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Hurricane disturbance regimes in temperate and tropical forest ecosystems

D. R. FOSTER and E. R. BOOSE

Abstract

We provide an overview of hurricane disturbance regimes in the north-eastern United States and the Caribbean, with a focus on ecological effects on temperate and tropical forests. Hurricanes in tropical regions occur with a higher frequency and reach higher intensity levels than in temperate regions. Slower movement of hurricanes in the tropics exposes forests to longer periods of damaging winds from a broader range of wind directions. At the regional to landscape level we are applying models of hurricane meteorology and topographic exposure to reconstruct wind conditions during historically important storms in order to compare these results with observations of forest damage, and to test two hypotheses: (1) regional gradients of hurricane frequency and intensity result from prevailing hurricane tracks and the configuration of coastlines and mountain ranges and (2) landscape gradients in wind exposure result from the interaction of peak wind directions and local topography. At the community level damage is controlled by windspeed, vegetation structure and composition, and site conditions. Damage patterns strongly control subsequent vegetation dynamics: (1) differential species damage determines the initial composition and structure of the vegetation, (2) leaf area establishment is controlled by damage type and forest composition, and (3) microenvironmental conditions and resource distribution are determined by the spatial pattern of residual vegetation. Field studies underline the offentimes low rate of initial mortality following catastrophic storms and the importance of releafing and sprouting in vegetation development. Changes in key ecosystem processes are often slight following even major hurricanes. Studies in Puerto Rico and New England document that nutrient retention was high, nutrient losses were minimal, soil moisture changed little, and minor changes in trace gas fluxes returned rapidly to pre-disturbance

levels. Rapid recovery of biotic control of ecosystem processes results from the retention of organic matter on-site and high rates of survival and resprouting by tree species.

18.1 Introduction

Disturbance processes affect natural ecosystems in complex ways and across a range of ecological scales. One productive means of assessing the relative importance and role of a particular disturbance factor is through analysis of the disturbance regime (*sensu* Heinselman, 1973), including its: (1) physical basis and controlling environmental factors; (2) temporal and spatial distribution; (3) direct impact on the biota and site conditions; and (4) indirect effect on the microenvironmental, biological and soil processes controlling ecosystem response. In this review we seek to provide an overview of the physical nature, spatial and temporal scope, and ecological effects of hurricane winds on forest ecosystems, and to highlight areas in need of further research.

There are notable opportunities for increased dialogue between physical and biological scientists regarding the physical basis of hurricane damage. Although tropical storm meteorology is quite well understood, there has been little attempt to link this information with studies of airflow at the stand and landscape level or with field measurements of forest damage. As a result, ecological and forestry studies often make naive assumptions concerning the characteristics of hurricane winds and their potential to damage forests. A clear understanding of the general characteristics of tropical storms is critical to the interpretation of individual wind events and damage patterns at a landscape scale.

The assessment of temporal variation in wind disturbance is equally critical. For coastal and some marine environments meteorologists have compiled long-term analyses of storm activity (e.g. Lamb, 1991). However, with rare exceptions, such as Stephens' (1955) work in central Massachusetts, the temporal context for wind disturbance in inland regions is lacking. Most estimates by ecologists of the long-term importance of hurricanes are based either on extrapolation of short time series or on composites of hurricane tracks, which contain little information concerning storm intensity. We clearly need additional tools for estimating the return interval of tropical storms of varying intensity.

It is widely assumed that spatial variation in wind damage may explain vegetation patterns and ecosystem characteristics at a landscape to regional scale (Odum, 1970; Committee on Global Change, 1988). For example, sites that are exposed to severe winds as a result of aspect or physiographic position may differ in forest structure or composition from adjacent sheltered lowlands (Cline & Spurr, 1942; Foster, 1988*a*). Similarly, regional gradients in hurricane frequency may alter climatically controlled vegetation gradients (Smith, 1946). Despite the potential importance of variation in wind at these spatial scales the subject is seldom addressed in ecological studies.

In the following overview we do not presume to fill all of these gaps, but rather to explore the relevant information for tropical and temperate regions. We begin with an overview of hurricane meteorology, especially characteristics that are relevant to ecological studies and to the development of modelling approaches to explore the temporal and spatial distribution of these storms. We then address regional and landscape-level considerations and elaborate on preliminary results from simple meteorological and landscape models. In terms of biotic response we review recent information on community-level damage and vegetation development following catastrophic storms. This overview of stand dynamics provides the context for interpreting ecosystem responses. The coverage in this review is admittedly selective and incomplete, reflecting both the contents of other chapters in this volume and the current state of knowledge.

18.2 Hurricane meteorology

Hurricanes occur in all tropical oceans of the world except the South Atlantic and the eastern South Pacific. While the processes that control hurricane formation are not fully understood, meteorologists have identified several necessary conditions, including very warm sea surface temperatures ($\geq$26 °C); an atmosphere free of vertical wind shear, temperature inversions, or dry layers that would inhibit developing cloud towers; and an external starting mechanism or energy source. Once formed, hurricanes often follow a parabolic path, drifting westward and slightly poleward with the tropical trade winds, then recurving eastward as they come under the influence of the prevailing westerlies of temperate latitudes (Fig. 18.1); however, there are many exceptions to this general pattern. Hurricanes that do follow a parabolic path over the oceans frequently become vigorous extratropical storms and may reach the polar oceans (Dunn & Miller, 1964; Simpson & Riehl, 1981; Anthes, 1982).

For the North Atlantic (including the Caribbean and Gulf of Mexico), sufficient data have been recorded to analyse the frequency, intensity and tracks of hurricanes over the last 120 years. As the hurricane season (June to November) progresses, there are regular shifts in the principal areas of storm formation and in the pattern of storm tracks. Hurricanes are most common

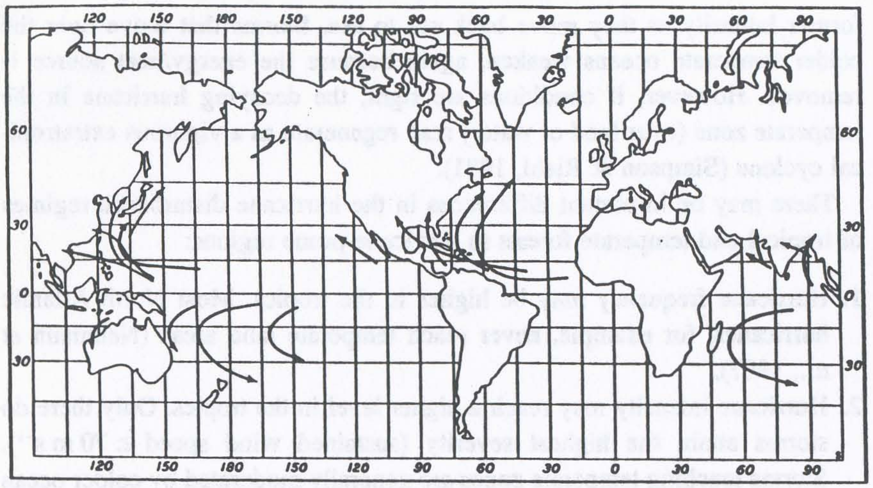


Fig. 18.1. Areas where hurricanes form. From Dunn & Miller (1964).

in September when ocean temperatures reach a maximum. Over the last 100 years (1886–1986) there have been an average of five hurricanes (sustained wind speed ≥ 32 m s^{-1}) per year (Neumann *et al.*, 1987). The frequency of severe hurricanes (sustained wind speed ≥ 50 m s^{-1}) varies over multidecadal cycles, and has recently been shown to be closely linked to summer rainfall amounts in the Western Sahel region of West Africa; these rainfall amounts appear to be linked in turn to natural global-scale climate variation in both tropical and extratropical regions (Fig. 18.2; Gray, 1990). The potential effects of human-induced global warming on hurricanes may include increases in hurricane frequency and intensity, and expanded areas of hurricane formation and impact (Emanuel, 1987; Hobgood & Cerveny, 1988; O'Brien *et al.*, 1992).

The mature hurricane is a great revolving vortex (counterclockwise in the northern hemisphere, clockwise in the southern) that reaches upward to an altitude of at least 7–8 km, and may extend outward to a radius of 1000 km. The eye at the centre of the hurricane is characterised by very low pressure and calm or light winds. Surrounding the eye, typically at a radius of 30 km (but variable from 10 to 80 km), is the eyewall, an area of intense convection where the highest windspeeds and heaviest precipitation normally occur. Sustained surface windspeeds (1 min average) as high as 88 m s^{-1} have been recorded, though in most hurricanes the maximum sustained speed is closer to 50 m s^{-1}. Outside the eyewall windspeeds normally decrease as a negative exponential function of the radius, so that sustained hurricane-force winds are rarely found beyond a radius of 100 km (Frank, 1977; Simpson & Riehl, 1981; Anthes, 1982).

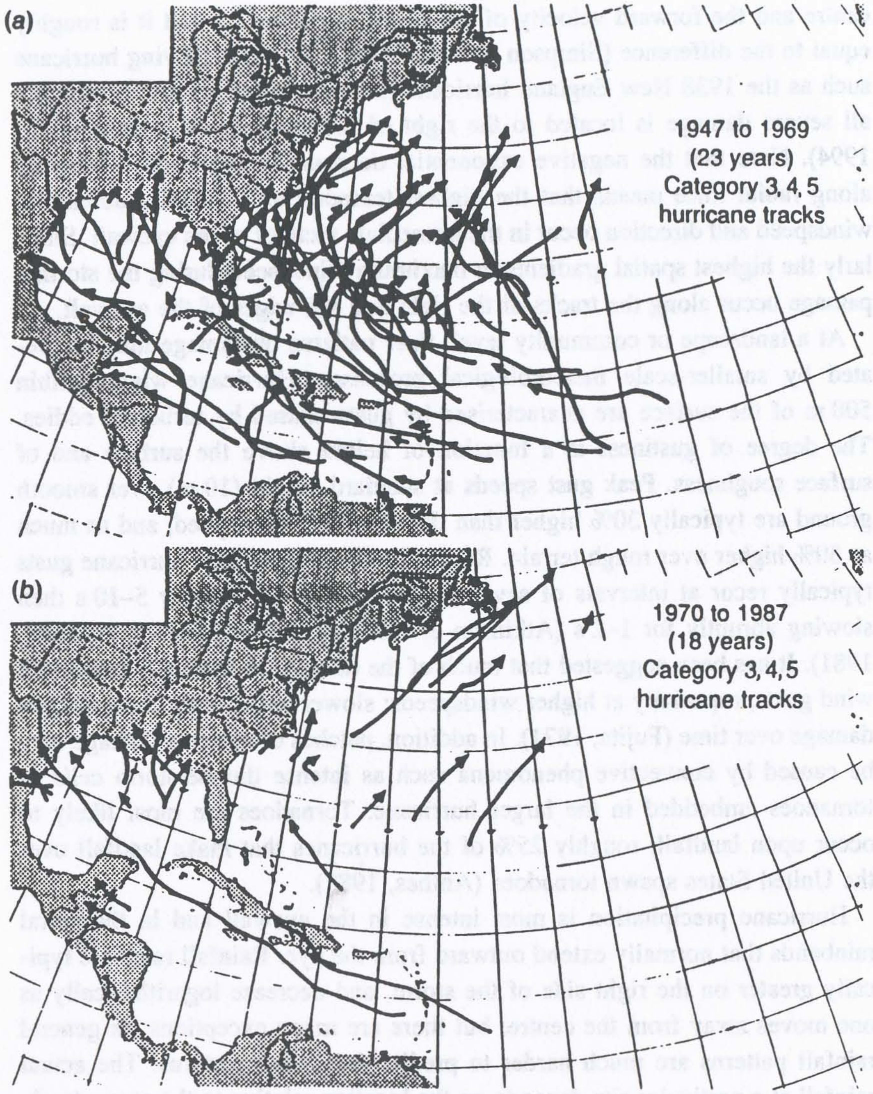


Fig. 18.2. Tracks of major hurricanes (sustained wind speed ≥ 50 m s^{-1}) in the North Atlantic for (*a*) the 23-year period 1947–69 when rainfall in West Africa was above average and (*b*) the 18-year period 1970–87 when it was below average. From Gray (1990).

On a regional scale, the area of widespread severe wind damage to forests rarely extends more than 100 km to either side of the storm track. Damage is often concentrated in areas directly impacted by the eyewall, and the worst damage normally occurs on the right side of the storm (in the northern hemisphere). On the right side the wind velocity relative to the ground is roughly equal to the sum of the rotational velocity of the wind around the centre and the forward velocity of the storm, while on the left it is roughly equal to the difference (Simpson & Riehl, 1981). In a fast-moving hurricane such as the 1938 New England hurricane (forward speed 25 m s^{-1}) virtually all severe damage is located to the right of the storm track (Boose *et al.*, 1994). Note that the negative exponential decrease in sustained windspeed along radial lines means that the highest temporal and spatial gradients in windspeed and direction occur in the immediate vicinity of the eyewall. Similarly the highest spatial gradients in maximum windspeed during the storm's passage occur along the tracks of the right and left edges of the eyewall.

At a landscape or community level, finer patterns of damage may be created by smaller-scale meteorological processes. Hurricane winds within 500 m of the surface are characterised by gusts caused by turbulent eddies. The degree of gustiness is a function of height above the surface and of surface roughness. Peak gust speeds at standard height (10 m) over smooth ground are typically 30% higher than the sustained windspeed, and as much as 50% higher over rough terrain. Recent studies suggest that hurricane gusts typically recur at intervals of several minutes, accelerating for 5–10 s then slowing abruptly for 1–2 s (Atkinson & Holliday, 1977; Simpson & Riehl, 1981). It has been suggested that much of the damage to forests is caused by wind gusts, especially at higher windspeeds; slower winds may cause fatigue damage over time (Fujita, 1971). In addition, patches of extreme damage may be caused by convective phenomena such as intense thunderstorm cells or tornadoes embedded in the larger hurricane. Tornadoes are most likely to occur upon landfall; roughly 25% of the hurricanes that make landfall over the United States spawn tornadoes (Anthes, 1982).

Hurricane precipitation is most intense in the eyewall and in the spiral rainbands that normally extend outward from the eye. Rainfall rates are typically greater on the right side of the storm, and decrease logarithmically as one moves away from the centre; but there are many exceptions. In general rainfall patterns are much harder to predict than wind patterns. The actual rainfall at a particular site depends on the location relative to the storm track, the distribution of rainfall around the storm, the speed of storm movement, and surrounding topographic features. Peak rainfall for a moderate hurricane averages 35 cm (Simpson & Riehl, 1981; Anthes, 1982).

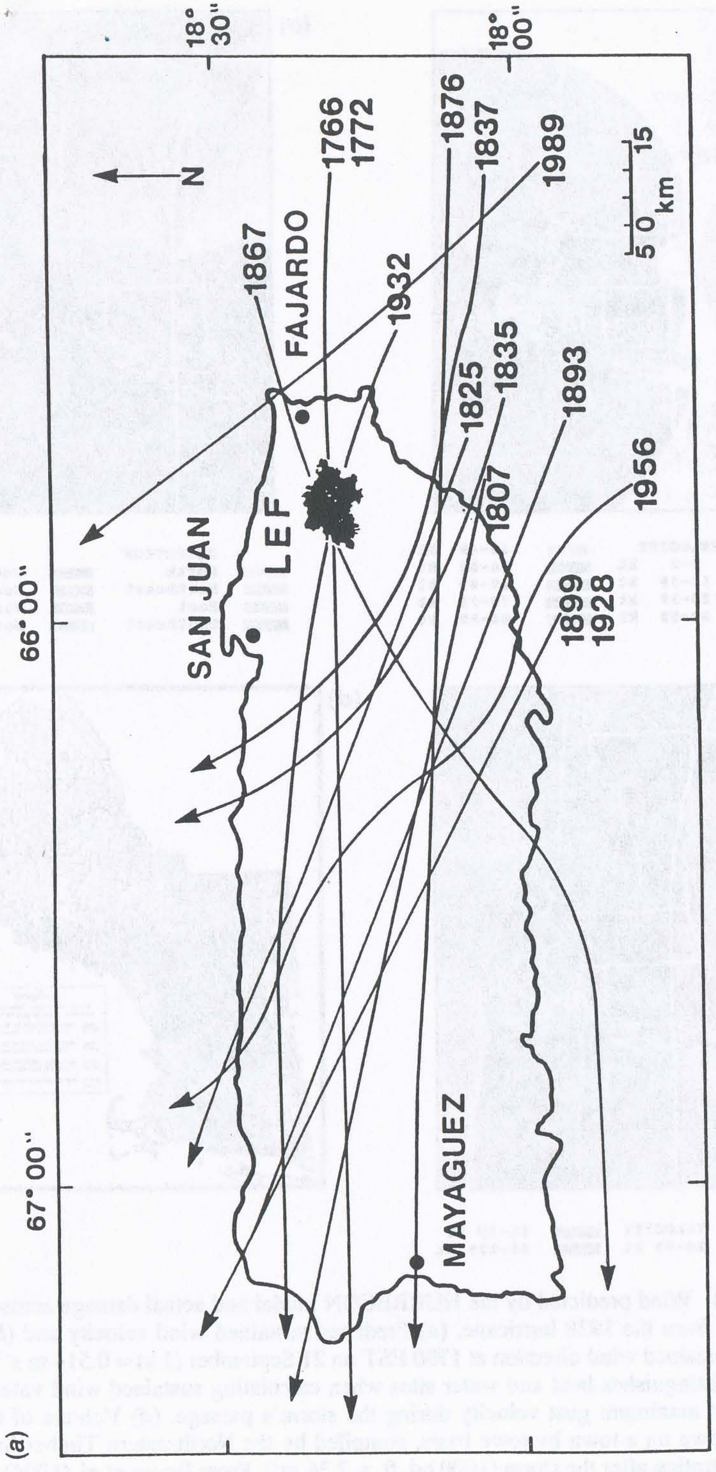
Hurricanes always weaken upon landfall, because the underlying energy source – warm ocean water – is removed. Such weakening is hastened in the vicinity of large mountain ranges because of increased surface friction. Upon landfall, windspeeds typically fall below hurricane levels in the first day. Rainfall rates may continue or even increase for several days. Hurricanes that pass over short stretches of land (e.g. small islands) frequently regain their former intensity as they move back out to sea. Storms that move over the colder temperate oceans weaken, again because the energy/heat source is removed. However, if conditions are right, the decaying hurricane in the temperate zone (over land or water) may regenerate as a vigorous extratropical cyclone (Simpson & Riehl, 1981).

There may be important differences in the hurricane disturbance regimes of tropical and temperate forests in hurricane-prone regions:

1. Hurricane frequency may be higher in the tropics. Most North Atlantic hurricanes, for example, never reach temperate land areas (Neumann *et al.*, 1987).
2. Hurricane intensity may reach a higher level in the tropics. Only there do storms attain the highest severity (sustained wind speed ≥ 70 m s^{-1}). Storms reaching temperate zones are generally moderated by colder ocean waters, an increase in the Coriolis force with latitude, and (frequently) the influx of cool, dry air into the storm (Byers, 1974; Simpson & Riehl, 1981).
3. Hurricanes in the tropics generally move more slowly than hurricanes in temperate zones. As a result, tropical sites may be subjected to longer periods of damaging winds and substantially greater rainfall from a single storm. In the faster-moving hurricanes of the temperate zone the area of highest winds is frequently shifted to the right side of the storm (see above), increasing the surface windspeed on that side but reducing the area of potential destruction and reducing the range of damaging wind directions.

18.3 Regional and landscape-level effects

The patterns of damage created by hurricane winds in a forested landscape are complex and may appear random or indecipherable (Shaw, 1983). The interaction of meteorological, physiographic and biotic factors that gives rise to such patterns has not been widely studied to date. At regional scales (~500 km) meteorologists have used damage to forests and to human structures as an indication of the strength and direction of the strongest surface winds for selected hurricanes at landfall (e.g. Fujita, 1971; Powell, 1982). At landscape scales (~10 km) ecologists have recognised the importance of hurricanes in establishing forest patterning and initiating vegetation dynamics (Naka, 1982; Denslow, 1985; Bellingham, 1991). Topographic exposure and forest structure and composition have been shown to explain much of the landscape pattern of damage in central New England in the 1938 hurricane



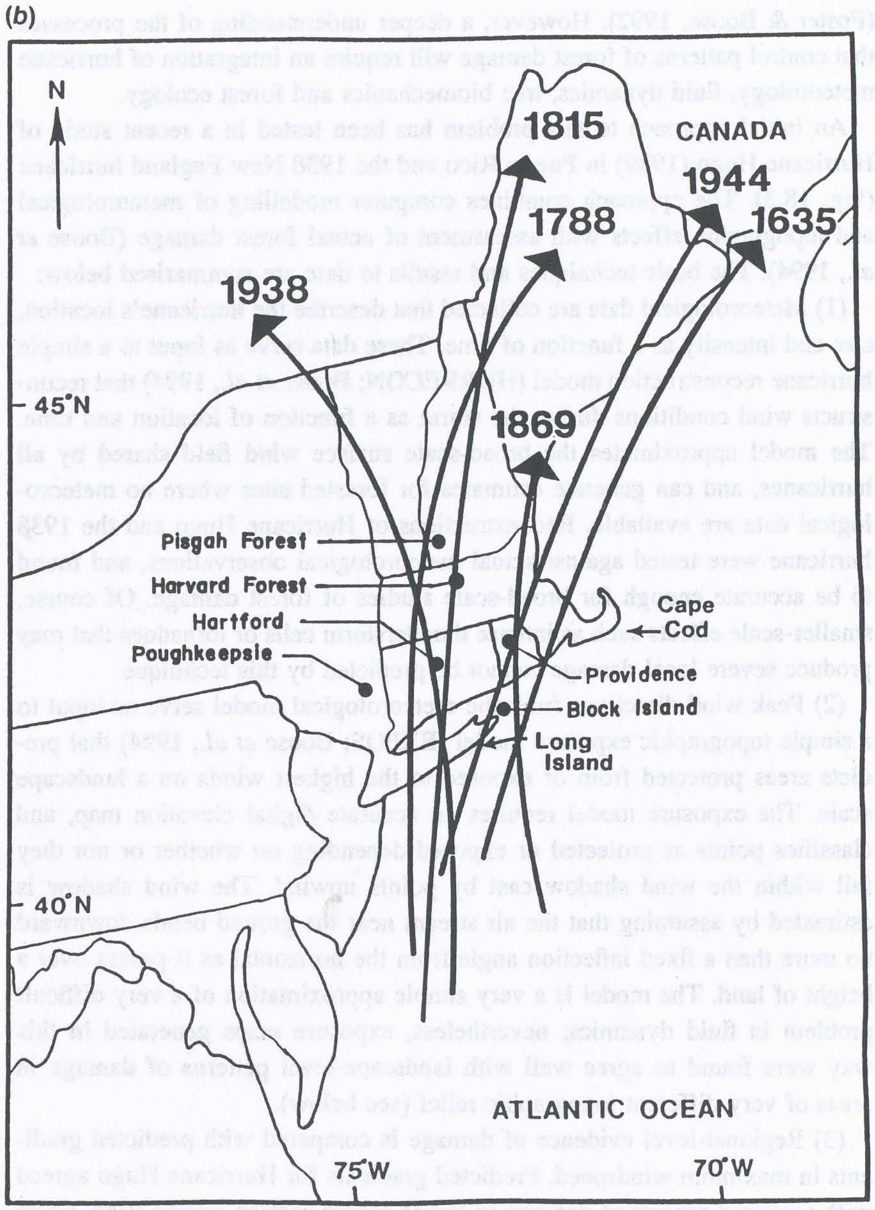


Fig. 18.3 (*a*) Tracks of severe hurricanes in Puerto Rico since 1700. LEF, Luquillo Experimental Forest; 1989, Hurricane Hugo. (*b*) Tracks of six severe hurricanes that caused significant forest damage in New England. From Boose *et al.* (1994).

(Foster & Boose, 1992). However, a deeper understanding of the processes that control patterns of forest damage will require an integration of hurricane meteorology, fluid dynamics, tree biomechanics and forest ecology.

An initial approach to this problem has been tested in a recent study of Hurricane Hugo (1989) in Puerto Rico and the 1938 New England hurricane (Fig. 18.3). The approach combines computer modelling of meteorological and topographic effects with assessment of actual forest damage (Boose *et al.*, 1994). The basic techniques and results to date are summarised below:

(1) Meteorological data are collected that describe the hurricane's location, size and intensity as a function of time. These data serve as input to a simple hurricane reconstruction model (HURRECON; Boose *et al.*, 1994) that reconstructs wind conditions during the storm as a function of location and time. The model approximates the broad-scale surface wind field shared by all hurricanes, and can generate estimates for forested sites where no meteorological data are available. Reconstructions of Hurricane Hugo and the 1938 hurricane were tested against actual meteorological observations, and found to be accurate enough for broad-scale studies of forest damage. Of course, smaller-scale effects such as intense thunderstorm cells or tornadoes that may produce severe local damage cannot be predicted by this technique.

(2) Peak wind directions from the meteorological model serve as input to a simple topographic exposure model (EXPOS; Boose *et al.*, 1994) that predicts areas protected from or exposed to the highest winds on a landscape scale. The exposure model requires an accurate digital elevation map, and classifies points as protected or exposed depending on whether or not they fall within the wind shadow cast by points upwind. The wind shadow is estimated by assuming that the air stream near the ground bends downward no more than a fixed inflection angle from the horizontal as it passes over a height of land. The model is a very simple approximation of a very difficult problem in fluid dynamics; nevertheless, exposure maps generated in this way were found to agree well with landscape-level patterns of damage in areas of very different topographic relief (see below).

(3) Regional-level evidence of damage is compared with predicted gradients in maximum windspeed. Predicted gradients for Hurricane Hugo agreed with scattered reports of damage to towns across eastern Puerto Rico, while predicted gradients for the 1938 hurricane matched detailed surveys of blowndown timber across New England (Fig. 18.4).

(4) Landscape-level patterns of damage for particular sites of interest are assessed through aerial photographs, archival records and/or field surveys. These patterns are analysed in the light of predicted gradients in maximum windspeed, predicted patterns of topographic exposure to the highest winds,

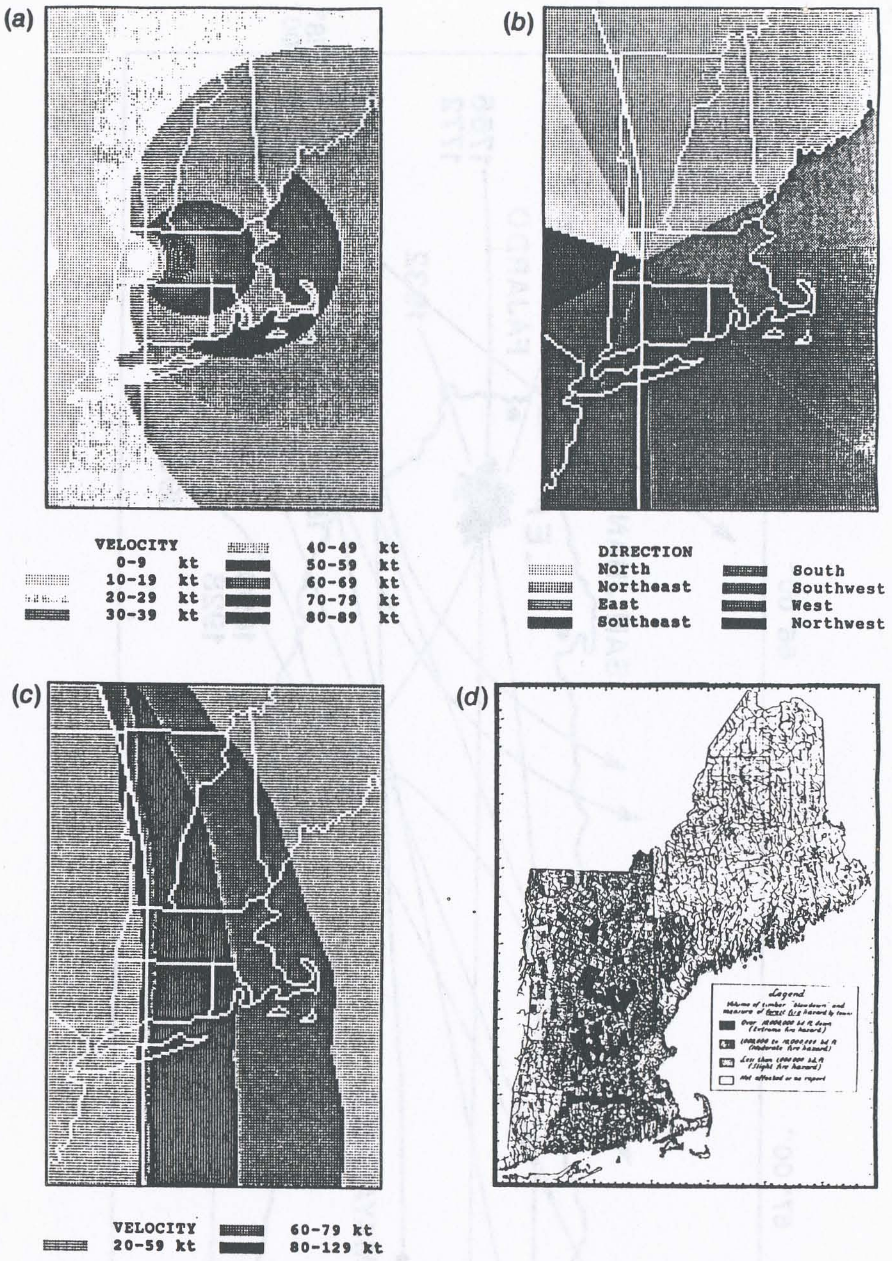


Fig. 18.4. Wind predicted by the HURRECON model and actual damage across New England from the 1938 hurricane. (*a*) Predicted sustained wind velocity and (*b*) predicted sustained wind direction at 1700 EST on 21 September (1 kt = 0.514 m s^{-1}). The model distinguishes land and water sites when calculating sustained wind values. (*c*) Predicted maximum gust velocity during the storm's passage. (*d*) Volume of timber blown down on a town by town basis, compiled by the Northeastern Timber Salvage Administration after the storm (1000 bd. ft. = 2.36 m^3). From Boose *et al.* (1994).

and available data on forest structure and composition. Results from the two hurricanes studied showed good agreement between predicted exposure and landscape-level patterns of damage (Fig. 18.5).

(5) The orientations of windblown trees at particular sites of interest are assessed through aerial photographs, archival records and/or field surveys. These orientations are analysed in the light of the modelled wind conditions for the site and local topographic features. In New England, treefall orientations closely matched predicted peak winds in the 1938 hurricane, while in Puerto Rico there was also fairly good agreement, with some apparent modification of wind direction by the mountainous terrain (Fig. 18.6).

Further analysis of other recent (twentieth-century) hurricanes for which good meteorological and forest damage data are available should improve this basic approach and refine the modelling techniques. An important ecological application of this approach will be to study long-term hurricane disturbance regimes at particular sites by extending the analysis to older storms (pre twentieth-century) to gain a better temporal perspective (even though data are less complete). Spatial variation in such regimes is anticipated. On a regional scale, we expect to find significant gradients of long-term hurricane frequency and intensity caused by prevailing historical hurricane tracks and the spatial configuration of coastlines and mountain ranges. On a landscape scale in hilly or mountainous areas, we expect to find significant gradients of long-term exposure to catastrophic hurricane winds caused by the interaction of prevailing peak wind directions and local topography. We expect that the range of peak wind directions at a particular site is constrained by historical storm tracks and storm velocity, and the location of coastlines and mountain ranges.

Work to date suggests that the following factors help to control regional scale (~500 km) hurricane wind damage to forests:

1. Regional wind velocity gradients resulting from hurricane size, intensity and proximity to the storm track. Note that hurricane size and intensity may change significantly during the storm's passage.
2. Large topographic features such as coastlines and mountain ranges which help to determine how much a hurricane will weaken before it reaches a particular site.
3. Regional vegetation zones resulting from differences in geology, climate and disturbance history. For example, high elevation forests, though often subject to higher wind speeds during a hurricane, may be better adapted to wind and suffer less damage than lower elevation forests.

At finer spatial scales, these regional factors may be modified by smaller-

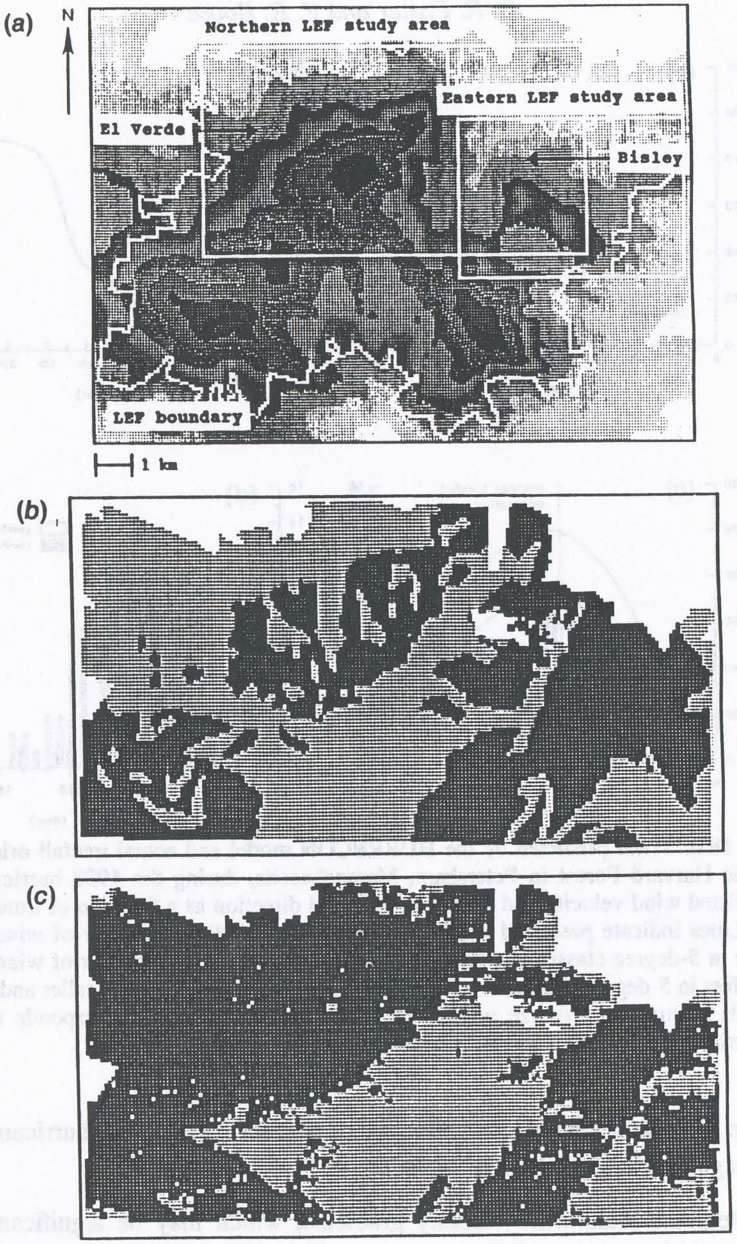


Fig. 18.5. Topographic exposure predicted by the EXPOS model and actual forest damage from Hurricane Hugo in the Luquillo Experimental Forest (LEF), Puerto Rico. (*a*) Study areas in the LEF. Elevation shown in 100 m contours ranges from 50 m to 1075 m a.s.l. (*b*) Forest damage in the Northern LEF study area. Light, <10% windthrow; dark, ≥10% windthrow. (*c*) Predicted exposure in the Northern LEF study area for the peak NNW wind predicted by the HURRECON model. Light, protected; dark, exposed. The lack of damage in exposed areas in the western portion of the study area parallels the predicted gradient in peak windspeed from east to west. From Boose *et al.* (1994).

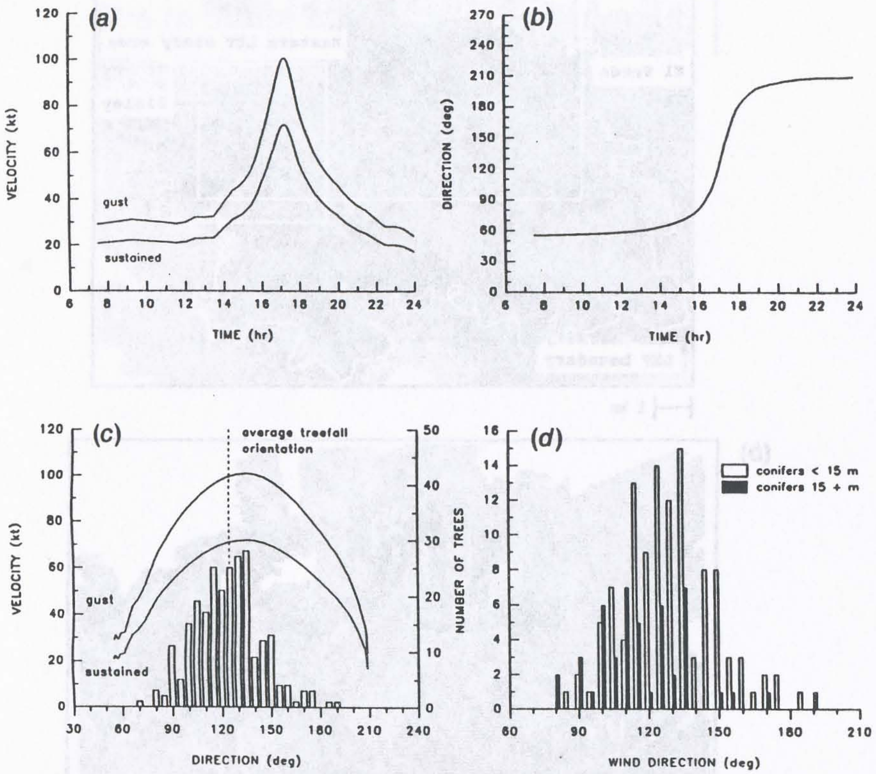


Fig. 18.6. Wind predicted by the HURRECON model and actual treefall orientation at the Harvard Forest in Petersham, Massachusetts, during the 1938 hurricane. (*a*) Predicted wind velocity and (*b*) predicted wind direction as a function of time (EST). (*c*) Lines indicate predicted wind velocity and bars indicate number of windthrown trees in 5-degree classes as a function of wind direction. (*d*) Number of windthrown conifers in 5-degree classes as a function of wind direction, showing taller and shorter stands separately. Average orientation angle for taller stands corresponds to wind directions earlier in the storm. From Boose *et al.* (1994).

scale processes. Factors controlling landscape-level (~10 km) hurricane wind damage to forests appear to include:

1. Regional-scale wind velocity gradients, which may be significant on a landscape scale as well, especially near the storm track. Intense thunderstorm cells or tornadoes may cause local patches or swaths of extreme damage, especially in the vicinity of the eyewall.
2. Variation in topographic exposure to wind. In hilly or mountainous areas topographic exposure may make the difference between little damage and complete destruction for the same forest type. The pattern and relative extent of protected and exposed areas vary with topography (Fig. 18.7).

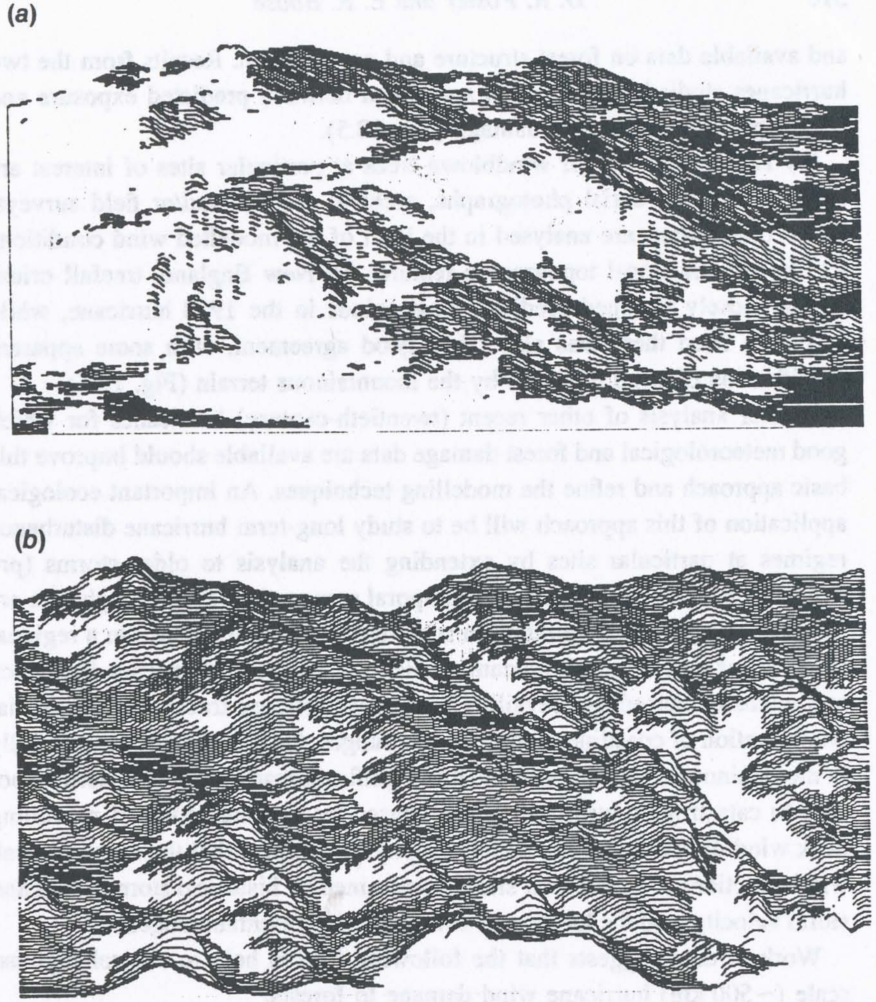


Fig. 18.7. Topographic exposure in contrasting landscapes predicted by the EXPOS model, using peak wind directions from the HURRECON model. Light, protected; dark, exposed. (*a*) Hurricane Hugo and mountainous terrain in the Luquillo Experimental Forest, Puerto Rico. (*b*) The 1938 hurricane and gently rolling terrain in the town of Petersham, Massachusetts. From Boose *et al.* (1994).

   Other complex topographic effects at this scale include acceleration of the wind over ridges and summits, and channelling of the wind up valleys and around protuberances.

3. Differential response of individual stands to wind disturbance as a function of species composition and structure, and rooting conditions (see next section). These factors may in turn be strongly influenced by the land-use and natural disturbance history of the stand.

18.4 Community-level effects

Stand dynamics initiated by hurricane damage are dependent on two interrelated processes: initial physical impact of the wind and subsequent regrowth. Damage is determined by windspeed and duration, vegetation structure and composition and site conditions, especially soil characteristics and site stability. Forest regrowth is largely determined by the distribution of surviving vegetation and resulting microenvironmental conditions.

Variation in site exposure, storm conditions and vegetation result in complex damage patterns in forested landscapes. However, when adequate pre-hurricane data are available many of the relationships among these variables are remarkably straightforward (Foster, 1988*b*; Peterson & Pickett, 1991; Foster & Boose, 1992; Zimmerman *et al.*, 1994).

The most complete effort to assess the relationships between forest characteristics and wind damage was that by Rowlands (1941) following the 1938 hurricane in New England. With samples stratified by wind exposure, soil drainage, stand age, structure and composition and with complete plot inventories before and after the storm it was possible to separate the relative importance of many factors. The results depict simple relationships between vegetation structure and composition and damage for exposed stands on well-drained soils (Foster, 1988*b*). Forest damage (percentage of windthrown trees) exhibited a positive relationship with stand height and age and negative relationship with density (Fig. 18.8). The slope of this relationship varied considerably with species composition: conifers (white pine, red pine, spruce) were much more susceptible to damage than hardwoods. In general, fast-growing and pioneer species were more susceptible than slower-growing, shade-tolerant species.

Within mixed forests of conifers and hardwoods the wind appeared to operate selectively on individuals according to their specific susceptibility. Thus, scattered white pine within an oak forest were preferentially windthrown (Rowlands, 1941; Foster, 1988*b*). The vertical distribution of damage also broadened with stand age. In young stands damage was largely confined to overstorey trees, whereas in older stands an increasing percentage of co-dominant, intermediate and understorey trees were damaged. Overall, uprooting of trees accounted for 75–90% of the windthrown stems.

These conclusions are supported by other research on the 1938 hurricane and different storms and forest types (Foster & Boose, 1992). New England studies suggest that fast-growing species are susceptible to damage as a result of tall stature, the concentration of foliage in the upper canopy and light wood (Jensen, 1941; Smith, 1946). Similar results have been reported from tropical sites, although a straightforward relationship based on size or wood strength is not always apparent (Putz, 1983; Basnet, 1992).

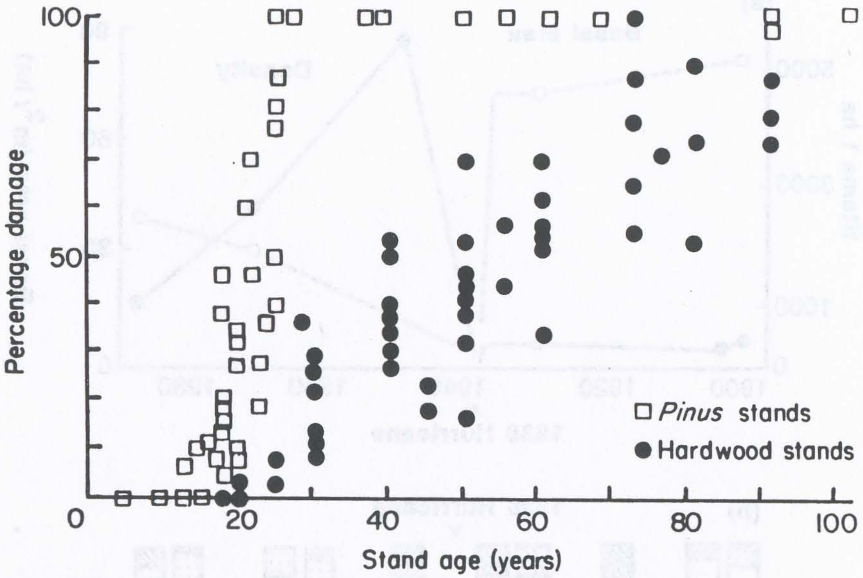


Fig. 18.8. Relationship between hurricane damage (measured as the percentage of individual trees damaged) and stand age for forests in central New England following the 1938 hurricane. Stand types are separated into conifer forests (primarily dominated by *Pinus strobus* and *P. resinosa*) and hardwood forest (consisting of *Quercus*, *Carya*, *Acer*, *Betula* spp.). From Foster (1988*b*).

The extent and type of damage affect subsequent vegetation dynamics in a number of important ways: (1) differential damage according to species, life history strategy and stratum will determine the initial composition and vertical arrangement of the vegetation; (2) re-establishment of leaf area through refoliation and sprouting is largely controlled by the type of damage suffered and species involved; (3) microenvironmental conditions and resource distribution are determined by the extent and structure of residual vegetation; and (4) site modification, including uprooting, controls many soil processes.

Differential species damage may produce abrupt changes in overstorey composition. For example, the 1938 hurricane transformed broad areas of New England from susceptible white pine forest to more resistant and more shade-tolerant hardwood stands comprised of oak, maple and birch (Clapp, 1938; Brake & Post, 1941). Similar responses occurred in old-growth white pine forests (Fig. 18.9; Henry & Swan, 1974). Additional studies suggest that selective damage to pioneer species by wind may actually advance succession (Jensen, 1941; Smith, 1946; Webb, 1986, 1989).

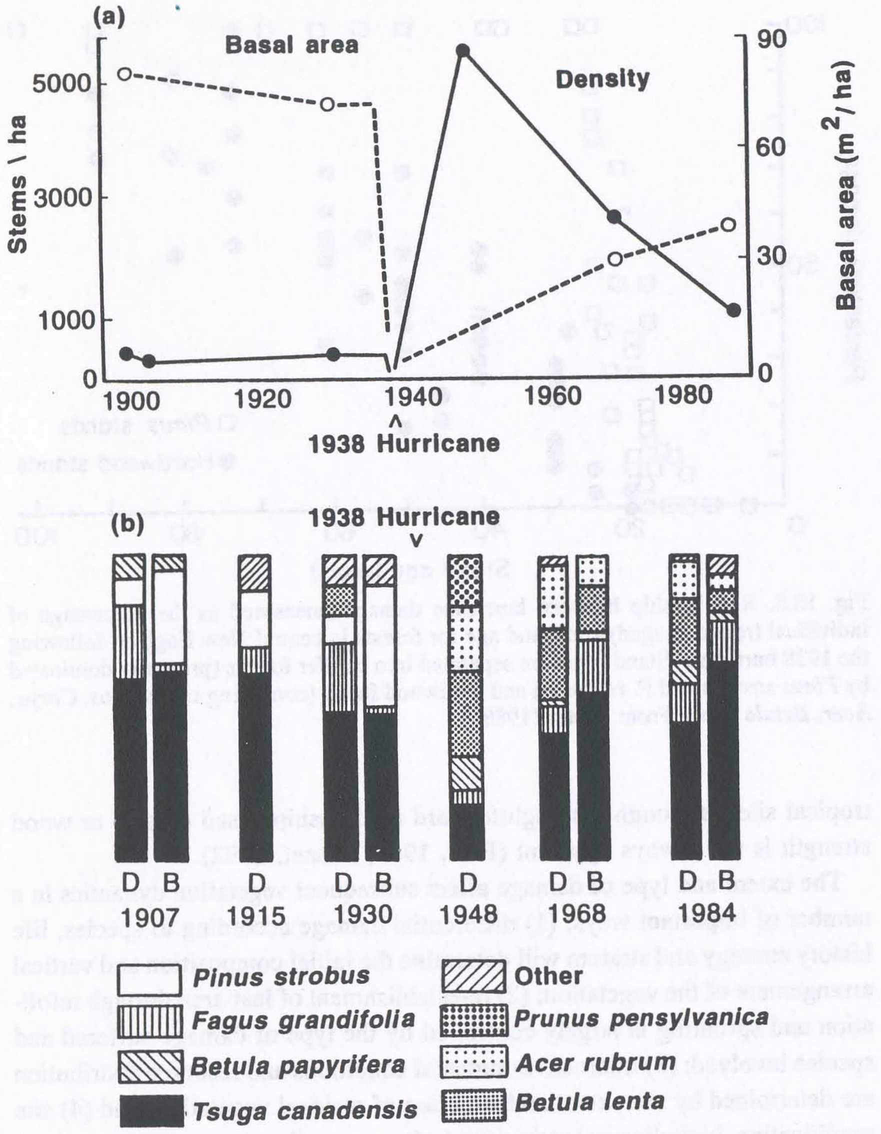


Fig. 18.9. Dynamics of the old growth white pine–hemlock forest on the Harvard Forest Pisgah tract, southwestern New Hampshire, following the 1938 hurricane. Changes from 1907 to 1984 are shown for (*a*) basal area and density and (*b*) relative density (D) and relative basal area (B). The forest stand was approximately 300 years old and undisturbed by human activity when it was completely windthrown by the hurricane. From Foster (1988*a*).

The extent of canopy removal and the type of damage strongly influence resource distribution and microenvironment heterogeneity (Figs. 18.10, 18.11). Of all microenvironmental factors affected, light is undoubtedly the most important in determining vegetation and ecosystem processes as it drives temperature and vapour pressure gradients and is critical to plant success (Sipe, 1990). Light quality, quantity and spatial pattern are determined by the size of canopy openings and rate of regrowth. For example, following Hurricane Hugo light at the seedling level increased from 23 to 404 µmol m^{-2} s^{-1} and was accompanied by a great increase in direct long beam radiation (Walker *et al*., 1992). However, this light environment was incredibly dynamic: regrowth from damaged stems and upgrowth from understorey vegetation rapidly reduced light levels near the ground. Light patterns are spatially and temporally complex, exhibiting tremendous variation across blowdowns and on a diurnal and seasonal basis (Chazdon & Fletcher, 1984; Walker *et al*., 1991; Carlton, 1993). As summarised by Sipe (1990) the light gradient in canopy gaps is also broad, spanning the range from full exposure to direct beam irradiance for much of the growing season to infrequent exposure to short sunflecks.

The mound and pit microtopography associated with uprooted trees forms important habitats in the post-hurricane landscape (Armson & Fessendon, 1973; Beatty, 1984; Denslow, 1985; Carlton, 1993). The extent of uprooting is strongly dependent on the long-term moisture status of the site; on wet sites root systems tend to be surficial and prone to uprooting. However, the effect of soil moisture on well-drained uplands is less clear and untested experimentally. For example, the extent of uprooting by an experimental hurricane created under relatively dry soil conditions was remarkably similar to that on similar sites following the 1938 hurricane, which was accompanied by over 20 cm of precipitation (Foster, 1988*b*; Lezberg & Foster, unpublished data). Other factors controlling uprooting include: tree characteristics (size, health, wood density and buttressing) and soil rockiness, drainage and depth (Brake & Post, 1941; J. E. Bertram, personal communication).

Windthrow microtopography may cover substantial ground in wind-prone forests. In New Brunswick, Canada, Lyford & MacLean (1966) identified 600 mounds and pits per acre covering approximately 50% of the surface. In Massachusetts, Stephens (1956) estimated that 15% of an old-growth forest site was windthrow microtopography; approximately 90% of this was produced by four severe hurricanes. Mounds averaged 6 m^2 in area and 60–100 cm in height, whereas pits were 30 cm deep and 2 m^2 in area.

Mound and pit topography increases site heterogeneity by creating soil microenvironments that vary in moisture, nutrients, temperature and stability

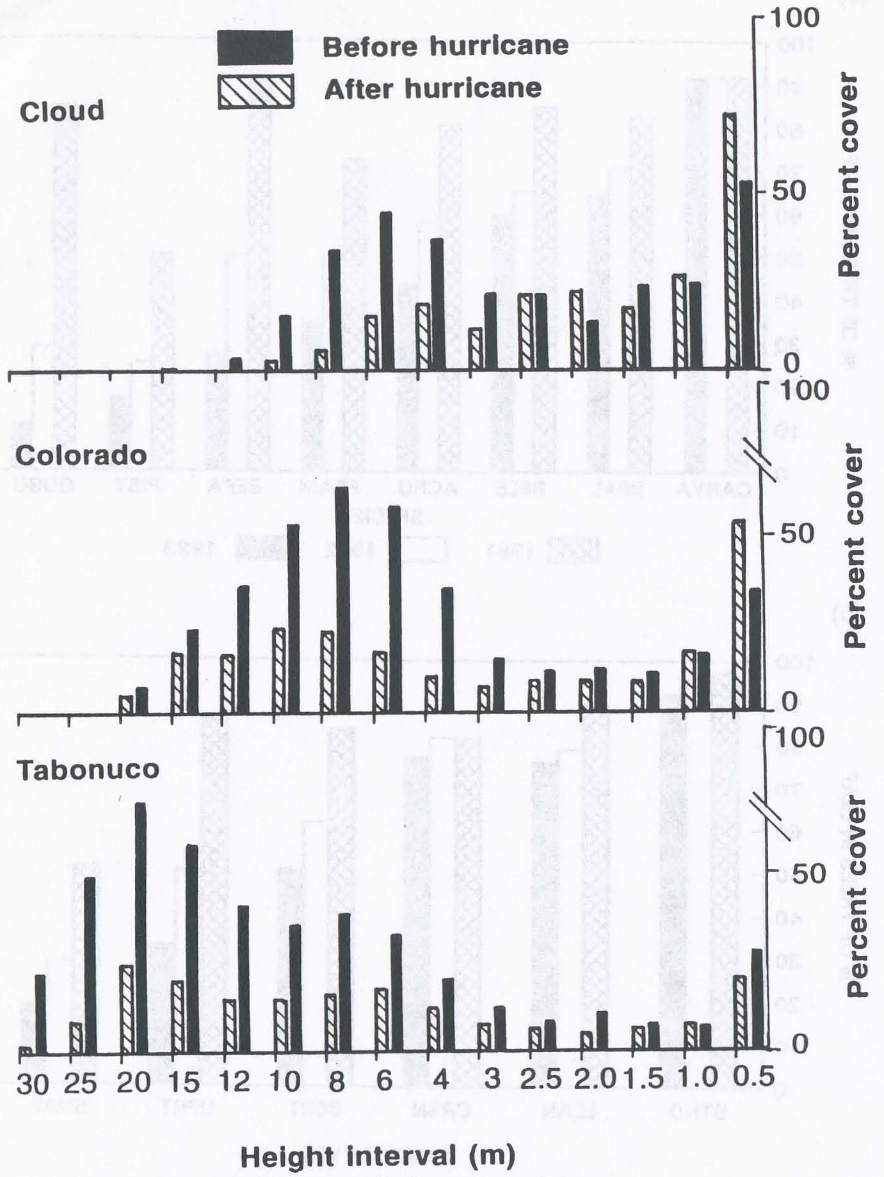


Fig. 18.10. Impact of Hurricane Hugo on the structure of forests in the Luquillo Experimental Forest, Puerto Rico. Vegetation height profiles taken before and after the hurricane for tabonuco (350 m elevation), colorado (750 m elevation) and cloud (1000 m elevation) forests. The horizontal scale shows the total points with cover as a percentage of the total number of grid points in each plot. The vertical scale shows the upper limit of each height interval. From Brokaw & Grear (1991).

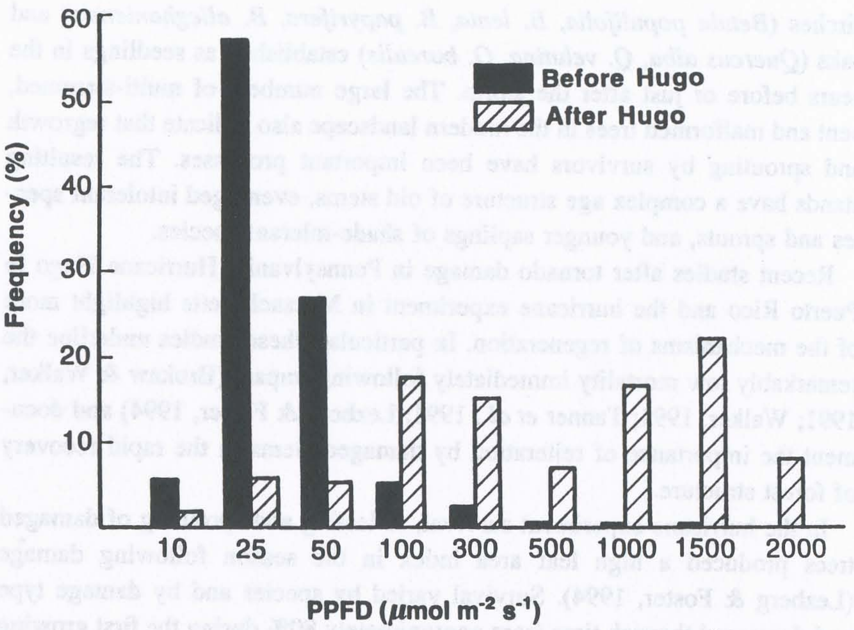


Fig. 18.11. The effect of hurricane damage on the light environment is illustrated by the frequency distribution of photosynthetic photon flux densities (PPFD; 1100–1300 hours local time) at Luquillo Experimental Forest, Puerto Rico, before (n = 21 660 records) and after (n = 34 548 records) Hurricane Hugo. From Walker *et al.* (1992).

(Peterson *et al.*, 1993). Mounds provide seed beds of exposed soil that may reduce competition and stimulate the germination of some buried seeds (Beatty, 1984; Carlton, 1993). As a consequence, mounds are frequently occupied by pioneer species, such as birches, with small, wind-dispersed seeds.

The successional changes initiated by catastrophic blowdown are dependent on the initial vegetation, type and intensity of damage, and subsequent environmental conditions. Long-term studies following the 1938 hurricane document complex patterns of vegetation development in which advanced regeneration, buried seeds, seedling establishment and vegetative reproduction were variously important for different species at different times (Henry & Swan, 1974; Hibbs, 1983; Foster, 1988*b*; D. R. Foster, unpublished data). In old-growth white pine and hemlock forests and old-field white pine forests, pin cherry was the only arboreal species utilising the buried seed strategy. Its abundance varied considerably among sites, but was never as great as documented in the clearcutting studies at Hubbard Brook (Marks, 1974). Shade-tolerant saplings of hemlock and beech were released as advanced regeneration. In contrast, many species, including red maple, the birches (*Betula populifolia, B. lenta, B. papyrifera, B. alleghaniensis*) and oaks (*Quercus alba, Q. velutina, Q. borealis*) established as seedlings in the years before or just after the storm. The large numbers of multi-stemmed, bent and malformed trees in the modern landscape also indicate that regrowth and sprouting by survivors have been important processes. The resulting stands have a complex age structure of old stems, even-aged intolerant species and sprouts, and younger saplings of shade-tolerant species.

Recent studies after tornado damage in Pennsylvania, Hurricane Hugo in Puerto Rico and the hurricane experiment in Massachusetts highlight more of the mechanisms of regeneration. In particular, these studies underline the remarkably low mortality immediately following impact (Brokaw & Walker, 1991; Walker, 1991; Tanner *et al.*, 1991; Lezberg & Foster, 1994) and document the importance of reiteration by damaged stems in the rapid recovery of forest structure.

In the hurricane experiment survival, re-leafing and sprouting of damaged trees produced a high leaf area index in the season following damage (Lezberg & Foster, 1994). Survival varied by species and by damage type and decreased through time from approximately 80% during the first growing season to 48% during the second (Fig. 18.12). Species differences are great: nearly 75% of the *Carya* and *Betula alleghaniensis* re-leafed during year 2, in comparison with 30% for *Quercus borealis* and *Pinus strobus*.

Sprouting frequency has increased steadily, with >50% of damaged stems sprouting in year 2 (Fig. 18.13). Again, considerably variation is noted between species; less than 30% of *Betula* stems sprout, in contrast to >60% of *Acer rubrum* and *Fraxinus americana* and nearly 95% of *Carya*. These observations on the experimental hurricane contrast with studies following the 1938 hurricane when pioneer, light-demanding species dominated. Differences may be due in part to variation in the forests studied. However, a plausible alternative is that timber salvage activities associated with the 1938 hurricane altered the trajectory of vegetation recovery (Brake & Post, 1941; NETSA, 1943). Logging following the hurricane was intended to reduce fire hazard and to recover the timber resource; it affected most of the impacted region and produced the largest timber salvage effort in United States history. In addition to cutting live and dead windthrown stems, loggers scarified the soil surface and concentrated slash into windrows for burnings. Collectively, these processes would have decreased the role of surviving vegetation and increased the role of light-seeded pioneer species that establish on bare mineral soil.

The importance of survival and reiteration affects interpretations of the role of hurricane impacts in controlling forest species composition and diversity.

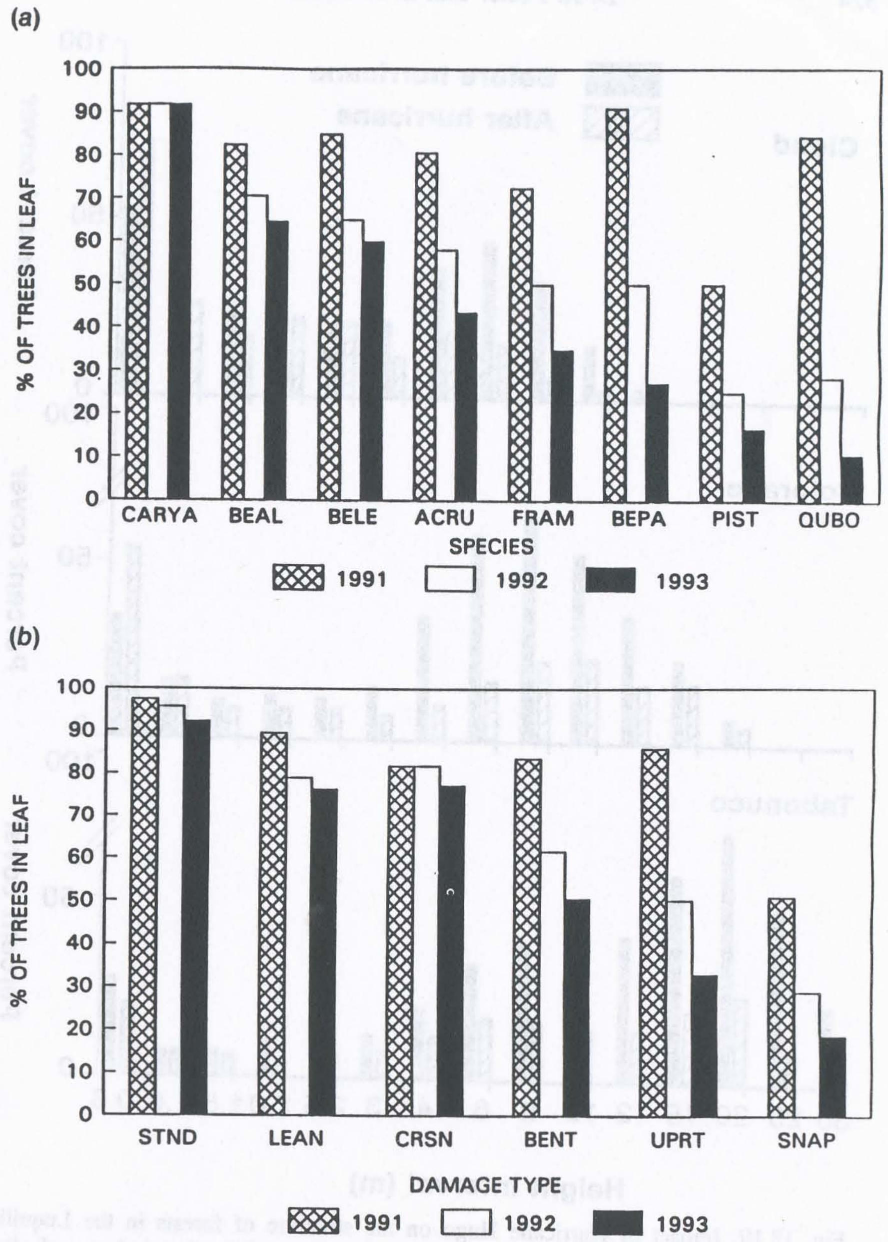


Fig. 18.12. Survival of trees following experimental hurricane on the Harvard Forest, Massachusetts. The percentage of live trees leafing out is shown by (*a*) species and (*b*) major class of damage for 3 years following the blowdown. Species acronyms are the first two letters of the genus and species: *Carya* spp., *Betula alleghaniensis, Betula lenta, Acer rubrum, Betula papyrifera, Fraxinus americana, Pinus strobus* and *Quercus borealis*. Damage classes: STND, standing; LEAN, leaning; CRSN, crown snap; UPRT, uproot.

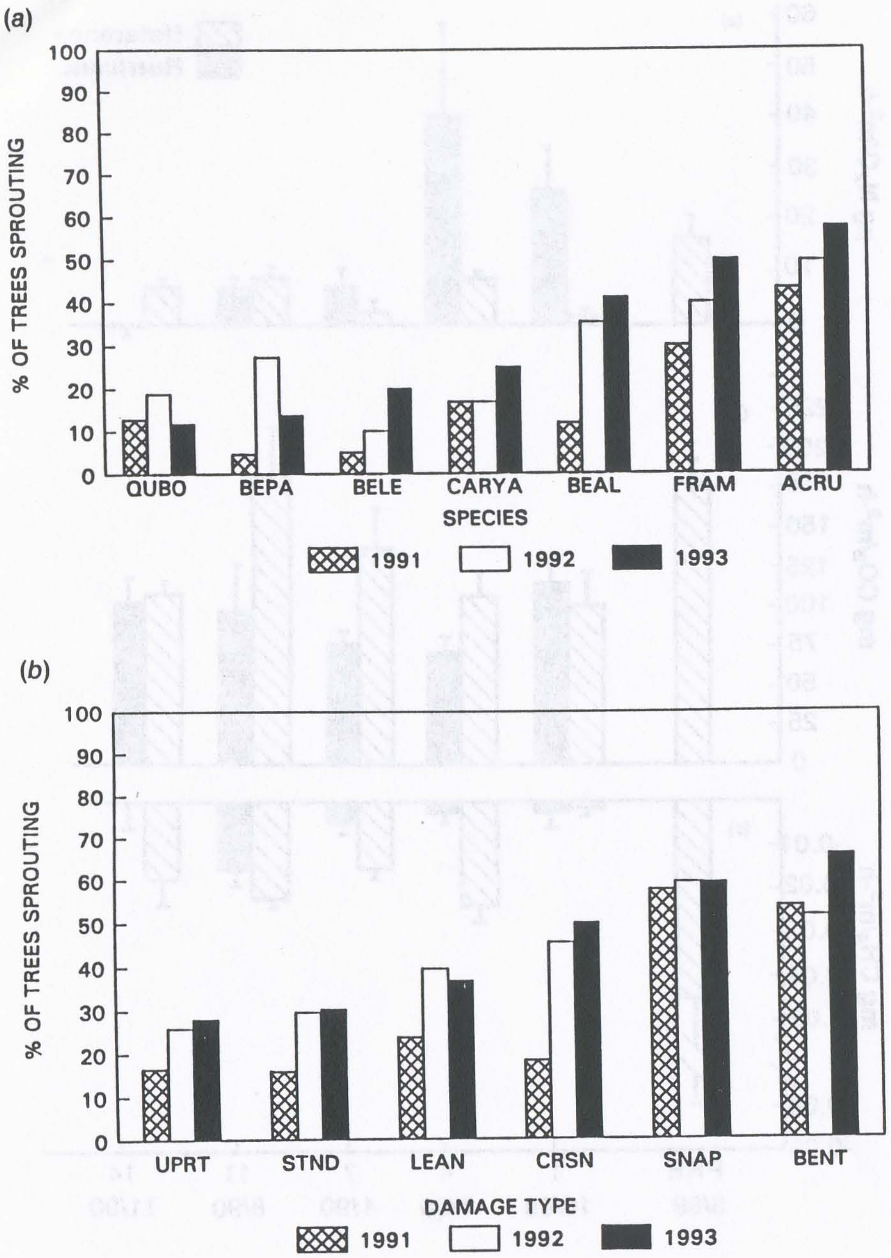


Fig. 18.13. The importance of vegetative reproduction in forest recovery following a hurricane is illustrated by the percentage of sprouts developing following experimental blowdown at the Harvard Forest, Massachusetts. The percentage of individuals developing sprouts is depicted by (*a*) species and (*b*) damage type for 3 years following the blowdown. Abbreviations as in Fig. 18.12.

Infrequent hurricane damage has been linked to the maintenance of high plant and animal diversity in some tropical forests (e.g. Lugo, 1988). This hypothesis is largely based on the intermediate disturbance hypothesis (Denslow, 1980) and is poorly tested. One attempt to assess the relationship between hurricane disturbance, floristic composition and diversity is a study in Puerto Rico. Using a stand development model (FORICO) Doyle (1981) demonstrated that dominance–diversity curves and the mixture of primary and pioneer species on forest plots matched model output based on an intermediate level of hurricane disturbance for eastern Puerto Rico (i.e. one hurricane every 9 years). This study has been cited as confirming the hurricane–diversity hypothesis (Lugo, 1988; Waide & Lugo, 1992; O'Brien *et al.*, 1992). However, conflicting results are generated by models that use multiple tree gaps and spatial interactions among stands (O'Brien *et al.*, 1992). There exists the real possibility that other disturbance factors (e.g. land-use) or plant–site relationships provide an alternative explanation of the forest composition.

In the absence of a definitive study, the relationship between hurricane disturbance and species diversity is speculative. The structural heterogeneity in standing vegetation, distribution of organic matter and microenvironments would appear to accommodate a broad range of species (Bormann *et al.*, 1974; Beatty, 1984). However, many studies suggest that survival and vegetative reproduction are the major mode of regeneration and document very little compositional change following major windstorms (Brokaw & Walker, 1991; Tanner *et al.*, 1991; Whigham *et al.*, 1991; Yih *et al.*, 1991).

18.5 Ecosystem processes

Of interest to ecologists, foresters and land managers is the impact of wind damage on ecosystem processes such as nutrient cycling, hydrology and atmospheric exchange. Of particular concern is the comparison of these impacts with the effects of human impacts, especially the salvage logging that often follows windstorms (Metropolitan District Commission, 1994). Hurricane damage results in many physical changes, including: redistribution of living and dead biomass; increase in organic inputs to the soil surface; reduction in canopy height, vertical stratification and leaf area; and exposure of mineral soil. Each of these direct impacts may alter characteristics of the soil and microenvironment that control ecosystem processes.

Information on ecosystem impacts from hurricanes is limited. Recent data have emerged primarily from the US LTER programme in which the Harvard Forest, Luquillo Experimental Forest and North Inlet projects are focussing on temperate forests in New England, tropical forests in Puerto Rico, and coastal forest and marsh ecosystems in South Carolina. Each offers an extensive, though preliminary view of ecosystem response to hurricane damage.

Severe hurricane impacts result in the immediate loss of most foliage and the collapse of vertical forest structure to boles and branches distributed within 3–4 m of the ground (Brokaw & Grear, 1991; Lodge *et al.*, 1991). Leaf litter inputs resulting from the single event may equal 2–7 times the annual litterfall at tropical sites (Tanner *et al.*, 1991; Walker *et al.*, 1991). Notably, the quality (e.g. nitrogen concentration) of this windblown litter is substantially greater than normal due to the abrupt defoliation before nutrient retranslocation (Whigham *et al.*, 1991; Tanner *et al.*, 1991). Nitrogen contents ranging from ×1 to ×3 and phosphorus concentrations of ×1 to ×5 that of average litter contributed to a massive input of organic matter and nutrients following Hurricane Hugo in Puerto Rico (Lodge & McDowell, 1991). In tropical environments, rapid decomposition of this nutrient-rich litter may increase standing stocks of calcium, potassium, magnesium, nitrogen, phosphorus and manganese (Whigham *et al.* 1991).

Nutrient dynamics in hurricane-damaged forests have been incompletely documented; however, data from temperate and tropical sites suggest that nutrient retention in soils and biomass is high, nutrient losses are slight, and recovery of ecosystem processes is more rapid than following logging (Steudler *et al.*, 1991; Lodge & McDowell, 1991; Bowden *et al.*, 1993). In the experimental hurricane in which 36% of the mature hardwood trees were uprooted and 32% were snapped or bent, emissions of important trace gases at the soil surface were remarkably similar to control values (Bowden *et al.*, 1993). Emissions of carbon dioxide and methane did not differ from those in the adjacent intact forest, whereas existing low emissions of nitrous oxide were lowered by 78%, but for only one season. Net nitrification was low and quite similar in control and experimental areas. A major conclusion from this experiment is that nutrient-poor temperate forests are resistant to changes in fluxes of carbon and nitrogen gases and are capable of establishing rapid control of ecosystem processes following hurricane disturbance. Despite catastrophic impact on forest structure this damage exerted little impact on nutrient cycling (Bowden *et al.*, 1993).

Slightly more disruption of biogeochemical processes is reported for tropical sites (Tanner *et al.*, 1991; Whigham *et al.*, 1991; Lodge & McDowell, 1991). Following Hurricane Hugo increases were detected in ammonium pools, net nitrogen mineralisation and net nitrification, although values generally peaked within 4 months of the storm and declined rapidly thereafter. Trace-gas emissions included large but relatively short-lived (<1 year)

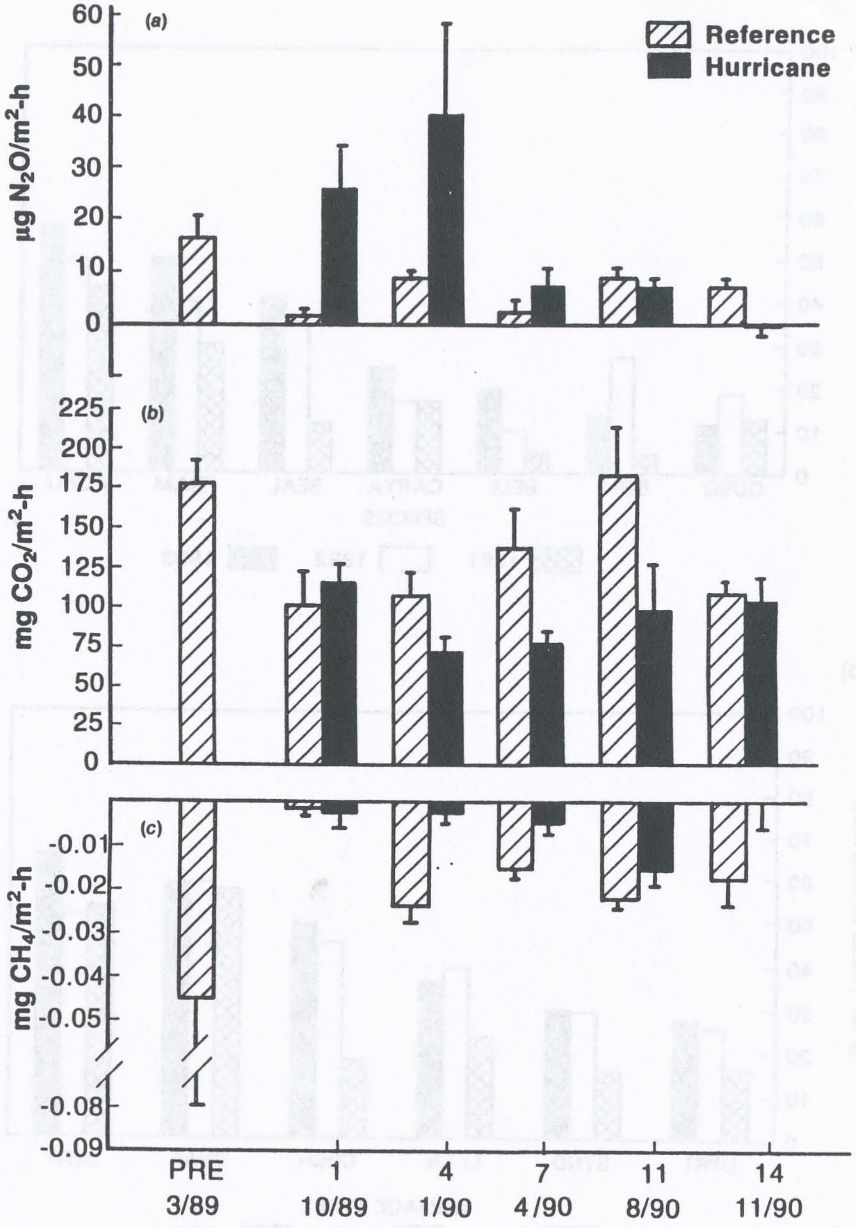


Fig. 18.14. Fluxes of (*a*) nitrous oxide, (*b*) carbon dioxide and (*c*) methane from reference and hurricane-damaged sites along a time sequence following Hurricane Hugo in Puerto Rico. Positive flux values indicate emissions from the soil to the atmosphere and negative values represent uptake by the soil. Flux rates are the means of four chamber measurements and bars show standard errors. From Steudler *et al.* (1991).

increases in nitrous oxide and decreases in methane and carbon dioxide (Fig. 18.14). The somewhat surprising decline in carbon dioxide flux probably resulted from reduced root respiration, as fine-root abundance has been noted to decrease substantially following hurricane damage (Steudler *et al.*, 1991; Tanner *et al.*, 1991). In comparison, effects upon nitrogen cycling and trace-gas fluxes were greater and more persistent after human disturbance (i.e. clearcutting of adjacent forest in Puerto Rico) than after the hurricane (Steudler *et al.*, 1991).

Numerous biotic mechanisms mitigate nutrient losses and restore pre-hurricane biogeochemical processes in forests (Vitousek *et al.*, 1979). Following windthrow most of the organic matter stays on-site and rates of vegetation survival and resprouting are remarkably high. In the New England hurricane experiment, initial survival of over 70% of the uprooted trees during the first year after damage created an extensive canopy 1–3 m above the ground. Sprouting of damaged trees, coupled with rapid expansion of fern, seedling and shrub layers, produced dense shade (Lezberg & Foster, 1994). As a consequence, soil temperatures were elevated only slightly and no change was detected in soil moisture (Bowden *et al.*, 1993). In Puerto Rico, rapid refoliation led to no detectable change in soil temperature and only a slight increase in soil moisture (Steudler *et al.*, 1991). Rapid establishment of biotic control of the soil environment, temperature and nutrient cycling appears to result from plant survival, expansion and regrowth (Bowden *et al.*, 1993; Carlton, 1993; Lezberg & Foster, 1994). In addition, microbes may immobilise and retain nutrients in the mineral soil and organic horizons (Lodge & McDowell, 1991).

As nutrient losses from ecosystems are often linked to hydrological changes, information on water balances and nutrient concentrations would be especially informative. The Luquillo Experimental Forest provides the only relevant data for hurricane impacts. Despite catastrophic damage to vegetation and great soil disturbance, nutrient exports were minimal as streams showed only minor peaks in nitrate concentrations for a 4 month period. In addition to other mechanisms discussed, low precipitation following Hurricane Hugo and nutrient retention by dense riparian vegetation may minimise stream nutrient loss (Scatena & Larsen, 1991).

The only regional analysis of hydrological impacts of hurricanes provides a striking, though perhaps misleading picture. In an ingenious use of double-mass plotting of streamflow from major watersheds following the 1938 hurricane, Patric (1974) showed that damaged watersheds (Connecticut and Merrimac Rivers) exhibited increased flows of 25 cm (4 × 10^6 acre feet) over a 5 year period in comparison with watersheds that were undamaged (Androscoggin River; Fig. 18.15). Increases peaked the first year and then declined consistently; more than 50% of the enhancement occurred in summer (Patric, 1974). Additional flow was interpreted as the result of substantial decline of evapotranspiration within the damaged area.

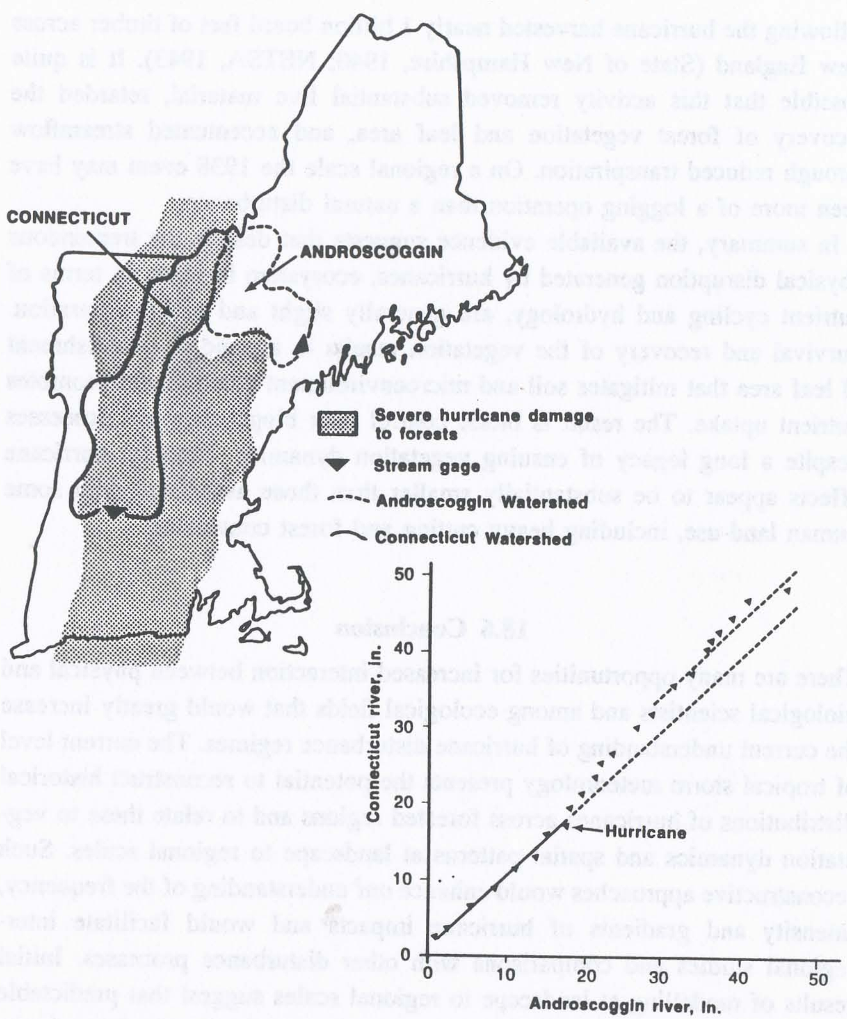


Fig. 18.15. Regional impact of the 1938 hurricane and associated salvage logging on river flow in New England. Figures show the study region with major river drainages and the extent of severe damage from the hurricane and cumulative summer flow (July, August, September) for the Connecticut river (within the damaged area) and the Androscoggin river (outside the damaged area) over a 5-year period. Modified from Patric (1974).

This interpretation appears sound; however, the additional flow may not necessarily be a direct result of the hurricane damage. Salvage operations following the hurricane harvested nearly 1 billion board feet of timber across New England (State of New Hampshire, 1940; NETSA, 1943). It is quite possible that this activity removed substantial live material, retarded the recovery of forest vegetation and leaf area, and accentuated streamflow through reduced transpiration. On a regional scale the 1938 event may have been more of a logging operation than a natural disturbance.

In summary, the available evidence suggests that despite the tremendous physical disruption generated by hurricanes, ecosystem impacts, in terms of nutrient cycling and hydrology, are generally slight and of brief duration. Survival and recovery of the vegetation results in a rapid re-establishment of leaf area that mitigates soil and microenvironment changes and promotes nutrient uptake. The result is biotic control over biogeochemical processes despite a long legacy of ensuing vegetation dynamics. Notably, hurricane effects appear to be substantially smaller than those associated with some human land-use, including heavy cutting and forest conversion.

18.6 Conclusion

There are many opportunities for increased interaction between physical and biological scientists and among ecological fields that would greatly increase the current understanding of hurricane disturbance regimes. The current level of tropical storm meteorology presents the potential to reconstruct historical distributions of hurricanes across forested regions and to relate these to vegetation dynamics and spatial patterns at landscape to regional scales. Such reconstructive approaches would enhance our understanding of the frequency, intensity and gradients of hurricane impacts and would facilitate inter-regional studies and comparisons with other disturbance processes. Initial results of modelling at landscape to regional scales suggest that predictable pathways and characteristics of storms may interact with physiography to develop long-term gradients of wind exposure.

Stand-level studies indicate that forest vegetation exhibits remarkable rates of recovery following intense canopy damage, but additional information on the response of some community-level characteristics, such as species diversity, is needed in a range of forest types. The important role of surviving plants in the re-vegetation process highlights the need for more study of plant reiteration and the physiology of damaged and sprouting plants.

The survival and vegetative reproduction of plants already established on hurricane-impacted sites explains in large part the very rapid recovery of biotic control of ecosystem processes. More study is needed of additional forest types and especially of hydrology, nutrient cycling and soil organic matter dynamics. Analysis of the role of microbial communities in nutrient immobilisation would complement the study of above-ground vegetation recovery.

Hurricanes have been recognised as an important disturbance process in a range of vegetation world wide. As a better understanding develops of the temporal and spatial variation in their impacts, and the actual range of vegetation and ecosystem response, we will be better able to identify their relative importance in controlling ecosystem structure and dynamics.

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