hurricane stems (r^2=.047, p=.522) and of pre-hurricane stems which were smaller than 4.00 cm in diameter in 1938 ($r^2=.312$; $p=.074$) show no significant correlation with the total densities of pre-hurricane stems.

Plots' average post-hurricane increments of hemlocks which were 4.00 to 7.99 cm in diameter in 1938 also appear to be negatively related to their densities of pre-hurricane stems which were greater than 3.99 cm in diameter in 1938, although this relationship cannot be statistically demonstrated.

Release and establishment data confirm the finding of previous studies that -- except for the 1938 hurricane -- disturbance within the Harvard tract over the past 200 years has been predominately narrow-scale (Fig. 7; Appendix B). No clear common patterns of pre-hurricane release and establishment can be discerned among plots, even those of similar slope postion. Only plot 7 shows evidence of significant post-hurricane disturbance (Appendix B). These results further reinforce the conclusion that differences in the hurricane's wind intensity, rather than patterns of pre- and post-hurricane disturbance, are primarily responsible for differences in the hurricane's effects.

DISCUSSION

Few forest disturbances could appear more homogeneous than a 10-ha blowdown that eliminates practically all trees larger than 20 cm dbh. Indeed, the overwhelming effects of hurricane blowdown have led some authors to conclude that fast-growing, shorter-lived species inevitably dominate the early post-blowdown forest (Hibbs 1983). Yet, any surviving advance growth is likely to exhibit some heterogeneity because of among-stand differences in physiography and pre-disturbance physiognomy (Foster 1988a; Foster & Boose 1992). The importance of this advance regeneration in post-disturbance stand development depends on its size, density, and post-disturbance growth and mortality. Advance regeneration of different size and species differs in its ability to overtop competitors. For example, Kelty (1984) found that *Tsuga canadensis* -- which constitutes 78 percent of the pre-hurricane stems within the sample plots -- usually needs a 3-m head start to overtop post-disturbance hardwood seedlings. The greater the density of advance regeneration able to overtop new stems or shorter advance growth, the lower the growth and survival rates of these overtopped stems (Marquis 1981). Consequently, among-stand dissimilarities in the density of advance regeneration 3 m tall can result in profound differences in post-disturbance development. Just such dissimilarities were found on the Harvard tract in 1942 (Harvard Forest Archives). Moreover, in the present study densities of hemlocks which were greater than 5.00 cm in diameter in 1938 ranged from 100-900 ha^{-1}. The minimum diameter (at the time of disturbance) of hemlock which reached the overstory in the Kelty study was approximately 5 cm. Thus, even though the 1938 hurricane destroyed almost the entire overstory and approximately 90 percent of the basal area of the Harvard tract forest, among-stand differences in surviving advance growth were apparently sufficient to produce considerable heterogeneity in post-hurricane development and physiognomy.

1938 Hurricane Damage

Evidence from this and other studies strongly suggests that physiographically mediated differences in hurricane damage were the primary cause of post-hurricane heterogeneity. Results from a 1942 survey and from this study indicate that the basal area and maximum height of surviving advance growth increased with decreasing slope position. The 1942 survey of a 2 m x 140 m transect found that although "little advance growth of any kind had persisted" on high slopes, the lower slopes were "dominated by hemlock and beech advance growth" which seemed destined to overtop most of the numerous seedlings that had emerged following the hurricane (Harvard Forest Archives). Similarly, the four ridgetop plots in this study contain no stems which were larger than approximately 8.5 cm in diameter in 1938, whereas each other plot contains at least three such stems, including at least one whose estimated 1938 diameter was 13 cm or greater. Of the 11 pre-1938 stems in plot 11 -- the most sheltered study plot -- at least 8 were larger than approximately 8.5 cm in diameter in 1938.

These dissimilarities might alternatively be explained by among-slope differences in pre-hurricane physiognomy or in post-hurricane mortality rather than in hurricane wind intensity. Evidence for such differences is lacking, however. Pre-hurricane release and establishment patterns seem uncorrelated with slope position (Appendix B), contradicting the hypothesis that the pre-hurricane development of advance growth differed with slope across the tract. Post-hurricane mortality would be expected to lessen rather than amplify among-plot differences in the density of larger advance regeneration because of the greater initial competition and mortality within denser plots (Peet & Christensen 1980). Additionally, data from this and other studies indicate that post-hurricane mortality has been relatively unimportant, except perhaps among lower-slope stems which were smaller than 4.00 cm in diameter in 1938 (see Results). No recent large downed stems were noted within the study quadrats, and only a few dead standing stems -- all post-hurricane hardwoods or understory pre-hurricane stems -- were observed. Schoonmaker (1992) concluded that less than 5 percent of downed wood on the tract in 1987 derived from post-hurricane treefalls. Moreover, if post-hurricane mortality were responsible for the relative paucity of ridgetop stems which were larger than 7.99 cm in diameter in 1938, then the post-hurricane growth and release rates of ridgetop stems should lag behind those of lower-slope stems. This is not the case (Fig. 8). In fact, release data (Appendix B) suggest that the only significant post-hurricane disturbance within the sample plots occured within mid-slope plot No. 7. A partially decayed downed stem within plot 7 appears to be associated with this disturbance. This plot also has fewer post-hurricane stems than predicted by the post-hurricane *versus* pre-hurricane density regression, perhaps because stems important in earlier post-hurricane development are no longer extant.

Data from the 1929 survey of the Pisgah region reinforce the conclusion that differing hurricane damage was the primary cause of post-hurricane patchiness, and cast further light on the patterns of this damage (Table 7). The densities of understory trees (individuals approximately 8 to 39 cm in diameter) and of saplings (individuals 0.3-4.6 m tall) did not differ significantly ($p>.42$) between ridgetop and

Table 7. Average densities (with standard errors) in 1929 of understory stems within eight ridgetop and five lower-slope plots on the Harvard tract. The densities within each size class do not differ significantly between slope positions. The exact locations of the 1929 plots are not known.

Diameter/ height class	Average density (stems/ha)	
	Ridgetop	Lower-slope
0.3-4.6 m	675±334	845±294
8-26 cm	319± 62	380±114
26-39	75± 24	75± 25

lower-slope plots within the Harvard tract in 1929 (the slope positions, but not the exact locations, of the 1929 study plots are known). Seven of the 13 1929 survey plots contained 26- to 39-cm dbh stems at densities of at least 100 ha^{-1}, whereas only two plots (Nos. 6 and 11) from the present study have 100 stems ha^{-1} which were greater than 26.0 cm in diameter in 1938. Current densities of stems which were between 8.00 and 25.9 cm in diameter in 1938 range from 300-800 ha^{-1} in lower-slope plots -- comparable to the 1929 survey values of approximately 100-875 stems ha^{-1} in this size class -- and from 0-100 stems ha^{-1} in ridgetop plots. Current densities of stems which were smaller than 8.00 cm in 1938 range from 1000-1900 ha^{-1} in ridgetop plots and from 200-1200 ha^{-1} in lower-slope plots, compared to approximately 50-2950 ha^{-1} in this size class in the 1929 plots. All these data suggest a pattern of total mortality of stems whose diameter exceeded approximately 35 cm; partial survival of lower-slope stems between 26.0 and 35.0 cm in diameter; high survival of lower-slope stems and nearly total mortality of ridgetop stems between 8.00 and 25.9 cm in diameter; and high survival of stems less than 8.00 cm in diameter.

Data from other studies also support these conclusions regarding hurricane damage patterns. Surveys of plots in the Petersham, Massachusetts, area following the 1938 hurricane found that almost all stems less than 3 m tall survived, and that damage increased with stem height and site susceptibility (Foster 1988b; Foster & Boose 1992). As noted above, 3 m or less in height is roughly equivalent to 5 cm or less in diameter, which corresponds closely with the smallest 1938 diameter class in the present study. A downburst in Wisconsin which left 46 trees ha^{-1} whose dbh exceeded 10 cm -- considerably fewer than in lower-slope plots but more than in ridgetop plots in the present study -- spared approximately 80 percent of stems of 2.5-10 cm dbh (Dunn, Guntenspergen, & Dorney, 1983).

Given the collective evidence, it seems reasonable to conclude that: (i) hurricane damage increased with slope position across the Harvard tract; (ii) physiographically mediated gradients in hurricane damage were the primary cause of post-hurricane heterogeneity; and (iii) hurricane damage was relatively slight for stems smaller than 5 cm in diameter.

Pre-Hurricane Heterogeneity and Post-Hurricane Patchiness

Data from the present study suggest that establishments and releases between approximately 1800 and 1938 occured in spatially and temporally discrete pulses following gap disturbance, leading to considerable forest heterogeneity. No overall synchronization of establishments and releases could be discerned among the sample plots (Appendix B). Most disturbance appears to have been relatively mild: 92 percent of the known pre-hurricane stems are of *Tsuga canadensis* and *Fagus grandifolia*, which can survive in lower light conditions than can the other, less shade-tolerant species found on the Harvard tract (Marshall 1927; Canham 1988; Leak 1991). Other species may be under-represented among extant pre-hurricane stems, however, because their higher juvenile growth rates would have caused them to be taller and more susceptible to hurricane damage (Kelty 1984; Foster 1988b). The presence of

Betula and *Acer rubrum* pre-hurricane stems in plots 1, 6, 8, 9, 10, and 11 indicates that relatively strong gap disturbance also occured during this period.

These results are supported by the 1929 survey data (Branch, Daley, & Lotti 1930). Basal areas and densities within the 13 Harvard tract plots ranged from 22-88 m^2 ha^{-1} and from 265-1600 stems greater than 5 cm dbh ha^{-1}. Five plots had no apparent gaps, four had gaps smaller than 200m^2, and four had gaps of approximately 200-400 m^2. Gap ages were not recorded, but field notes indicate they were asynchronous (Harvard Forest Archives). Gap origins included windthrows or deaths of single overstory trees (mainly *Pinus strobus*), and multiple-tree mortality from lightning, windthrow, or *Armillaria mellea* damage. Seventy-seven percent of understory stems were of *Tsuga canadensis* or *Fagus grandifolia*. Results from recent stand reconstructions within the Harvard tract also indicate that gap disturbance predominated from 1665 to 1938, producing spatial heterogeneity (Henry & Swan 1974; Schoonmaker 1992).

Current evidence of differences in pre-hurricane physiognomy is overwhelmed by the effects of the hurricane in among-slope-position comparisons, and is at best inconclusive in within-slope-position comparisons. The surviving pre-hurricane vegetation presents only a fragmentary and perhaps highly distorted picture of pre-hurricane physiognomy and development, and some dissimilarities among plots of similar slope position undoubtedly result from patchiness in hurricane damage (due to additional components of the physiographic damage gradient, differences in damage from falling stems, and other factors) and in post-hurricane development as well as from pre-hurricane heterogeneity. Nevertheless, considerable heterogeneity did exist within the pre-hurricane forest, and it undoubtedly accounts for much of the post-hurricane dissimilarities among plots of similar slope position. Furthermore, some apparent pre-hurricane differences among mid-slope plots are corroborated by downed wood data. Plots 6, 8, and 9 -- unlike other mid-slope plots -- show relatively strong pulses of establishment and growth in the late 19th and early 20th centuries, indicating relatively intense disturbance (Appendix B). Of the seven pre-hurricane birches found in mid-slope plots, at least three and possibly five established in these three plots during this time. These plots also have the lowest 1936-1945 release rates, suggesting that their pre-hurricane overstories were comparatively thin as a result of this recent disturbance. All these conclusions are supported by downed wood densities, which range from approximately 150-250 stems ha^{-1} in plots 6, 8, and 9, compared to approximately 400-450 stems ha^{-1} in the other mid-slope plots (Harvard Forest Archives).

Post-Hurricane Dynamics

Because of the slope-position gradient in the size structure of surviving stems, post-hurricane growth of hemlock advance regeneration varied across this gradient. Hemlocks which were 4.00-7.99 cm in diameter in 1938 grew faster and reached the overstory more often in ridgetop plots than in mid-slope plots (Tables 2 & 6), almost certainly because of the lack of competition from larger stems. Hemlocks which were 8.00-11.99 cm in diameter grew faster in mid-slope plots than in plot 11, which has the most sheltered slope postion and the greatest number of stems which were larger than 11.99 cm in diameter in 1938. Growth differences were less significant for hardwoods than for hemlocks, probably because hardwoods are typically taller than hemlocks of the same diameter (Hough 1935).

Because the characteristics of surviving advance growth did not depend solely on slope position, however, plots with similar slope positions exhibit some differences in their average post-hurricane increments. Hemlocks which were 4.00 to 7.99 cm in diameter in 1938 grew considerably slower in plots 8 and 9 than in other mid-slope plots, probably because of the relatively high densities of larger pre-hurricane stems in plot 9 and of pre-hurricane birches in plot 8 (Fig. 5). Birches can expand their crowns and thereby occupy available growing space faster than can *Tsuga canadensis* or *Fagus grandifolia* (Hibbs 1982; Runkle & Yetter 1987), which dominate the pre-hurricane cohorts of other mid-slope plots.

Growth data on pre-hurricane hemlocks which were smaller than 4.00 cm in diameter in 1938 present an interesting contrast to the preceding results. Despite the differences in pre-hurricane physiognomy and in hurricane damage, hemlocks of this size differ little in their overstory accession rates and average post-hurricane increments among slope positions or among plots. This is because most such hemlocks have been overtopped, usually by larger pre-hurricane stems in lower-slope plots or by post-hurricane stems in ridgetop plots. These findings resemble those of Kelty (1984, 1986), who noted that hemlocks shorter than 1.5 m at the time of catastrophic disturbance were soon overtopped by younger hardwoods, whereas hemlocks taller than 3 m at the time of disturbance reached the overstory. Although the 1938 heights of cored stems are unknown, an estimate based on regression analysis of published height *versus* dbh data for old-growth hemlock (Hough 1935) is 2.6 m average height for stems 4 cm in diameter. Thus, it is likely that most hemlocks smaller than 4.00 cm in diameter were also considerably shorter than 3 m. From the same regression, the estimated average diameter of 1.5 m hemlocks is 2.4 cm, close to the median 1938 diameter of stems which were less than 4.00 cm in diameter in 1938.

1990 Characteristics

Differences in available growing space immediately following the hurricane have led to enduring differences in stand characteristics (Fig. 9). Stands with higher densities of larger advance growth had less available space, leading to lower growth and survival of post-hurricane and of small pre-hurricane stems (Oliver & Stephens 1977; Peet & Christensen 1980; Marquis 1981). This explains the strong negative correlation between plots' current densities of stems which were larger than 3.99 cm in diameter in 1938 and their current densities of post-hurricane and smaller pre-hurricane stems. Most stems larger than 3.99 cm in diameter were able to overtop and exclude post-hurricane hardwoods. Larger gaps between this taller advance regeneration were filled by hardwoods, which outstripped small (<4.00 cm in diameter) hemlocks. Consequently, plot 10, the lower-slope plot with the fewest stems which were greater than 3.99 cm in diameter in 1938, has the most post-hurricane hardwoods of any lower-slope plot (and the only understory stems of *Acer rubrum* and *Betula lenta*). The composition of surviving advance growth might also have been important: for example, plot 10 has only three hemlocks which were larger than 3.99 cm in diameter in 1938, compared to at least five in other lower-slope plots. Several studies have found a negative association between the densities of young hemlock and of understory seedlings (Hett & Loucks 1976; Rogers 1978; Whitney 1990).

Relatively shade-intolerant hardwoods might be expected to dominate for some time following catastrophic hurricane disturbance. Accordingly, Hibbs (1983) speculated that "hemlock would rarely become dominant in 40 yr" following "a large wind disturbance in the pre-colonial forest of central New England." Yet, the effect of the hurricane on lower-slope stands appears to have been to increase the relative importance of hemlock, the predominant shade-tolerant species on the Harvard tract. In 1990, hemlock constituted 70 percent of the basal area within lower-slope sample plots and 46 percent within ridgetop plots, compared to 31 percent in the 1929 survey plots. Data collected in 1984 from the lower-slope permanent plots (see Methods) show that 46 years after the hurricane hemlock constituted at least 80 percent of the basal area in all but plots 8 and 10. As discussed above, plot 10 has fewer large pre-hurricane stems and more post-hurricane stems than other lower-slope plots. The comparatively high hardwood density and basal area in plot 8 result not from greater post-hurricane recruitment (actually, plot 8 has no post-hurricane trees) but from advance regeneration of saplings which apparently established following relatively intense disturbances around 1800 and in the late 1870's.

Thus, within 40 years of the 1938 hurricane, advance regeneration (most of it hemlock) had gained dominance over much of the tract's lower slopes. These lower-slope stands -- unlike the former old-field *Pinus strobus* stands surveyed by Hibbs (1983) in his study of post-hurricane succession -- contained sufficient advance regeneration of sufficient size to overtop and largely exclude post-hurricane hardwoods. In contrast, the low densities of advance regeneration taller than 3 m within ridgetop plots and (apparently) within the Henry & Swan plot (also located on the ridgetop; Fig. 3; Henry & Swan 1974) enabled relatively shade-intolerant species to invade and survive in large numbers. Even so, these species are dwindling in importance because of their high mortality relative to hemlock. The densities of *Acer rubrum* and *Betula lenta* within ridgetop permanent plots (see Methods) declined 14 and 20 percent between 1984 and 1990, while *Tsuga canadensis* density increased 16 percent. Barring severe disturbance, hemlock will eventually dominate these stands.

If nothing else, these findings should dispel any notions that the disturbance history and species composition of the Henry & Swan plot (Henry & Swan 1974) are characteristic of the entire Harvard tract. Henry & Swan suggested that a series of four catastrophic windstorms, culminating in the 1938 hurricane, caused the composition of the Harvard tract overstory to shift from *Pinus strobus* - *Tsuga canadensis* to *Tsuga canadensis* -Hardwood. In contrast, data from the present study and from other surveys (Branch, Daley, & Lotti 1930; Foster 1988a; Schoonmaker 1992) contain no evidence either of catastrophic disturbance during the 40 years preceding the hurricane or of a sustained, broad-scale increase in the importance of hardwoods following the hurricane. Although the hurricane certainly caused long-term change in the composition of the Harvard tract forest, it was more through the near-elimination of *Pinus strobus* and the mass release of *Tsuga canadensis* advance growth than through any promotion of hardwood regeneration.

Among-stand differences in early post-hurricane physiognomy have also led to persistent differences in basal area. The overstories of lower-slope plots, unlike those of ridgetop plots, are dominated by stems which were larger than 7.99 cm in diameter in 1938 (Table 1). Lower-slope understories, unlike ridgetop understories, include many stems which were larger than 3.99 cm in diameter in 1938. Because growth rates of overstory and understory stems differ little between lower-slope and ridgetop plots (Table 2), lower-slope plots have maintained their initial post-hurricane lead in basal area (Table 5).

This mechanism of among-stand basal area differentiation is entirely different than that described by Kelty (1984, 1989) for pure hardwood, pure hemlock, and hemlock/hardwood (mixed) stands in central and southern New England. In Kelty's study, mixed stands had greater basal area than pure hardwood stands primarily because of the additive contribution of the dense hemlock understory to the red-oak-dominated overstory. Hardwood stands had much sparser understories because of the relative shade-intolerance of the important hardwood species (*Quercus rubra*, *Acer rubrum*, *Betula lenta*, *B. papyrifera*, and *Prunus serotina*). Similarly, mixed stands outproduced pure hemlock stands, apparently because hardwoods (particularly *Quercus rubra*) outperformed

Tsuga canadensis in the overstory and because hemlocks grew faster under hardwoods than under hemlocks. Kelty therefore concluded that -- given sufficient interspecific niche differentiation -- mixed stands outproduce pure stands.

Stands in this study show an opposite trend: hemlock-dominated stands exceed mixed stands in basal area. The main reason for this contrast appears to be the lack of canopy-niche differentiation among the species presently abundant on the Harvard tract. In the mixed stands studied by Kelty, *Quercus rubra* increasingly dominated the overstory by outgrowing *Betula lenta, Acer rubrum,* and other hardwoods. Other studies have found similar evidence of canopy differentiation among these species (Oliver 1975; Hibbs 1983). *Acer rubrum, Betula alleghaniensis*, *B. lenta*, and *Fagus grandifolia* constitute most of the hardwoods within the study plots. None of these species has gained dominance over the others or over larger hemlock regeneration following the hurricane, and all have slowed markedly in radial growth. Moreover, understory hemlock is growing no faster in mixed stands than in hemlock-dominated stands (Table 2). Consequently, hemlock-dominated lower-slope plots have been able to maintain their initial post-hurricane lead over mixed ridgetop plots.

The disagreement between these results and Kelty's is partly due to differences in methodology. Kelty compared stands of equal age, whereas the lower-slope hemlock stands in this study are older than the ridgetop mixed stands. As the results from this study illustrate, however, hemlocks gain the overstory following disturbance precisely because they have an age and size advantage over newly established hardwoods. To compare hemlock stands with mixed stands of equal age, then, is to ignore the very processes by which hemlock stands originate following disturbance. Probably the fairest such comparison is between hemlock and mixed stands which were of similar height immediately following contemporaneous disturbance. The presence in this study of plot 8, sited within a lower-slope mixed stand, allows just such a comparison. Interestingly, this plot has the lowest basal area of any lower-slope plot, while the lower-slope plots with the highest percent basal area of hemlock -- Nos. 6, 7, and 11 -- have the highest basal areas. These results further demonstrate that interspecific canopy differentiation -- leading to greater basal area -- is absent within the study plots.

In contrast to the post-hurricane performances of *Acer rubrum, Betula alleghaniensis*, *B. lenta*, and *Fagus grandifolia*, one of the two individuals of *Quercus rubra* found within the plots shows accelerating radial growth which exceeds that of any other hardwood stem. It has overtopped neighboring hardwoods and hemlocks and appears on the verge of dominance. Perhaps this species' superior ability to sustain high growth rates allows both the overstory and hemlocks beneath it to grow faster. Its architecture may also be important. *Quercus rubra* has upright branches which may make more space available for understory growth. Kelty (1986) speculated that "the high growth rates of the taller understory hemlocks may depend on the relatively open crowns of red oak . . . as well as the later date of leaf development in spring for red oak, to allow sufficient sunlight to reach their crowns".

Because of the lack of stratification among overstory species, basal areas within the present Harvard tract forest may never equal pre-hurricane levels. The pre-hurricane overstory was dominated by *Pinus strobus*, which may occupy a canopy niche similar to that of *Quercus rubra*. *Pinus strobus*, however, showed little regeneration after the hurricane, partly because of competition from hemlock advance regeneration. Interestingly, pollen and forest litter studies have found evidence of abundant oak as well as *Pinus strobus* and *Tsuga canadensis* in the pre-1635 forest (Henry & Swan 1974; Schoonmaker, 1992). The oak was apparently destroyed by the 1665 fire, and has never recovered. Consequently, catastrophic disturbance has led to the supplanting of two fast-growing, shade-intolerant species by a slow-growing, shade-tolerant one.

CONCLUSION

Previous studies have found that the 1938 hurricane left a complex mosaic of damage (Foster 1988a & 1988b; Foster & Boose 1992). Foster & Boose (1992) classified damage from the hurricane into five categories (ranging from no overstory damage to greater than 75 percent overstory damage), none of which constituted more than 36 percent of the total area surveyed. The present study reveals yet a further order of patchiness. Although the hurricane destroyed the overstory over all but the western fringe of the Harvard tract, differences in wind intensity and in pre-hurricane physiognomy caused the size structure of surviving advance growth to differ across the tract. These differences have led to important differences in post-hurricane development and in current characteristics. Furthermore, despite the hurricane's devastation, surviving advance growth was of sufficient size and abundance to dominate much of the post-hurricane forest.

These results demonstrate that relatively fine-scale patchiness in the immediate effects of catastrophic disturbance can result in considerable forest heterogeneity. The nature of such patchiness and the mechanisms by which it generates diversity deserve further study.

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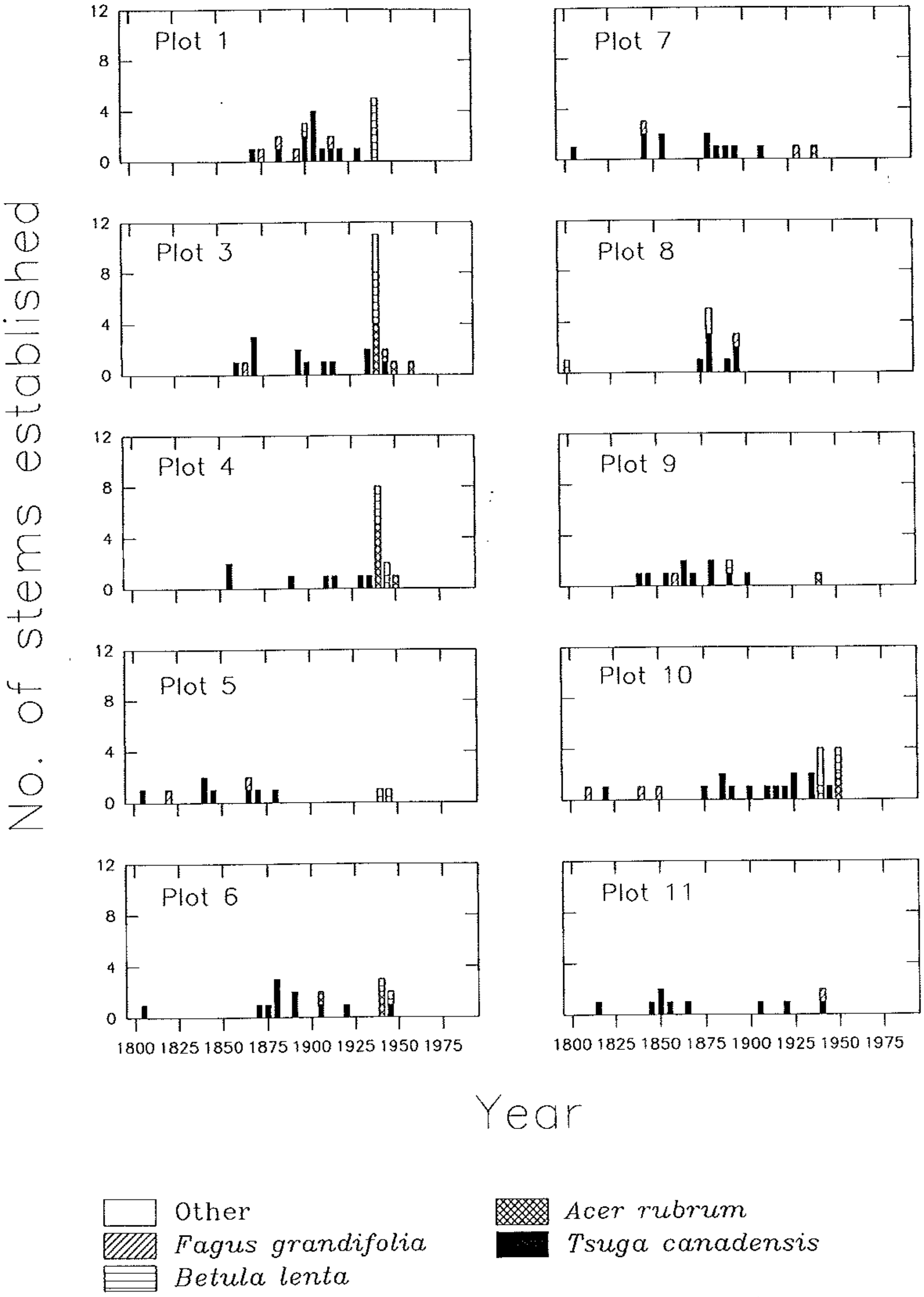
APPENDIX A

To corroborate the 1942 survey's finding that the size of surviving advance growth increased with decreasing slope position, the data on the 1938 diameters of cored stems (Fig. 5) were analyzed. First, the 1938-diameter data for each plot were categorized into four diameter classes: 0.01-3.99 cm, 4.00-7.99 cm, 8.00-11.99 cm, and ≥12.00 cm. The number of stems in each class were then compared among plots through weighted average cluster analysis of Canberra Metric dissimilarity values [$\Sigma|x_{1p}-x_{2p}|/(x_{1p}+x_{2p})$, where x_{qp} denotes the number of individuals in size class p in plot q]. Finally, a dendrogram (Fig. 4) of the weighted average dissimilarity values was constructed.

APPENDIX B

Figure B-1. Establishment patterns of extant stems by species by sample plot.


No. of stems established
Plot 1
Plot 3
Plot 4
Plot 5
Plot 6
Plot 7
Plot 8
Plot 9
Plot 10
Plot 11
0
4
8
12
1800
1825
1850
1875
1900
1925
1950
1975
Year
Other
Fagus grandifolia
Betula lenta
Acer rubrum
Tsuga canadensis

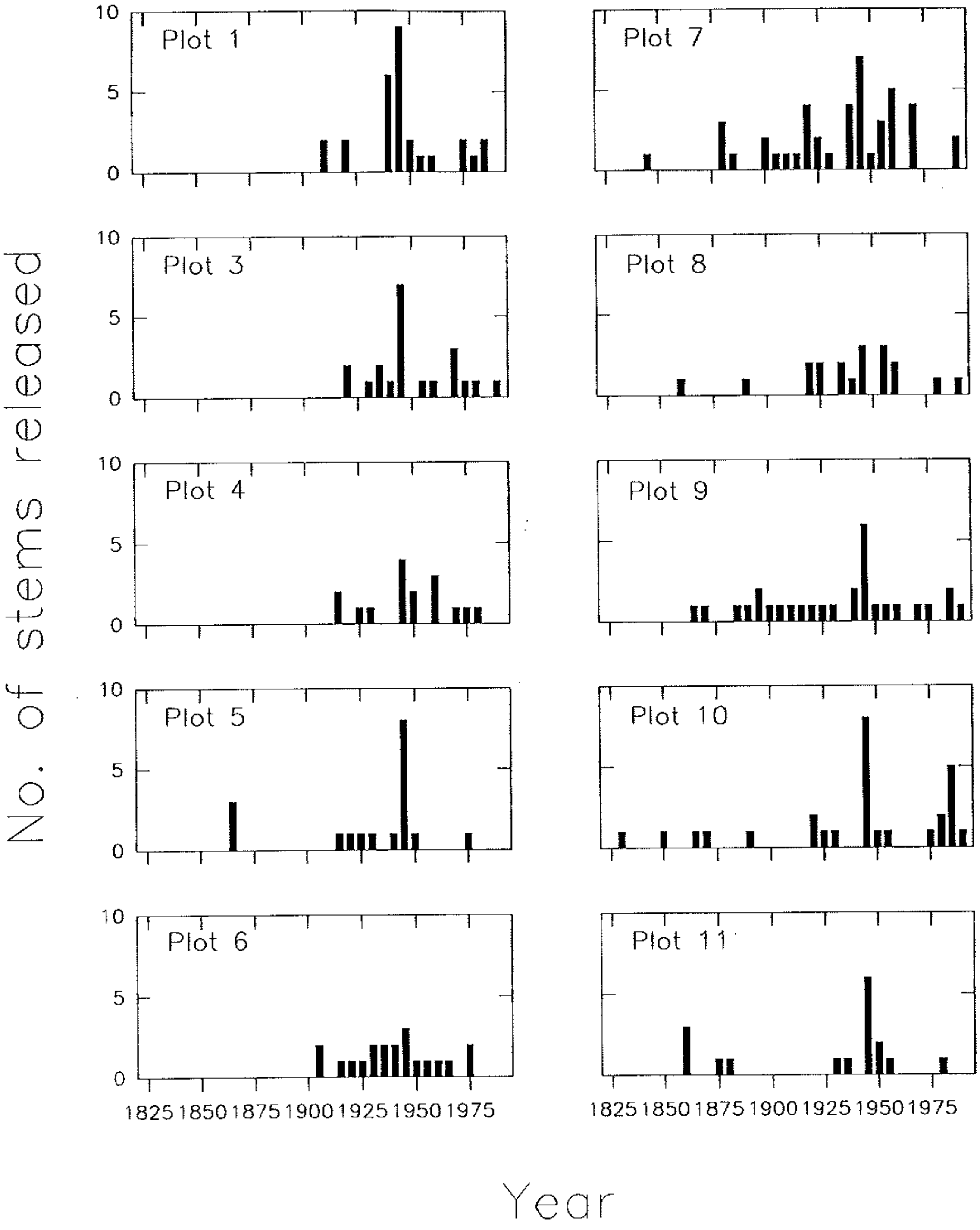


Figure B-2. Growth release patterns of extant stems by sample plot.

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