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ECOSYSTEMS OF DISTURBED GROUND

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Chapter 8

BACKGROUND CANOPY GAP AND CATASTROPHIC WIND DISTURBANCES IN TROPICAL FORESTS

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INTRODUCTION

Disturbance has been defined in various ways (e.g., Sousa, 1984; Rykiel, 1985; van Andel and van den Bergh, 1987; Pickett et al., 1989), in part because disturbance theory must deal with a wide variety of phenomena under that name (Pickett et al., 1989). A useful definition of disturbance for forests is "a relatively discrete event causing a change in the physical structure of the environment" (Clark, 1990). In forests, this change in physical structure refers primarily to damage and removal of aboveground biomass (Grime, 1979), and removal of the litter layer and mixing of surface soil layers (e.g., Putz, 1983). Changes in the physical structure of the environment (Clark, 1990) are concomitant with changes in environmental variables below the main canopy (e.g., soil resources, light quantity and quality, and temperature: Chazdon and Fetcher, 1984; Bellingham et al., 1996). For individual disturbance events, the size of the canopy opening is often correlated with most of the direct and indirect changes in environmental variables and resource levels (Brokaw, 1985b). Even small gaps (Canham and Marks, 1985) provide opportunities for regeneration and adult growth (Sousa, 1984; Oliver and Larson, 1990). Consistent with the above definition, in this chapter we focus on forest-canopy disturbances that occur as discrete events in time. We are primarily concerned with those relatively small canopy disturbances (background canopy gap disturbance) caused by a variety of agents and larger disturbances caused by major windstorms (catastrophic wind disturbance). A modification of Clark's (1990) definition of the scale of wind-generated disturbances, which represents a continuum of disturbance (Everham and Brokaw, 1996; Lugo and Scatena, 1996), is useful because it

can be used to divide disturbances into those that we will consider to be background canopy disturbances ($<10^3$ m^2: Table 8.1), the scale most often used to investigate tree-fall dynamics in forests, independent of the causes of the tree-falls (Brokaw, 1985a) and catastrophic wind disturbances ($>10^3$ m^2: Table 8.1). We only indirectly deal with major disturbance events (e.g., fire, floods, river meanders, landslides, shifting agriculture) that both open the canopy and more substantially disturb the soil, understory, and litter layer (see Uhl, 1982a; Lugo et al., 1983; Johns, 1986; Oliver and Larson, 1990; Lugo and Scatena, 1996).

Some types of canopy disturbances have been described by the concept of "patch dynamics" (White and Pickett, 1985), in which the disturbance effects are relatively discrete spatially, and where there is a "shifting mosaic" of patches of different ages. After disturbance, the patch changes through time and regains characteristics of the older patches. This concept applies well to canopy gaps formed by the fall of one to a few trees and blow-downs where many trees are felled together (see Sousa, 1984; White and Pickett, 1985; Whitmore, 1989; Clark, 1990). The concept is problematic in that gap edges are not always

Table 8.1
Scale of wind-generated disturbances in neotropical moist forests [1]

Type of disturbance	Approximate area of effect (m^2)
Hurricanes/typhoons	10^5–10^7
Blow-downs/wind-throws	10^3–10^5
Single tree-falls	10^2–10^3
Branch falls	10^1–10^2

[1] Modified from Clark (1990).

obvious, openings do not always extend through all canopy layers (Lieberman et al., 1989), small gaps may be closed from the side (Runkle and Yetter, 1987), and patches may also be internally heterogeneous (White and Pickett, 1985). In contrast to discrete gaps, hurricane disturbance may often, though not always, be better described as "diffuse" (Pickett and White, 1985), particularly where the canopy is thinned and no discrete patches are formed (Everham and Brokaw, 1996). In this chapter we focus on background canopy disturbances that create canopy gaps extending to the understory [see Brokaw (1982a) and Popma et al. (1988) for definitions of canopy gaps] and catastrophic wind disturbances of both discrete and diffuse nature.

One can view disturbances as having causes and effects (Rykiel, 1985) to which ecological systems respond (van Andel and van den Bergh, 1987). Three largely similar dichotomous groupings of causes of disturbance have been used (but see Lugo and Scatena, 1996): endogenous versus exogenous (White and Pickett, 1985), internal versus external (Vooren, 1986; van der Meer and Bongers, 1996b) and biotic versus abiotic. Endogenous causes (e.g., disease, competition, epiphyte and vine loading of canopies, and herbivory) originate from within the biotic community while exogenous causes (e.g., drought, wind, lightning, and rainfall) originate from without (White and Pickett, 1985). Endogenously caused disturbances may largely occur through the gradual fall of trees that died standing, hereafter referred to as standing mortality (Vooren, 1986; Krasny and Whitmore, 1992; van der Meer and Bongers, 1996b). Exogenously caused disturbances can occur gradually (e.g., from standing mortality owing to drought) or suddenly (e.g., from wind-throw). There is interaction between these two groups of causes (White and Pickett, 1985). For instance, though major wind disturbance obviously has a largely exogenous component, trees weakened by disease are more prone to damage (Putz and Sharitz, 1991; see also Everham and Brokaw, 1996). Wind is an important cause of canopy disturbance, and probably the primary cause of canopy disturbance in forests where large tropical storms or other strong, though localized, wind storms are common occurrences (see Lugo et al., 1983; Shaw, 1983; Brokaw, 1985b; Walker et al., 1991; Lugo and Scatena, 1996) and where other causes of major disturbance are not operative (Leighton and Wirawan, 1986; Foster, 1990). Vegetative response to disturbance depends on characteristics of the disturbed site (e.g., severity of damage), species availability

(e.g., propagule availability and survival through the event), and post-disturbance species performance such as growth rates, sprouting ability, and survival (Pickett et al., 1987; Pickett and McDonnell, 1989; Lugo and Scatena, 1996).

Our objectives in this chapter are to build on the work of Everham and Brokaw (1996) and other reviewers by describing the causes and effects of background canopy disturbance (Denslow, 1980; Hartshorn, 1980; Brokaw, 1985a,b) and catastrophic wind disturbance (Lugo et al., 1983; Glitzenstein and Harcombe, 1988; Brokaw and Walker, 1991; Tanner et al., 1991; Lugo and Scatena, 1996; Zimmerman et al., 1996) in tropical and subtropical forests, and comparing vegetative response to catastrophic wind events with response to background canopy disturbance. Finally, we describe ecosystem response to catastrophic wind disturbance.

CAUSES AND EFFECTS OF CANOPY DISTURBANCE

Wind storms in the tropics – distribution and patterns

Within the tropics, winds that are not associated with catastrophic events usually impact forests during periods of rainfall that occur chiefly in areas of atmospheric disturbance and persist for days, moving irregularly around the landscape, but often toward the west. The distribution, size, and intensity of tropical rainstorms varies temporally and spatially (Schwerdtfeger, 1976; Lauer, 1983), but storms that are potentially strong enough to generate winds causing canopy disturbances can generally be organized into three types:

(1) The Intertropical Convergence Zone produces winds, that are rarely strong, over the oceans and widely over continents during rainy seasons. Forest disturbances associated with these types of windstorms are most often associated with individual or small groups of rain squalls.

(2) Northern cold fronts (*nortes*) in certain longitudes (e.g., in the northern Caribbean) penetrate into the tropics and become part of the trade-wind system. Strong winds and showers or thunderstorms are commonly associated with these systems.

(3) Larger-scale easterly-winds produce squall-line systems. These occur in West Africa, across the tropical Atlantic to the Caribbean, and infrequently in the central and western Pacific. Wind velocities

of more than $20\,\mathrm{m\,s}^{-1}$ are associated with these systems.

These three types of wind disturbances occur throughout the tropics, but their occurrence and intensity are difficult to predict and their impacts are poorly known. Richards (1996) suggested that all tropical areas are subject to wind disturbances before and during convectional rainstorms and thunderstorms, and he cited several examples to demonstrate the range of impacts that wind disturbances can have. In Sarawak, winds associated with squalls created canopy gaps as small as 0.04 ha (equivalent to felling a single tree) but they can also cause catastrophic damage; areas as large as 80 ha, for example, were damaged by wind in swamp forests dominated by *Shorea albida*. Other authors have also documented the importance of wind as an agent of background canopy disturbance (e.g., Whitmore, 1989).

Winds that cause background canopy disturbance can also create catastrophic disturbances that would be difficult to predict under any circumstances. Uhl et al. (1988a), for example, found that local rain and windstorms mostly accounted for the background rate of canopy disturbance in the São Carlos *terra firme* forest in Venezuela, but that windstorms also "occasionally knock down whole sections of forest". Kellman and Tackaberry (1993) found that "extreme winds of atypical orientation" caused trees to fall in a direction that was not uniformly distributed. Numerous accounts of blow-down and wind-throw disturbances can be found in the literature, but almost all of them are qualitative descriptions (e.g., Richards, 1996; Whitmore, 1989; citations in Clark, 1990; Nelson et al., 1994). Bruenig (1989) used aerial photographs taken in different years to demonstrate the importance of windstorms in creating wind-throws in forested wetlands in Borneo. Bruenig found that the rates of single-tree gaps varied among forest types from 0.2–3.0% of the area per year, but that the rate of disturbance in one forest type appeared to be about 1% for single tree-fall gaps and for openings created by wind-throws. Bruenig suggested that forests with taller trees and trees with a high height/diameter ratio are more susceptible to lightning and wind-throw. Forested wetlands appear to be particularly susceptible to blow-down and wind-throw disturbances because the trees have very shallow roots. Clearly, there have been too few quantitative studies to characterize the importance of blow-downs and wind-throws in tropical forests, even though their impacts on forest structure and species composition are long-lived (Hubbell and Foster, 1986).

Most catastrophic wind disturbances are associated with tropical cyclones, the general term for hurricanes and typhoons, which are the most destructive types of windstorms in the tropics and subtropics; their damaging effects can extend far into the temperate zone (Encyclopædia Britannica, Inc., 1992; Boose et al., 1994). They are intense storms (as large as 150–250 km across) with maximum wind speeds that are, at least, $32.7\,\mathrm{m\,s}^{-1}$. Heavy rain is also usually associated with tropical cyclones. The number of tropical cyclones per year, world-wide, varies between approximately 30 and 100, and they occur primarily near Southeast Asia, the Caribbean, and adjacent waters (Vega and Binkley, 1993), and in the southwest Pacific and Australian waters (Fig. 8.1). In addition to disturbing natural ecosystems, tropical cyclones also cause enormous economic destruction and human suffering (Encyclopædia Britannica, Inc., 1992).

Background canopy disturbance

Overview

Canopy disturbance is now viewed as integral to an understanding of tropical forest ecology (Hartshorn, 1978; Whitmore, 1975), and much of the data cited in this chapter were obtained as part of efforts to characterize what we have defined as the "background" pattern of disturbance in tropical forests, disturbances that are usually caused by branch-falls, standing dead trees, and the fall of one to several adjacent trees. The average rate of gap formation in humid lowland tropical forests has been reported to be $1\,\mathrm{ha}^{-1}\,\mathrm{yr}^{-1}$ with a range of 0.7–2.6, opening ~1–2% of the forest per year with a range of $0.5–3.6\%\,\mathrm{yr}^{-1}$ (Denslow, 1987; Swaine et al., 1987; Whitmore, 1989; Hartshorn, 1990; Jans et al., 1993; Yavitt et al., 1995; Lugo and Scatena, 1996). Average gap size, shortly after gap formation, ranges from 54 to $120\,\mathrm{m}^2$ (see review in Jans et al., 1993). Small gaps are much more common than large gaps (Lawton and Putz, 1988; Uhl et al., 1988a; Chandrashekara and Ramakrishnan, 1994). In lowland moist and wet forests, the largest gaps range considerably in size. Brokaw (1982a,b) measured gap sizes of $232\,\mathrm{m}^2$ and $342\,\mathrm{m}^2$ in an old forest on Barro Colorado Island (BCI), Panama. Yavitt et al. (1995) measured a gap size of $604\,\mathrm{m}^2$ in a young forest there. Sanford et al. (1986) measured gaps as large as $781\,\mathrm{m}^2$ at La Selva, Costa Rica. Gap turnover is a function of
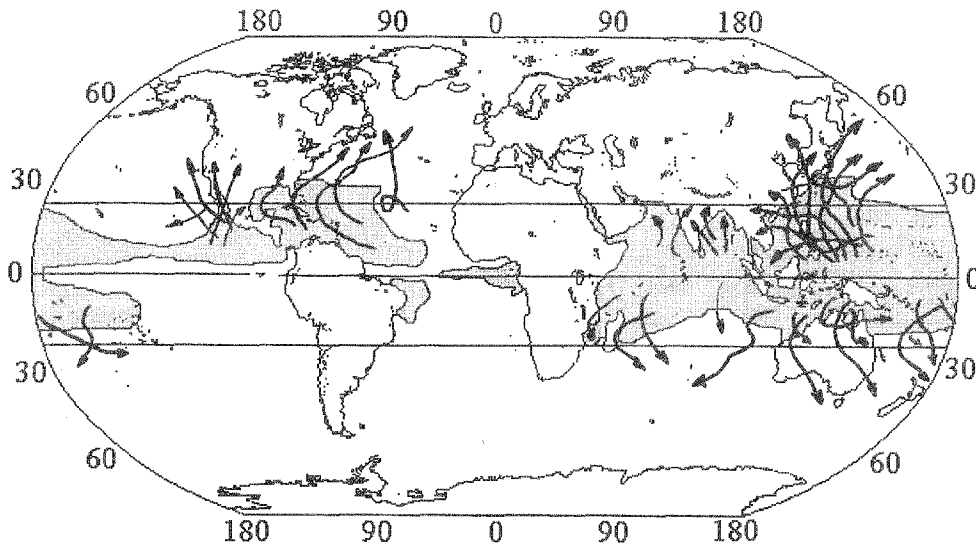
Fig. 8.1. Major tracks (arrows) and frequency (shaded areas) of hurricanes and typhoons. Source: Encyclopædia Britannica, Inc. (1992).

the size of gaps and their rate of occurrence and can be thought of as the number of years it would take to cover 100% of the forest in gaps (assuming there is no gap overlap). Estimated gap turnover rates range from 60 to 145 years in humid lowland forests (see review in Jans et al., 1993), and rates of gap formation can vary considerably from year to year (Martínez-Ramos et al., 1988; Lawton and Putz, 1988; Dickinson et al., 1999). The variation is even greater when rare and large disturbance events are included in the estimates of turnover rates (Brokaw, 1985b; Leighton and Wirawan, 1986; Whigham et al., 1990).

Variation among forests

Similarities among forests in gap size, frequency, and turnover have been emphasized (Lawton and Putz, 1988; Hartshorn, 1990; Kapos et al., 1990; Jans et al., 1993; Yavitt et al., 1995). The similarities, however, are likely owing to a bias towards studying humid lowland forests in the neo-tropics (P. Hall, pers. commun., 1997) not obviously affected by major periodic disturbance (see summary data above). There are fewer data on background canopy disturbance rates for forests subject to major periodic disturbances, dry tropical forests, montane forests, wetland forests, and paleotropical forests, but differences among forest types are to be expected. Several examples follow. In a wet forest in Puerto Rico periodically disturbed by periodic catastrophic wind events, mean gap size (76 m^2) and gap formation rate (0.8 gaps ha^{-1} yr^{-1}) are below the mid-range values for humid forests not impacted by periodic

major disturbance (Scatena and Lugo, 1995). The gap formation rate in a semideciduous forest in the Mexican Yucatan (1300 mm annual rainfall) periodically hit by major disturbance is exceedingly low at 0.2 gaps ha^{-1}, resulting in 0.07% of the forest being disturbed in an average year (Dickinson et al., 1999). The average gap size in the Yucatan forest (<50 m^2) is similar, after correcting for a lower minimum gap size, to an elfin montane forest in Costa Rica (Lawton and Putz, 1988), and at the low end for humid lowland tropical forests. Similarly, maximum gap sizes also are lower for the Yucatan site (>180 m^2; Dickinson et al., 1999), a montane forest site (>135 m^2; Lawton and Putz, 1988), and in a West African forest with a long dry season (244 m^2) studied by Jans et al. (1993). Jans et al. also reported a correspondingly long gap turnover time (244 years) for that site. Compared with humid lowland neo-tropical forests, gap turnover times also were long (154–375 yr) in two equatorial Southeast Asian forests (Jengka Forest Reserve, Peninsular Malaysia: Poore, 1968; Samarinda, East Kalimantan, Borneo: Riswan et al., 1985). Long gap turnover times can be partly explained by small gap size in the Jengka (Whitmore, 1975). East Kalimantan is periodically affected by severe droughts, which may explain long turnover times there (Leighton and Wirawan, 1986).

In the following section and in Table 8.2, we describe what we expect to be the main sources of variation among sites in background canopy disturbance (also see Brokaw, 1985b). These include: wind regime, forest

Table 8.2
Predictions about variation in background canopy disturbance regimes

#	Prediction
1	Dry, high-altitude forests, and extremely nutrient-poor forests should have the lowest average gap size owing to small crown sizes.
2	Forests dominated by tall trees with thin crowns will have linear gaps, with less effect on understory light levels.
3	Forests subject to natural and anthropogenic major disturbance (fires, blow-downs, hurricanes, agricultural clearing, logging, landslides, flooding events, and river meanders) will have smaller gaps and a lower rate of gap formation than forests that do not experience such events or that have not experienced such an event in >200 years.
4	Shallow rooting of trees on fertile, extremely nutrient-poor, or waterlogged soils will increase the rate of tree-fall and prevalence of uprooting (and soil disturbance), while seasonally dry forests and forests on moderately infertile and well-drained soils will exhibit low rates of tree-fall and more stem-snapping.
5	Forests on slopes will have a higher rate of tree-fall than forests on flat terrain only if soils and parent material are unstable and rooting is shallow.
6	Forests with high abundance of woody vines should exhibit larger gap sizes and more frequent gaps.
7	High rates of standing mortality will result in a smaller average gap size and lower overall rates of gap formation.
8	Except where continuous strong winds have large effects on structure, forests with higher frequencies of strong, gusty winds (e.g., where rainstorms are more frequent) should have higher rates of gap formation than forests where winds are less gusty.
9	Dry tropical forests should have smaller gaps and lower rates of gap formation than humid forests, owing to smaller crown sizes, a more stable tree architecture, higher rates of standing mortality, periodic fire (if applicable), and a shorter period in which most gap causal factors operate.

structure (as affected by site conditions, biogeography and species composition, and prior catastrophic disturbances), tree anchorage, standing mortality, and vines and epiphytes. The effects of wind are often mediated by the other factors. We also compare dry and wet tropical forests, which appear to differ in several of the above factors, and we predict that they will prove to vary considerably in background canopy disturbance.

Wind regime

Forests subject to more frequent strong and gusty winds should have more canopy disturbances than forests where winds are calm (Grace, 1977; Richards, 1996; see also Table 8.2, Prediction 8). In terms of damage to trees, high mean wind speeds, strong gusts, and abrupt changes in wind direction are probably most likely to cause damage (Gloyne, 1968; Grace, 1977). Within a given forest, sites that are most exposed to gusty winds have higher tree-fall rates (see review in Brokaw, 1985b). Strong gusts (from 780 to over $100\,\text{km}\,\text{hr}^{-1}$) have been reported to occur on multiple occasions in a given year in several sites (Bultot and Griffiths, 1972; Lawton and Putz, 1988; Uhl et al., 1988a). Whitmore (1975) suggested that variation among forests in the frequency of convectional storms and squall lines would explain variation among forests in disturbance. Squall lines along the Malaysian Peninsula are reported to be the

most important cause of large gaps (Whitmore, 1975). The generally calmer winds of equatorial Southeast Asia have been hypothetically linked to high rates of standing mortality and low overall gap formation rates in forests there (P. Hall, pers. commun., 1997). In forests with distinct dry seasons, a peak in gap formation occurs during the middle of the wet season [see review in Brokaw (1985b), and also Matelson et al. (1995)], although not all wet season gaps can be ascribed to wind (see below). Ninety percent of the gaps sampled at La Selva in Costa Rica were formed during the 6 wettest months (Hartshorn, 1989), and in a cloud forest in Monteverde (Costa Rica) 70% of the gaps formed in one year were caused during one severe, but common type of storm (see Lawton and Putz, 1988). Dry tropical forests are also likely to have more wind-induced damage during the wet season, as most of the strong wind gusts occur during the wet season (Bultot and Griffiths, 1972). In addition to causing individual tree-fall gaps, wind damage can enlarge existing gaps by toppling trees at the gap edge (Bruenig, 1989; Whitmore, 1984), or cause clustering of gaps owing to increased turbulence around existing gaps where the canopy is uneven (Poorter et al., 1994).

Wind is often the *coup de grace* to a tree made vulnerable by such things as disease, poor rooting conditions owing to waterlogged soils, and rain-loading

(Gloyne, 1968; Whitmore, 1975; Brokaw, 1985b; Richards, 1996). Though rain-loading of the canopy can cause large, live trees to fall in calm, rainy weather (Strong, 1977), standing mortality cannot generally be directly attributable to wind, although extreme winds may lead to eventual standing mortality (Shaw, 1983; Whigham et al., 1991). Where gap formation by standing mortality is minimal, we expect that the largest proportion of gaps would be caused by uprooting, snapping, and live limb-fall owing to wind. Trees fall in the direction of the prevailing winds in a subalpine temperate forest, strong evidence of the importance of wind in those environments (Wooldridge et al., 1995).

Wind speeds vary in several ways, most importantly perhaps with geographic setting and the frequency of storms (Whitmore, 1975). Average coastal wind speeds are generally higher than inland wind speeds at the same altitude (Grace, 1977). Windstorms may often be more common somewhat inland from the coast owing to orographic rain storms (Dale, 1959; Whitmore, 1975). Average wind speed increases with altitude (Grace, 1977), although canopy gaps do not seem to become more frequent at higher altitudes (Lawton and Putz, 1988; Matelson et al., 1995). Trees whose physiognomy is shaped to a large degree by strong and continuous winds, such as trees in exposed cloud forests, are not as prone to wind damage as trees that are not so conditioned (Lawton and Putz, 1988; Brokaw, 1985b; Richards, 1996). This is likely in large part owing to the increased turbulence associated with rough rather than smooth canopy topographies (Gloyne, 1968; Grace, 1977). Topography significantly affects wind speed and direction above canopies (Grace, 1977). When wind speeds are high, forests on the lee side of ridges can experience severe turbulence (Grace, 1977).

Wind is responsible for the formation of disturbances over a wide range of scales, from single tree-falls (e.g., Denslow, 1987) to blow-downs (Dunn et al., 1983; Uhl et al., 1988a; Clark, 1990; Nelson et al., 1994), and swaths of hurricane-disturbed forest (Everham and Brokaw, 1996; Richards, 1996). In forests that are not typically affected by major wind disturbance, the incidence of multi-tree wind-throws may be the most important factor in disturbance regimes and resulting patterns of species abundance differentiating one forest from another (Denslow, 1987).

Forest structure

Effects of site conditions: Variation among forests in above-ground structure (shoot characteristics, including crown size, average tree height, and allometry) should be reflected in the size distributions of tree-fall gaps, their effect on light conditions at ground level, and on the frequency of gap creation. A positive relationship between tree size (measured as trunk diameter) and gap size [i.e., area of the hole in the canopy that extends to ground level: see Brokaw (1982a) and Popma et al. (1988)] has been documented (Brokaw, 1982a; Lawton and Putz, 1988; Clark and Clark, 1996). Small gap sizes in montane and drier forests are a reflection of this (see p. 226 above). It is not clear whether bole height, bole thickness, or crown size most influences gap size. However, the findings that the height at which the bole gave way has little effect on gap size (Lawton and Putz, 1988) and that gaps formed by uprooting trees are no larger than gaps formed by snapped trees (Jans et al., 1993) indicate that crown size is most important (Richards, 1996; see also Table 8.2, Prediction 1). All else being equal, large crowns are on tall thick boles (King, 1991) and are poised to do maximum damage to surrounding trees when they fall.

Tree architecture varies with wind regime, rainfall, soils, topography, altitude and latitude [see review of hypotheses regarding physiological limits on tree size by Stevens and Perkins (1992)]. Rainfall patterns are primary determinants of above-ground forest structure (Beard, 1955; Holdridge et al., 1971; Ellenberg, 1979; Lieberman et al., 1996). Forests with the highest densities of emergents that have large crowns should occur in lowland tropical wet and moist forests on well-drained soils (Holdridge et al., 1971; Grubb, 1989), especially on lower slopes or in areas with little topographic relief (Ashton and Hall, 1992). Forest height in a wet Puerto Rican forest is highest on better drained areas and lowest where soils are often waterlogged (Lugo et al., 1995). Kira (1978) found that the tallest forests at a number of Southeast Asian sites occur where rainfall was around 2000 mm yr^{-1} and was evenly distributed throughout the year. Tree height drops both in wetter sites and in sites with decreasing amounts and increasing seasonality of rainfall. In concert, the height to diameter ratio decreases in drier and more seasonal forests, that is, a tree of 1 m dbh becomes shorter (Kira, 1978). Thus, crown size may not decrease as quickly as tree height with decreasing rainfall. High stand turnover rates (as at La Selva) should lead to low densities of very large trees (Lieberman et al., 1985; Clark, 1996). Stand and basal area turnover appear to increase generally in

productive sites (Phillips et al., 1994), consequently, such sites may have more, but smaller, gaps. Forests on extremely nutrient-poor soils should also have small tree-fall gaps as the trees are typically of low stature, although the effects of low nutrient status are often confounded with periodic moisture deficits (Whitmore, 1975; Grubb, 1989). Kapos et al. (1990) found larger gaps, and larger trees, on a relatively nutrient-rich site than on a nutrient-poor site.

Periodic drought in eastern Borneo killed the largest and tallest trees, leading to a broken emergent stratum (Leighton and Wirawan, 1986; Richards, 1996: see below). Large trees on ridges are particularly vulnerable to drought-related mortality, since the soils dry quickly (Leighton and Wirawan, 1986; Ashton and Hall, 1992; Richards, 1996). This effect may have contributed to lower rates of gap formation and lower gap sizes on ridges compared with slopes in West African seasonal forests (Poorter et al., 1994). Rooting was impeded on hill crests (Poorter et al., 1994), perhaps compounding an effect of periodic drought.

Tree height and crown size decrease with increasing altitude (Holdridge et al., 1971; Whitmore, 1975; Ellenberg, 1979; Lieberman et al., 1996). Consistently stronger winds at higher altitudes (Grace, 1977) lead to shorter trees with thicker boles, primarily due to the mechanical effects of continuous winds on tree growth (Lawton and Dryer, 1980; Telewski, 1995). Also, there appears to be a temperature effect on forest height along altitude gradients (Pendry and Proctor, 1996). A hypothesis that there should exist a pattern of increasing crown width from the temperate to the tropical zone was proposed by Terborgh (1985), but King (1991) did not find such a pattern.

Forests dominated by tall trees with small crowns produce small gaps that are often linear in shape, providing little opportunity for regeneration of light-demanding species (Putz and Appanah, 1987; see also Table 8.2, Prediction 2). The distribution of forests in which tall trees with small crowns predominate is unclear, but examples include certain zones in Sarawak peat swamps (Whitmore, 1975) and Pasoh Forest Reserve in Peninsular Malaysia (Putz and Appanah, 1987). Both of these sites are nutrient-poor, and trees also experience periodic moisture stress (Whitmore, 1975; Putz and Appanah, 1987). Canopy trees in the tallest forests may generally show a reduction in crown expansion as compared with canopy trees in somewhat shorter forests (King, 1996).

Biogeographic and species-composition effects: Biogeographic effects on forest structure may occur; they should not be confused with site effects, and the effects of past disturbance on species composition. Variation in species composition within and among biogeographic regions may affect disturbance regimes when different species have different stem architecture (Beard, 1945a; Wadsworth and Englerth, 1959; Jans et al., 1993), wood properties (Putz et al., 1983), rooting patterns (Everham and Brokaw, 1996), and modes of death (Brokaw, 1985b). The high density of very tall, emergent trees in some dipterocarp-dominated forests may be related to unique aspects of the reproductive biology and ecology of this Southeast Asian family (Ashton, 1988). Forests in Borneo often have a towering emergent canopy of dipterocarps, and on certain sites 80–100% of all individuals in the upper canopy are dipterocarps. Forests east of Wallace's Line (where dipterocarps are less species-rich), in Africa and in the Neotropics typically have a sparse cover of emergent trees above the main canopy (Ashton, 1988). Higher densities of large emergents may lead to larger gaps when emergents fall. High rates of standing mortality in certain equatorial forests in Southeast Asia (Table 8.3) may also have a biogeographic component (Hall, 1991).

Effects of prior catastrophic disturbances: While most studies on background canopy disturbance have been done in forests not subjected to major disturbance, major disturbances have large and long-term effects on canopy structure (Johns, 1986; Foster, 1988; Saldarriaga et al., 1988) and subsequent background canopy gap disturbance (Spies and Franklin, 1989; Lorimer, 1989). Any disturbance that results in high mortality of large canopy trees would be expected to lead to a period of lower rates of formation of large tree-fall gaps and smaller gap sizes, as the large dead canopy trees are replaced by individuals from smaller size classes (Hartshorn, 1978; Brokaw, 1982b; Denslow and Hartshorn, 1994; Dahir and Lorimer, 1996; see also Table 8.2, Prediction 3). Such disturbances (see Johns, 1986) include blowdowns (Whitmore, 1975), fire (Leighton and Wirawan, 1986), landslides (Guariguata, 1990), agricultural clearing (Saldarriaga et al., 1988), logging, flooding events (Mori and Becker, 1991; Gullison et al., 1996), severe droughts (Leighton and Wirawan, 1986; Woods, 1989) and river meanders (Foster, 1990). As the frequency of large-scale disturbances increases, tree-fall gaps may

Table 8.3
Standing mortality of tropical forest trees

Region	Climate[1]	Standing mortality[2] (%)	Soil fertility[3]	Source
Bako, Sarawak, NW Borneo	4167 [0]	84	low	Hall (1991)
Mersing, Sarawak, NW Borneo	3905 [0]	68	high	Hall (1991)
Lambir, Sarawak, NW Borneo	2874 [0]	65	moderate	Hall (1991)
Lower Montane Venezuela	1650 [2]	64	–	Carey et al. (1994)[4]
Lowland Venezuela	2725 [1–2]	60	–	Carey et al. (1994)[5]
Pasoh, peninsular Malaysia	1900 [1]	45	low	Putz and Appanah (1987)
Paracou, French Guiana	3000 [3]	44	low	Durrieu de Madron (1994)
La Selva, Costa Rica	4000 [0]	40	high	Lieberman and Lieberman (1987)
Amazonas, Brazil	2186 [4]	26	low	Rankin de Merona et al. (1990)
Barro Colorado Island, Panama	2656 [3]	14	high	Putz and Milton (1982)
Amazonas, Venezuela	3500 [0]	≥ 10	low	Uhl (1982b)

[1] Annual rainfall in mm. The number of consecutive months with precipitation below 100 mm is shown in brackets.
[2] All stems that died after excluding stems for which the cause of mortality was unknown. Consequently, estimates in the Table differ somewhat from the original citation.
[3] Soil fertility, often estimated by the current authors.
[4] Data are averaged over 9 plots in the State of Merida.
[5] Data are averaged over 8 plots in the States of Merida, Delta Amacuro, and Bolívar.

occur less and less frequently, and eventually become inconsequential to tree population dynamics (Lorimer, 1989). In the Luquillo Experimental Forest in Puerto Rico, where hurricane return times are about 60 years, periodic hurricanes open more of the canopy than do background canopy gaps, in all topographic positions apart from the often waterlogged riparian valleys (Lugo and Scatena, 1996). Extreme cases of a reduction in the importance of background canopy gaps may occur in the "hurricane scrubs" of North Queensland, Australia (Webb, 1958) and in forests in the Caribbean that are damaged frequently and severely (Beard, 1945b). Even minor hurricanes would be expected to reduce tree-fall rates in the years after the hurricane event, as wind disturbance would fell trees that had rot in their trunk or were poorly rooted in the substrate (Putz and Sharitz, 1991). Major canopy disturbances also tend to reduce canopy height owing to the felling of the tallest trees during severe wind events (Wadsworth and Englerth, 1959; Foster, 1988). In forests subjected to frequent major canopy damage, tree heights should remain lower as a result of bole thickening and reduced height growth in response to increased lateral illumination (see Holbrook and Putz, 1989). These effects on tree size should tend to reduce gap size when trees fall.

Recovery following complete canopy removal may provide a maximum bound on the time to recovery of forest canopy structure. The gap disturbance regime (frequency and size) of seasonally dry forests receiving around 2600 mm of rainfall on Barro Colorado Island, Panama, following abandonment of agriculture, was similar to nearby primary forest after 70–80 years (Yavitt et al., 1995). In upland, nutrient-poor, wet-forest sites in the upper Amazon basin, stems 40–60 cm dbh were prevalent in a stand 60 years old, but after clearing it took 190 years for these forests to regain the previous basal area and biomass (Saldarriaga et al., 1988). After approximately 200 years, forests which formed on the trailing edge of river meanders were still undergoing structural changes in species composition towards larger emergents, which would continue to impact background canopy disturbance (Foster, 1990). Recovery following catastrophic wind disturbance, measured in a variety of ways, may take from decades to centuries, depending in part on severity of damage (Everham and Brokaw, 1996). Catastrophic wind events in Puerto Rico recur at a frequency less than the time to forest recovery (Lugo and Scatena, 1996).

Tree anchorage

Deeply rooted species (Touliatos and Roth, 1971) and forests in which most individuals are deeply rooted

(Brokaw, 1985b) or otherwise firmly anchored by root grafting (Basnet et al., 1992) or root penetration into soil parent material on shallow soils (Wadsworth and Englerth, 1959; Basnet et al. 1992) suffer less damage in general and less uprooting in particular from strong winds (Everham and Brokaw, 1996; see also Table 8.2, Prediction 4). Deep rooting is impeded in waterlogged soils (Hartshorn, 1978) or where impermeable soil horizons occur (Richards, 1996). Rooting depth may be superficial in soils where deeper layers are exceedingly nutrient-poor or highly acid (Richards, 1996). Relatively shallow rooting also appears to occur in soils with high fertility in wet forests (Brokaw, 1985b). On the other hand, deep rooting appears to occur on soils of moderately low fertility, with somewhat open nutrient cycles, and where seasonal drought confers a premium on deep rooting (Richards, 1996). In support of the hypothesized relationship between rooting patterns and gap formation, Kapos et al. (1990) found lower rates of tree-fall on a more infertile soil. Hartshorn (1978) found higher rates of tree-fall on waterlogged soils where deep rooting was impeded (see also Scatena and Lugo, 1995; Lugo et al., 1995).

Firm anchorage may result in a lower frequency of tree-fall and a higher proportion of bole-snapping relative to uprooting (Richards, 1996). Uprooting, as opposed to bole snapping, creates disturbance in the soil and litter layer, which is important in vegetation response. Whether a tree was uprooted or snapped may have little effect on gap size, however (Lawton and Putz, 1988; Jans et al., 1993), because uprooting or snapping may often depend more on wood characteristics than on tree size (Putz et al., 1983). In contrast, in Nouragues, French Guiana, relatively small uprooted trees tended to create gaps that were larger than would be expected from their size (van der Meer and Bongers, 1996a). The increase in gap size was owing to slightly higher numbers of fallen trees in gaps caused by uprooted trees on shallow soils where, compared with the parts of the plot with deeper soils, there was poor root-system development and anchorage. Everham and Brokaw (1996) in a review of uprooting during catastrophic wind events, found that the highest rates of uprooting occurred on the wettest sites. Wadsworth and Englerth (1959) reported high rates of uprooting on deep soils and high rates of stem breakage on shallow soils. Uhl et al. (1988a) reported a blow-down in which 80% of trees were uprooted on nutrient-poor soils where tree roots were shallow.

However, most stems that die outside of these blow-downs do so after snapping (Uhl, 1982b).

Of the forests listed in Table 8.4, few had percentages of uprooting above 50%, after excluding standing mortality and other modes of tree damage and gap formation that do not involve uprooting or trunk breakage. The highest rate was at La Selva, a wet site with relatively nutrient-rich soils. In most forests (Table 8.4), the majority of tree-fall and gap-making events cause little or no soil disturbance. Although there are no strong patterns evident in the Table, several dry and moist forest sites (e.g., Amazonas, Pasoh, Tai and Zagne) had low to moderate rates of uprooting. As expected if relative soil fertility affects uprooting, increasing soil fertility from Tai to Zagne and Para coincides with increasing rates of uprooting. Jans et al. (1993) explained the higher percentage of uprooting at Para (compared with nearby sites Zagne and Tai) to impeded rooting owing to waterlogging of soils and higher gravel content at Para. In contrast, the high rate of stem snapping at Tai (Vooren, 1986; Jans et al., 1993) was attributed to good rooting conditions (Jans et al., 1993). The relatively large size of gaps caused by uprooting in parts of the sample plot with shallow soils appears to account for the increase in the proportion of uprooting among gap-makers over what might be expected from the proportion of uprooting among fallen trees as a whole (compare the 1996a and 1996b data of van der Meer and Bongers in Table 8.4). We have no explanation as to why the leeward cloud forest at Monteverde had a relatively low percentage of uprooting (Matelson et al., 1995) compared with all other sites and with Monteverde windward cloud forest (Lawton and Putz, 1988). In considering the data in Table 8.4, it must be borne in mind that high rates of standing mortality should generally lead to low overall rates of gap formation (e.g., the Sarawak and Pasoh sites in Tables 8.3 and 8.4).

Topographic position influences anchorage and tree-fall rates, but its effects appear to depend on the instability of the soil and underlying parent material, and on waterlogging or other factors that lead to shallow rooting (Table 8.2, Prediction 5). There are few data on the effects of slopes on canopy gap formation. Canopy gaps may often be more frequent on slopes than on flat terrain (Oldeman, 1978; Berner, 1992; Lugo et al., 1995), but not at all sites (Kapos et al., 1990; Hubbell and Foster, 1986; Scatena and Lugo, 1995). In a Costa Rican montane oak–bamboo forest, an increase in gap-formation probably involved

Table 8.4
Relative percentage of gap-makers or fallen trees that were either uprooted or snapped across the main stem

Site	Sample [1]	Climate [2]	Soil fertility [3]	Uprooted (%)	Snapped (%)	Source
La Selva, Costa Rica	GM	4000 [0]	high	90	—	Hartshorn (1980)
Lower Montane Venezuela	FT	1650 [1–2]	–	69	31	Carey et al. (1994) [4]
Bako, Sarawak, Borneo	FT	4167 [0]	low	56	44	Hall (1991)
Lambir, Sarawak, Borneo	FT	2874 [0]	moderate	54	46	Hall (1991)
Lowland, Venezuela	FT	2725 [1–1.5]	–	52	48	Carey et al. (1994) [5]
Monteverde,[6] Costa Rica	GM [7]	>2500 [–]	–	48	52	Lawton and Putz (1988)
Mersing, Sarawak, Borneo	FT	3905 [0]	high	47	53	Hall (1991)
Nouragues, French Guiana	GM	3000 [3]	low	45	55	van der Meer and Bongers (1996a)
Para, Ivory Coast	GIST	2100[8] [4]	low[9]	43	57	Jans et al. (1993)
Zagne, Ivory Coast	GIST	1650[8] [4]	low[9]	40	60	Jans et al. (1993)
Pasoh, Malaysia	FT	1900 [1]	low	40	60	Putz and Appanah (1987)
Amazonas, Brazil	FT	2186 [4]	low	36	64	Rankin de Merona et al. (1990)
Nouragues, French Guiana	FT	3000 [3]	low	34	66	van der Meer and Bongers (1996b)
Monteverde,[6] Costa Rica	FT	>2500 [–]	–	26	74	Matelson et al. (1995)
Barro Colorado Island, Panama	FT [7]	2656 [3]	high	25	75	Putz et al. (1983)
Tai, Ivory Coast	FT [7]	1875[8] [4]	low[9]	23	77	Vooren (1986)
Barro Colorado Island, Panama	FT	2656 [3]	high	22	78	Putz and Milton (1982)
Noh Bec, Quintana Roo, Mexico	GM [7]	1500 [6]	moderate	18	82	Dickinson et al. (1999)
Tai, Ivory Coast	GIST	1875[8] [4]	low[9]	15	85	Jans et al. (1993)

[1] Data sources differed in whether the sample included gap-makers (GM), gap-makers from single tree-fall gaps (GIST), or fallen trees (FT) – whether they caused gaps or not.
[2] Annual rainfall in mm. The number of consecutive months with <100 mm of precipitation is shown in brackets.
[3] Often estimated by the current authors.
[4] Data are averaged over 9 plots in the State of Merida.
[5] Data are averaged over 8 plots in the States of Merida, Delta Amacuro, and Bolivar.
[6] Leeward (Lawton and Putz, 1988) and windward (Matelson et al., 1995) cloud forest. Rainfall does not include cloud deposition.
[7] Trees that fell over at ground level, often owing to a rotten base, are included in the "snapped" category because they cause minor soil disturbance.
[8] Estimated by M. Dickinson.
[9] F. Bongers, pers. commun., 1997.

higher growth and mortality rates on slopes, down-slope leaning of boles, and larger crown volumes on the down-slope side of trees (Berner, 1992). Asymmetric crowns may increase the probability of tree-fall even on flat sites (Young and Hubbell, 1991; Richards, 1996). Soil instability on slopes amplifies the effects of other conditions that would predispose a tree to being toppled (Denslow, 1987), but soil types and their parent materials are differentially resistant to slippage (Guariguata, 1990) and differentially suitable for anchorage. For instance, in palm forests in the Luquillo Experimental Forest in Puerto Rico, tree falls are more frequent on steep slopes with shallow clayey and often waterlogged soils (Lugo and Scatena, 1996; Lugo et al., 1995). In contrast, Wadsworth and Englerth (1959), also in Puerto Rico, noted that uprooting during hurricane winds was prevented in shallow soils on slopes by root penetration into cracks in stable parent rock, as compared with deeper soils in valleys. As may be the case with the palm forests noted above, waterlogging appears to exert a stronger effect than slope in the Bisley catchments of the Luquillo Experimental Forest where background canopy gap formation rate is highest on waterlogged soils in riparian valleys, but lower on slopes and in upland valleys (Scatena and Lugo, 1995).

Standing mortality

Standing dead trees tend to form smaller gaps (Brokaw, 1985b; Putz and Appanah, 1987; Hall, 1991; Krasny and Whitmore, 1992; Jans et al., 1993; Midgley et al., 1995) than tree-falls, and high rates of standing mortality should translate into lower overall rates of gap formation because many trees that die standing will not form discernable canopy gaps (Table 8.2, Prediction 7; see also Putz and Appanah, 1987). The depressive effect of high rates of standing mortality on rates of canopy gap formation and on gap sizes should be particularly acute where the trees that die standing are larger than the trees that are uprooted or snapped, as is the case in certain lower montane and lowland sites in Venezuela (Carey et al., 1994) and at Mersing, Sarawak (Hall, 1991), but not in La Selva, Costa Rica (Lieberman et al., 1985). The depressive effect of standing mortality of large trees on gap size is exemplified by a study of three West African sites, among which gap-size distribution and rate of formation did not differ, owing to a preponderance of gaps formed by branch-fall from standing dead emergents in the site with the largest trees (Vooren, 1986; Jans et al., 1993). If rates of uprooting and snapping had been equal, gap sizes should have been larger at the site with the larger trees (Jans et al., 1993).

The proportion of canopy gaps caused by dead or dying trees varies considerably: 72% in a temperate forest in New York (U.S.A.) (Krasny and Whitmore, 1992); 70% in a South African forest (Midgley et al., 1995); at least 50% in a West African forest (Jans et al., 1993); 27% in a semi-deciduous forest in the Yucatan (Dickinson et al., 1999); and at least 2% in a cloud forest at Monteverde, Costa Rica (Lawton and Putz, 1988). Standing mortality often leads to gaps that may best be described as gradual gaps (Krasny and Whitmore, 1992), formed by slowly dying trees that drop limbs one by one or by uprooting or snapping after the tree has died. Accordingly, some of the percentages above are probably underestimates of the role of standing mortality in gap creation.

Although there are few sites for which data are available, the highest rates of standing mortality appear to be in equatorial Southeast Asia (Table 8.3). Comparably high rates of standing mortality have also been reported in two temperate forests (Krasny and Whitmore, 1992; Midgley et al., 1995). Data suggest that gap formation rates are also lower in equatorial Southeast Asia (see p. 226 above; see also Putz and Milton, 1982). Rates of standing mortality should be highest where wind gusts are not frequent and strong trees are not architecturally prone to structural failure, trees are deeply rooted, and rare and severe droughts occur. From Table 8.3, it appears that soil fertility has little effect, although the site with the highest rate of standing mortality has low soil fertility (Hall, 1991). Average annual rainfall appears to have no effect, although Hall (1991) attributed high rates of standing mortality to periodic moisture deficits in freely draining soils. Such moisture deficits can occur quickly under certain soil conditions (Richards, 1996). The locations of sites (Table 8.3) examined by Hall (1991) did not appear seriously affected by the 1982–1983 drought that caused such severe mortality in east Bornean forests. Lack of frequent strong gusty winds may also help explain high rates of standing mortality in equatorial Southeast Asia (P. Hall, pers. commun., 1997), while high rates of tree snapping in the Venezuelan Amazon (Uhl, 1982b) may account for the lowest proportion of standing mortality in Table 8.3. Wind appears to be an important cause of tree-fall in Barro Colorado Island and La Selva (p. 227; see also Brokaw, 1985b), forests with low rates of standing mortality. Different rates of standing mortality among forests may also be related to differences among species in propensity to die standing (Seth et al., 1960; Brokaw, 1985b; Jans et al., 1993; Condit et al., 1995). In a French Guianan forest dominated by species with pyramidal crowns, standing death was more common, while in forests with predominately umbrella-shaped crowns, wind-throw was more common (Riéra, 1995). Senescence (Swaine et al., 1987), lightning strikes (Putz and Appanah, 1987; Lawton and Putz, 1988; Bruenig, 1989; Smith et al., 1994; Magnusson et al., 1996), defoliation by herbivores (Whitmore, 1975), fungal pathogens (Whitmore, 1975; Swaine et al., 1987) and termites (Putz and Appanah, 1987) also cause standing mortality.

Vines and epiphytes

High abundance of woody vines may increase gap frequency, while high frequencies of vine interconnections among adjacent trees may increase gap size (Putz, 1984; see also Table 8.2, Prediction 6). Woody vines appear to increase the likelihood that a tree will fall or die due to increased mechanical stress on the shoot and to shading of the tree's foliage (Putz, 1984). In a somewhat different way, epiphytes may increase rates of gap formation by adding weight to the

canopy of trees in wet montane forests, especially in the wet season (Strong, 1977; Matelson et al., 1995). Vines may increase gap size by pulling down trees that are either linked with the gap-making tree or are hooked by woody vine tangles on the falling tree (Putz, 1984). There is ample evidence for this effect from vine-cutting experiments preceding logging operations (Putz, 1985). In contrast, woody vines may also have a dampening effect on tree-fall frequency and gap size by stabilizing trees through their connections with neighbors (Putz, 1984). Vine abundance is highest in areas subject to disturbance (Webb, 1958; Whitmore, 1974; Hegarty and Caballé, 1991) and may be least in forests on nutrient-poor soils (Grubb, 1989).

Dry to wet forest gradient

It has been suggested that tropical dry forests should be less dynamic than tropical wet forests (Hartshorn, 1978; S.H. Bullock, pers. commun., 1996). But there have been few studies in which gap size and disturbance frequency have been described for a forest receiving less than 2000 mm of rainfall. Jans et al. (1993) and Dickinson et al. (1999) provide evidence suggesting that rates of gap formation and gap sizes are lower in forests with long dry seasons (see above, p. 226). The pattern of decreasing gap disturbance rates along the wet to dry forest gradient is obviously not well established, but several hypotheses have been advanced as to why drier forests should have lower rates of gap disturbance than wetter forests (see Table 8.2, Prediction 9):

(1) Trees in drier forests have smaller crowns which produce smaller canopy gaps (Holdridge et al., 1971). However, as forest height decreases, it takes less of a gap to create an equivalent light gap, as gap aperture is the key variable (Canham et al., 1990; Lawton, 1990). Also, light limitation in the understory of the shortest forests may not be the most serious problem for tree regeneration (Lieberman and Li, 1992) so that light gaps lose their importance. Below-ground gaps may become effectively smaller for a given gap aperture, because of higher root/shoot ratios in drier forests (Cuevas, 1995).

(2) Trees become shorter for a given trunk diameter as annual rainfall decreases and seasonality increases (Kira, 1978). Short trees with thick boles should be less subject to snapping (Putz et al., 1983), and shorter boles present a shorter moment arm that should lead to decreases in uprooting. Accordingly, rates of gap formation should be lower.

(3) Trees more often die standing in drier forests, leading to smaller tree-fall gaps (S.H. Bullock, pers. commun.). High rates of standing mortality would be expected on drier sites because of better anchorage, relative low height/diameter ratios, shorter periods during which gap-causing agents operate, and relatively low rain-loading of the tree canopies. Although standing mortality has been found to be important in forests that receive 2000 mm rainfall per year or less (Vooren, 1986; Putz and Appanah, 1987; Jans et al., 1993), it is also a feature of wet and moist forests, and there are too few data from drier forests to assess this hypothesis (Table 8.3). Standing mortality is associated with droughts in dry and moist tropical forests (Whigham et al., 1990; Swaine, 1992; Condit et al., 1995). Evidence from the 1982–1983 El Niño Southern Oscillation event support the notion that forests experiencing a yearly dry season may be less affected than wetter forests (Richards, 1996). Condit et al. (1995) reported 3% mortality (versus 2% during a non-drought period) on Barro Colorado Island, Panama, a forest where there are three months with less than 100 mm of rainfall. In contrast, mortality rates were substantial in forests in which rainfall does not typically drop below 100 mm in any given month. Woods (1989) reported 12–28% mortality in previously logged wet forest in Sabah, Malaysian Borneo. Similarly, Leighton and Wirawan (1986) reported 37% and 71% mortality of large trees ($\geqslant 60$ cm dbh) on two ridge plots, and 39–60% mortality of large trees ($\geqslant 50$ cm dbh) on mostly dry ridges at another site, in East Kalimantan on the island of Borneo. On wetter alluvial soils, mortality was approximately half as great as on ridges (Leighton and Wirawan, 1986; see also Ashton et al., 1995). Severe droughts of the magnitude of the 1982–1983 event recur in east Borneo at intervals of fifty to several hundred years (Leighton and Wirawan, 1986).

(4) Rates of tree mortality are lower in drier forests, therefore rates of gap formation are lower. In contrast to this expectation, Lugo and Scatena (1996) found no relationship between relative mortality ($\% \, yr^{-1}$) and rainfall in a large sample of sites (see also Swaine, 1992). As disturbance-regime data are usually area-based, we used data from Phillips and Gentry (1994) to test for a relationship between rainfall (range 1500–4746 mm yr^{-1}) and the number of stems that died per hectare per

year. As with relative mortality, no relationship was found ($F_{(2,28)} = 0.35$; $R^2 = 0.02$; $P = 0.71$).

(5) Drier forests may burn periodically (Uhl et al., 1988b; Swaine, 1992; Snook, 1993), leading to long periods without appreciable formation of tree-fall gaps as forest structure recovers (Dahir and Lorimer, 1996).

(6) Rates of gap formation are lower in drier tropical forests owing to a shortened wet season, while gap-causing agents (such as gusty wind, rainfall, and lightning strikes) are operative over longer periods in forests that receive high rainfall and are aseasonal.

(7) Less rain-loading of tree canopies occurs in dry forests because of lower epiphyte biomass (Holdridge et al., 1971). Lower rates of gap formation should result.

Catastrophic wind disturbances

Blow-downs and wind-throws in which a number of trees are damaged or killed are larger disturbances than those created by the death of single trees (Table 8.1). Art (1993) has defined blow-downs as "an extensive toppling of trees by wind within a relatively small area, greatly altering the small-scale climate within the ecosystems". Blow-downs and wind-throws appear to be fairly common in tropical and subtropical forests, but clearly there have been too few quantitative studies to characterize their importance in tropical forests, even though their impacts last for a long time and clearly influence forest dynamics (Hubbell and Foster, 1986).

Hurricanes and typhoons are the most destructive types of tropical windstorms. They occur in all regions of the world, and their impacts can be devastating (e.g., Yih et al., 1991). Many areas with vast expanses of tropical forest (e.g., South America, Africa, large areas in Asia and Australasia), however, are not impacted by hurricanes and typhoons (Fig. 8.1). In recent years, there have been a large number of articles in which the impacts of hurricanes and typhoons are considered and several authors have written summary articles (e.g., Brokaw and Walker, 1991; Tanner et al., 1991; Smith et al. 1994; Everham and Brokaw, 1996).

While it is possible to predict an average return time for hurricanes within tropical and subtropical areas (Everham and Brokaw, 1996), there are few examples where it has been shown that the structure and dynamics of the forest are strongly influenced

by periodic hurricane events (Roth, 1992; Zimmerman et al., 1994) as much as or more than by background canopy gaps. It has been predicted, however, that forest structure and floristics would be influenced by repeated hurricane or typhoon damage (e.g., Odum, 1970; Fraver et al., 1998). Coastal mangroves may represent one of the few types of tropical and subtropical forests in which periodic wind disturbance has a dominant influence on the physical structure of the canopy (Roth, 1992).

Predictions about the distribution and intensity of hurricanes and typhoons may mean little when one is considering a particular area of tropical forest, because the damage effects are greatest near the center of the storm, and there are few examples to demonstrate that specific forests have been heavily damaged by hurricanes at a frequency equaling the regional return frequency. Three examples demonstrate this point. Hurricane Gilbert heavily damaged a forest in the northeast Yucatan Peninsula in 1988 (Whigham et al., 1991; Harmon et al., 1994; Whigham et al., 1998). The northeast Yucatan was struck by 50–60 hurricanes between 1886 and 1968 (Alaka, 1976) which would represent a return time of approximately 1.6 years for the region. Our studies have been ongoing since 1984. Hurricane Gilbert has been the only storm during that 12-year period to do any significant damage to the forest. Long-term residents could not remember any storm that damaged the local forests as much as Hurricane Gilbert did. Records of hurricanes passing through the Sian-Ka'an Biosphere Reserve, south-central Yucatan Peninsula, show the same pattern. The area encompassed by the reserve has been struck by 11 hurricanes between 1893 and 1982 and each of them followed a different path (López Ornat, 1983), indicating that few areas would have been heavily damaged more than once or twice during the period of approximately 90 years, even though the return interval, based on long-term records for the area, would be about nine years. The Luquillo Experimental Forest in Puerto Rico is one of the few areas where long-term climatological and vegetation data are available to evaluate the occurrence and impact of hurricanes. The northeastern portion of Puerto Rico was struck by approximately 45 hurricanes between 1886 and 1968 (Alaka, 1976) for a return frequency of 1.8 years. Heavy to moderate damage to the Luquillo Forest occurred three times between 1928 and 1932 (a 1.3-year return interval) but the next damaging storms did not occur until 24 years (1932–1956)

and 33 years (1956–1989) had passed (Zimmerman et al., 1994). Since Hurricane Hugo in September 1989, four hurricanes have passed near the Luquillo Forest, but none has caused any significant damage (J. Zimmerman, pers. commun., 1996).

The extent of hurricane and typhoon impacts can range from very small to very large, and the impacts in any particular location will be influenced by a number of factors, both biotic (e.g., stem size, stem condition, species, presence of pathogens, structural complexity of the stand) and abiotic (e.g., storm intensity, topography, soil characteristics, disturbance history) (Everham and Brokaw, 1996; Imbert et al., 1996). Topography, for example, has been shown to be important in the Luquillo Forest in Puerto Rico where the landscape is rugged compared to the more uniform landscape of New England (Lugo, 1995). The factors which mediate the effects of wind as a cause of background canopy disturbance may often be obscured in intense hurricanes and typhoons (Everham and Brokaw, 1996).

COMMUNITY AND ECOSYSTEM RESPONSES TO CANOPY DISTURBANCE

Background canopy gaps, blow-downs, and catastrophic wind events in tropical and sub-tropical forests create a continuous range of conditions that set the stage for community and ecosystem response (Lugo and Scatena, 1996; Vandermeer et al., 1996). We first describe community-level responses by focusing on both changes in species composition and pathways of initial response to mainly catastrophic wind disturbance. We then compare responses between background canopy disturbances and catastrophic wind disturbances. We close this section by discussing changes in ecosystem processes, associated primarily with catastrophic wind disturbance events that cause large changes in the physical structure of forests.

Community-level responses

A framework for understanding responses

The interplay between characteristics of the disturbed site (see p. 228 above), species availability, and post-disturbance species performance determine changes in species composition and relative abundance immediately following the disturbance, and set the stage for long-term successional changes (Pickett et al.,

1987; Pickett and McDonnell, 1989; Everham and Brokaw, 1996; Vandermeer et al., 1996). Species availability (Pickett and McDonnell, 1989) after a wind disturbance includes propagules (seeds for most species) that are dispersed into a site at the time of the disturbance event, occur in a seed bank (generally in the soil in tropical forests; Garwood, 1989), or are dispersed to the site after the event from reproductive individuals that either occur outside the area of disturbance or were present in the disturbed area and recovered from damage incurred during the disturbance (Noble and Slatyer, 1980; Everham and Brokaw, 1996). Species availability also includes intact or damaged adults and juveniles that were present at the time of the disturbance. Sprouting of persistent meristems from roots and stems of intact or damaged plants is an important component of recovery (Everham and Brokaw, 1996).

Species performance (i.e., establishment and growth of individuals that originated from seed or persisted through the disturbance event) is determined by the autecology of the species (e.g., germination, growth, and assimilation patterns), environmental conditions (e.g., light and soil moisture) prior to and following the disturbance, and species interactions (e.g., disease, herbivory, and competition; Pickett and McDonnell, 1989). Throughout the literature on responses to catastrophic wind disturbances and background canopy gaps, species have been grouped by relative shade tolerance (Brokaw, 1985b; Clark and Clark, 1987; Denslow, 1987; Swaine and Whitmore, 1988; Brokaw and Scheiner, 1989; Everham and Brokaw, 1996). The grouping of plants into shade intolerant and shade-tolerant species necessarily involves breaking up a continuum of conditions and responses, as well as lumping species with different life-history attributes. Thus there is room for much refinement (Clark and Clark, 1992; Grubb, 1996) in categorizing species responses. We believe that the most useful approach for comparing species responses to wind disturbances is to differentiate species that have relatively abundant seedlings and saplings below a closed canopy (shade-tolerant) from those that may persist for relatively short periods below a closed canopy, but grow very little, if at all, beyond their seed reserves (shade-intolerant: Clark and Clark, 1987; Swaine and Whitmore, 1988). Pioneer species (Whitmore, 1989; Clark and Clark, 1992; Kennedy and Swaine, 1992) are a subset of the shade-intolerant group of species, and are short-lived, grow quickly in high light, and have light wood.

Table 8.5

Predictions about absolute change in species composition and the prevalence of different pathways of response to catastrophic wind disturbance in tropical forests

#	Prediction

Species composition

1   Absolute change in patterns of species relative abundance (species composition) should be greatest where catastrophic wind events have the longest return interval

2   Large changes in species composition should be associated with catastrophic wind events that damage forests established on old fields or plantations

3   Little change in species composition should occur in forests frequently hit by catastrophic winds, because of dominance by species that resist and are resilient to damage (i.e., survive well and sprout readily)

Response pathways

4   Regrowth from damaged stems predominates after catastrophic wind events in the tropics

5   The importance of regrowth decreases with increasing mortality rates, damage, and uprooting

6   The importance of regrowth should be greatest in wet sites within humid tropical forests, in high-altitude tropical forests, and in dry tropical forests

7   The importance of release of understory trees after catastrophic wind disturbance is currently underestimated, primarily owing to a lack of long-term studies of regrowth

8   Recruitment of short-lived shade-intolerant species with dormant seeds should be greatest where mortality and damage is greatest and uprooting more common

9   Recruitment of short-lived shade-intolerant species should be minimal in forests with a long return time for catastrophic events

10   Recruitment of shade-intolerant species with non-dormant seeds should be minimal in catastrophic wind disturbances owing to reductions in populations of seed dispersers and nonexistent or inconsequential post-event fruiting

11   Repression by vines of tree release and recruitment should occur where damage is severe and frequent

12   Repression by vines should affect species composition of recovery owing to differential abilities among tree species to shed and avoid vines

Shade-intolerant species are most likely to regenerate from seeds that germinate at the time of gap formation (Lieberman and Lieberman, 1987; Kennedy and Swaine, 1992), while the shade-tolerant species are more likely to colonize a gap from established seedlings or saplings (Brokaw, 1985b; Brokaw and Scheiner, 1989; Connell, 1989; Brown and Whitmore, 1992) or from sprouts of damaged seedlings or saplings (Putz and Brokaw, 1989). This may often be primarily a function of mortality rates below a closed canopy (see Lieberman et al., 1990). The response of shade-intolerant species to wind disturbances is further influenced by whether the species have or do not have a dormant seed bank (e.g., Garwood, 1989). Species that do not maintain a dormant seed bank can only respond to a wind disturbance if seeds are recruited to the site from individuals at the site that produced seed shortly before or after the disturbance, or from reproductive individuals not at the disturbance site but close enough for seeds to be dispersed by wind or animals.

Responses to catastrophic wind disturbance
Major pathways of response to catastrophic wind disturbance: Responses to catastrophic wind disturbances have been discussed in terms of recovery pathways (Everham and Brokaw, 1996), including: (1) regrowth from sprouting of damaged stems; (2) release of established seedlings and saplings of primarily shade tolerant species that were present in the understory at the time of disturbance; (3) recruitment of seedlings of primarily shade-intolerant species from dormant seeds in the soil seed bank, or from seed dispersal to the site just before or following the disturbance; and (4) repression of vegetation by fast-growing species of vines, herbs, and shrubs. Table 8.5 lists 12 generalized predictions about community responses to catastrophic wind disturbance. In this section we discuss the basis for each of the predictions. We expect exceptions to the generalizations, because they are based on a review of the literature which includes findings from catastrophic wind events of widely different intensities and from forests that differ in disturbance history, soils, and

type (e.g., wet and dry forests, lowland and montane, temperate and tropical).

Change in species composition: Absolute change in relative abundance patterns (species composition) in response to a catastrophic wind event should depend, in large part, on the characteristics of the disturbed site and on the species composition of the forest before the event, both of which are related to the severity, frequency, and recency of past events (Richards, 1996; see also Table 8.5, Predictions 1–3). The greatest change in species composition has been predicted to occur in forests that are infrequently impacted by catastrophic wind disturbances. This response is mostly owing to the increased importance of shade-intolerant species which often have low abundance prior to the disturbance and have increased opportunities for recruitment following the disturbance (Richards, 1996). Wind damage in forests with a low frequency of disturbance should be greater because canopy trees are taller and the topography of the forest canopy is more irregular and thus more prone to wind damage (Foster and Boose, 1992; Poorter et al., 1994; Everham and Brokaw, 1996; Richards, 1996). An exception to this prediction occurred in Nicaragua where storms are infrequent, hurricane damage was severe, and recruitment was limited (Boucher et al., 1994; Vandermeer et al. 1995, 1996). The absolute change in species composition would not be expected to be great in forests that suffer frequent wind disturbance, where species are better adapted to resist and respond to damage (Frangi and Lugo, 1991; Richards, 1996).

Large changes in species composition have been shown to occur in the temperate zone when a canopy of relatively shade-intolerant species is heavily disturbed and replaced by shade-tolerant species that were present in the understory (Spurr, 1956; Webb, chapter 7, this volume). This general process has been termed accelerated succession (Spurr, 1956; Abrams and Scott, 1989). In contrast, catastrophic wind events in the tropics are often characterized by little change in species composition (Everham and Brokaw, 1996). Differences between tropical and temperate forests may be due, in part, to the fact that many of the temperate forests in which studies have been done developed on sites that had been previously disturbed by logging or had been cleared for agriculture and then abandoned (Spurr, 1956; Foster, 1988). The same type of response may be anticipated in the tropics where plantations (Lugo, 1992; Parrotta, 1995; Fu

et al., 1996) and secondary forests (Lugo, 1992) often have a diverse understory differing in composition from the canopy trees and where plantations often are more severely damaged during catastrophic events than natural primary and secondary forests (see Everham and Brokaw, 1996; Fu et al., 1996). Plantations or natural forests dominated by fast-growing, soft-wooded species would be highly susceptible to wind damage and resulting mortality (Putz et al., 1983; Zimmerman et al., 1994; Fu et al., 1996) and should show low levels of regrowth (Zimmerman et al., 1994).

Relatively little change in species composition would be expected where species are resistant and resilient to damage. The importance of resistant and resilient species should increase in forests that are frequently damaged by wind (Brokaw and Walker, 1991; Frangi and Lugo, 1991; Walker, 1991; Bellingham et al., 1994; Zimmerman et al., 1994; Matelson et al., 1995; Everham and Brokaw, 1996; Scatena and Lugo, 1995). Hard-wooded, shade-tolerant species have been found to survive damage well and to sprout more readily than soft-wooded species (Putz et al., 1983; Zimmerman et al., 1994). Also, palms appear to resist wind damage and readily recover from defoliation (Frangi and Lugo, 1991). Forests that experience frequent windstorms, but that are not severely damaged owing to the dominance of resistant and resilient species, should be dominated by shade-tolerant species with seedling and sapling pools (Richards, 1996). Limited opportunities for recruitment in gaps would result from both reduced damage to established trees and a pulsed pattern of disturbance with many years between events, rendering inviable a life-history involving short life-span and recruitment from seed in gaps (Noble and Slatyer, 1980). Also, as we argue below (pp. 239–241), there are several general barriers to recruitment in tropical cyclonic-storm disturbances that would appear to make recruitment a less than ideal regeneration strategy.

Regrowth by sprouting: In their review, Everham and Brokaw (1996) suggested that regrowth from surviving stems predominates following catastrophic wind disturbance in the tropics because most events cause low to moderate damage and mortality (Table 8.5, Predictions 4–6). Sprouting occurs after mechanical damage to individuals that were damaged by wind, by falling debris, or by the fall of large individuals. Several variables appear to influence the importance of recovery by regrowth. Everham and Brokaw (1996) predicted that regrowth would become less important as direct

or indirect mortality from wind disturbance increased. Also, the importance of recovery by regrowth may decrease as the proportion of uprooted trees increases; uprooted stems are, in some cases, less likely to sprout than snapped trees (Putz et al., 1983; Bellingham et al., 1994; Everham and Brokaw, 1996). On moister sites, sprouting appears to be a common tree response, but increases in density due to sprouting may be negated by increased mortality of uprooted trees, which appears to be common on wet sites (Everham and Brokaw, 1996). The importance of stem sprouting as a major pathway of recovery following wind disturbance also appears to be greater in drier forests and in forests at higher elevations (Ewel, 1977; Ewel, 1980; Murphy and Lugo, 1986), although this tendency has not been evaluated in terms of forest response to hurricane damage.

Release: Our predictions regarding release as an important recovery mechanism are based on only a few studies of this phenomenon in tropical forests (Table 8.5, Prediction 7). There are at least four reasons why the importance of release after catastrophic wind events is likely to be underestimated. First, for seedlings and saplings, the difference between release and regrowth is trivial; to be in either response category, the plants had to be present before the disturbance event. Damaged seedlings and saplings would fall into the regrowth category, while individuals that were not damaged would arbitrarily fall into the release category. Second, we expect that short-term studies of regrowth seriously overestimate the eventual importance of sprouts, because of the development of disease associated with wounds and a concomitant decrease in wind-firmness (Roth and Hepting, 1943; Shigo, 1984; Putz and Sharitz, 1991). Large trees often cannot recover effectively after severe damage (Oldeman, 1978), and may be very likely to die, even long after the event that damaged them (Shaw, 1983; Walker, 1995). Third, catastrophic wind disturbance may initiate changes in canopy dominance, beginning with an increase in the importance of short-lived pioneers which, after several decades, are replaced by shade-intolerant species that persist until the next disturbance event (Weaver, 1986).

The fourth reason why release may be underestimated comes from evidence that catastrophic events appear to lead to enhanced growth of suppressed seedlings and saplings. Defoliation and structural damage to canopy trees results in an increase in the amount of light in the understory, at least for a couple

of years (Fernández and Fetcher, 1991; Bellingham et al., 1996). In Nicaragua, although the majority of stems were sprouts, released seedlings and saplings appeared to account for a large proportion of the stems encountered in post-hurricane inventories (Yih et al., 1991; Boucher et al., 1994; Vandermeer et al., 1995). In Puerto Rico, falling litter and debris from Hurricane Hugo killed 60% of the seedling pool of one species, but the remaining seedlings of that species responded with a strong increase in growth (You and Petty, 1991). An increase in growth in smaller trees following hurricane disturbance was observed in the Yucatan following Hurricane Gilbert (Whigham et al., 1991). The abundance of the long-lived *Shorea parvifolia* in the storm forest of Kelantan disturbed in the late 1800's may be an example of an important episode of release (Wyatt-Smith, 1954). Release has also been found to be important in temperate forests recovering from catastrophic wind disturbance (e.g., Spurr, 1956; Foster, 1988; Platt and Schwartz, 1990; Merrens and Peart, 1992; Webb, chapter 7, this volume). Even if regrowth of damaged stems is more important than release among the set of individuals that successfully captures space in the canopy after a given disturbance event, a generalized release response in past disturbance events will still have played a central role in that prevalence of regrowth (Foster, 1988; Connell, 1989; Clark and Clark, 1992; You and Petty, 1991).

Recruitment: Recruitment rarely appears to be the dominant recovery pathway following catastrophic wind disturbances (Everham and Brokaw, 1996; Table 8.5, Predictions 8–10). Recruitment, nonetheless, is generally a component of recovery (Weaver, 1986; Frangi and Lugo, 1991; Walker, 1991; Bellingham et al., 1994). Recruitment should be greatest following wind disturbances that cause extensive damage and mortality, particularly in forests that are infrequently impacted by major storm events (Everham and Brokaw, 1996; Richards, 1996). Recruitment is, however, likely to vary spatially within the area impacted by wind disturbances. The greatest damage is more likely to occur near the center of the storm than at the periphery (Lugo et al., 1983; Richards, 1996), and recruitment would thus be more important near the storm center. Recruitment would also be expected to be more important in topographically exposed sites that are more heavily damaged (Bellingham, 1991; Frangi and Lugo, 1991; Foster and Boose, 1992); particularly

at higher-elevation sites where damage is more severe and less spatially variable (Beard, 1945a,b; Brokaw and Grear, 1991).

Several examples in which high levels of recruitment have occurred seem to counter the general perception that regrowth is the primary recovery mechanism following wind disturbance. Whitmore's (1974) 21-year study of the role of catastrophic wind disturbance in tropical forests contrasted sites on Kolombangara, in the Solomon Islands, that were subject to severe damage by past hurricane events with those that had been more sheltered from hurricane damage. The canopies of the more hurricane-prone areas were dominated by long-lived shade-intolerant species while the sheltered sites had a high representation of non-pioneer species. The shade-intolerant species suffered heavy damage during disturbance events, yet recruited well afterwards from seed. Snook (1993) also reported successful recruitment by long-lived shade-intolerant species after hurricanes in the Yucatan Peninsula of Mexico.

Lack of recruitment by shade-intolerant species following catastrophic wind disturbances may be related to the presence of few large gaps, lack of exposed soil, the presence of a thick litter layer, and lack of propagules (Everham and Brokaw, 1996; Walker, 1999). Catastrophic wind events create a range of gap sizes dominated by small gaps, although the size distribution shifts to a larger average gap size as storm intensity increases (Everham and Brokaw, 1996). Except for patches that are severely damaged, the canopy may not remain open long enough for pioneers to avoid suppression, as regrowth following defoliation and minor branch damage can be rapid (Bellingham et al., 1994).

Perhaps more important than a lack of large gaps is the high deposition of litter and lack of disturbance to the substrate and understory necessary for germination and establishment of pioneer seedlings (Weaver, 1986; Everham and Brokaw, 1996). "Litter gaps", where the litter layer is removed and mineral soil is exposed, are thought to be indispensable for high rates of germination and establishment of small-seeded species in general and pioneers in particular (Putz, 1983; Putz and Appanah, 1987; Raich and Christensen, 1989; Kennedy and Swaine, 1992; Molofsky and Augspurger, 1992; Grubb, 1996). Litter gaps are often associated with uprooted trees, nurse logs, and steep slopes (Grubb, 1996). Uprooting mixes the soil, which may enhance germination rates (Putz, 1983; Putz and

Appanah, 1987). Experimental litter removals after a hurricane were particularly beneficial to pioneer species (Guzmán-Grajales and Walker, 1991). The importance of litter gaps is supported by the finding that fires that follow hurricanes, by removing litter, lead to high levels of establishment of pioneer species, particularly if fire intensity is high enough to kill vegetation that would otherwise sprout profusely (Oliver and Larson, 1990; Snook, 1993; Everham and Brokaw, 1996).

Even if conditions are right for germination, growth and survival of shade-intolerant seedlings, dormant or newly dispersed seeds may not be available (Schupp and Fuentes, 1995; Everham and Brokaw, 1996). Lack of a response to major disturbance by short-lived shade-intolerant species has been attributed to the absence of both a seed bank and reproductive individuals owing to a long disturbance return time or the spatial pattern of disturbance (Noble and Slatyer, 1980; Uhl et al., 1988a; Brand and Parker, 1995; Peterson and Carson, 1996). One possible example of lack of response by short-lived shade-intolerant species owing to lack of propagules were the severely hurricane-damaged Nicaraguan forests described by Boucher et al. (1994) and Vandermeer et al. (1995). The hurricane return time for the area is long, perhaps too long for adults and seed banks to persist between events. Because major wind disturbances should significantly reduce background rates of canopy gap formation (Dahir and Lorimer, 1996), there may be few opportunities for regeneration between events.

Unique problems of seed input may be associated with catastrophic winds. When defoliation is extensive, seed fall just after the event can be minimal (Lindo, 1968), although defoliation has been reported to trigger a large flowering response, at least in some species, and lead to an increase in seed fall compared to normal levels (Everham and Brokaw, 1996; Lugo and Scatena, 1996). This later seed rain may often be irrelevant, however, because of a premium on early establishment (Brokaw, 1985a; Brown and Whitmore, 1992; Kennedy and Swaine, 1992) and because the seed bank is likely to be the predominant source of viable seeds in background canopy gaps (Garwood, 1989) where defoliation does not occur. In large gaps created by catastrophic winds, seed rain may be further constrained among wind-dispersed pioneer species by the distance to potential seed sources. A large proportion of species have animal-dispersed seeds (Swaine and Whitmore, 1988; Levey et al.,

1994), and the dispersers often avoid large gaps in the canopy (Schupp et al., 1989). Seed and fruit dispersers may leave hurricane-damaged areas because of a lack of seeds and fruit (Ackerman et al., 1991; Yih et al., 1991). One might expect that, where hurricane damage is most severe, flowering and fruiting would be most attenuated. This would particularly affect those species that do not have dormant seeds, a seeding and sapling bank, or a strong sprouting response, but might have little effect on pioneers. If this is the case, it could partially explain the lack of an overwhelming recruitment response in some severely damaged forests (Boucher et al., 1994; Vandermeer et al., 1995, 1996).

Repression: Long-term repression of recovery as a result of the proliferation of herbs and vines (Everham and Brokaw, 1996) appears to be infrequent in the tropics (Table 8.5, Predictions 11, 12). In high-altitude dwarf forests in Puerto Rico, recovery was dominated by ferns and grasses (Weaver, 1986; Walker et al., 1996), although the cause of a lack of tree recovery was not clear. In gaps in Samoan lowland forest created by catastrophic winds, dense growth of grasses and ferns suppressed tree regeneration (Wood, 1970). These would seem to be examples of the arrested-succession effect, where shrub and herb communities delay invasion by trees in the temperate zone (Putz and Canham, 1992). The climbing habit of vines, however, creates a different situation.

Repression by vines has been documented in several severely and frequently disturbed forests. Frequent hurricanes in wet forests of northeastern Australia can lead to the formation of "cyclone scrub", a short-statured forest with emergent climber towers and abundant vines throughout the canopy (Webb, 1958). These forests occur where winds from frequent storms are locally intensified by topography (Webb, 1958). A similar situation occurs in Nigeria as a result of frequent tornados (Jones, 1955a,b). Recruitment and release can be suppressed by vines in large blow-downs (Lindo, 1968; Wood, 1970) and after intensive logging (Putz, 1991) where forest structure is conducive to vine proliferation (Hegarty and Caballé, 1991; Putz, 1985). Soil disturbance owing to logging promotes high levels of vine establishment (Putz, 1985, 1991). Proliferation of vines appears to delay forest structural development, but, except for frequently disturbed forests (Webb, 1958), the effect is temporary (Wyatt-Smith, 1954; Webb, 1958; Whitmore, 1974; Whitmore, 1975). Putz (1980) listed several characteristics that enable trees

to avoid and rid themselves of vines, these include: fast height and diameter growth, regular self-pruning of branches, large compound leaves, and vine-removing symbionts. The ability to avoid and shed vines provides a mechanism by which vine repression may alter the species composition of trees following severe damage (Table 8.5). In support of this general expectation, vine tangles in big gaps ($\geqslant$ 1 ha) in Costa Rica exclude "all but the very fast growing pioneers" (Hartshorn, 1980). Also, palms are "climber shedders/vine tangle surmounters par excellence" owing to their methods of leaf production and shedding (Putz, 1980).

It is apparent that not all severely damaged forests are prone to repression by vines (Walker et al., 1996). One possible example of this is the "hurricane forests" of the Caribbean island of St. Vincent, where damage is frequent and uprooting predominant, but where vine proliferation is apparently absent (Beard, 1945b). If blow-down is not prevalent, severe winds and major branch loss may rid trees of vines. In the forests damaged by Hurricane Gilbert in northeastern Yucatan (Whigham et al., 1991), almost all vines were eliminated from canopy trees, but they survived the disturbance and within a month most began to branch profusely. For the first year after the disturbance it appeared that vines would play an important role in recovery, but within five years almost all of the vine branches that were marked in 1988 had died, and most of the trees were still free of vines even though some had heavy vine loads prior to the hurricane (D. Whigham and E. Cabrera, pers. observ.). This could potentially explain the lack of vine repression in some relatively wind-resistant forests.

Contrasts between responses to catastrophic wind and other canopy disturbances

It should be apparent that much of the literature upon which an understanding of response to catastrophic wind disturbance is based comes from studies of background canopy disturbance, and response to background canopy gaps is often a good model for understanding response to catastrophic wind events (Ackerman et al., 1991; Everham and Brokaw, 1996). However, Ackerman et al. (1991) suggested that response to background canopy disturbance is an imperfect analog for response to both the least and the most severe damage by tropical cyclonic storms, while moderate damage should most closely approximate background canopy disturbance. Comparisons are made difficult, in part, because recovery in background

canopy gaps is typically studied only where gaps extend into the understory (Brokaw, 1982a; Popma et al., 1988; Lieberman et al., 1989). In contrast, in studies of catastrophic wind disturbance, gaps (or heavily disturbed patches) are not generally distinguished from areas where only upper canopy damage occurs (Frangi and Lugo, 1991; Walker, 1991). We are not aware of any studies which explicitly compare regeneration in sites dominated by background canopy disturbance with that in forests damaged by catastrophic events [(the closest would be that of Whitmore (1974)]. Forests whose disturbance regimes are dominated by catastrophic wind events should differ from forests dominated by background canopy disturbance in the frequency of large gaps, in the lack of seed sources for various reasons, and in poor recruitment even where seeds are present. Foster and Boose (1992) and Everham and Brokaw (1996) conceived of a gradient of disturbance from small gaps, created by standing dead trees or branch falls, to larger gaps formed by the uprooting or breakage of one or many trees, and, at the extreme, to large gaps with indistinct edges created by damaged and defoliated trees during a catastrophic wind event. Less severe catastrophic wind events may cause minimal upper-canopy damage, and there may only be a few small gaps that extend to the understory (Everham and Brokaw, 1996). When compared with background canopy disturbance, catastrophic wind events can create equally small gaps as well as much larger gaps (Foster and Boose, 1992; Everham and Brokaw, 1996). For both types of disturbance, small gaps are much more frequent than large gaps, although, despite their low frequency, large gaps may cover a comparatively large area (see Lawton and Putz, 1988; Brokaw, 1985b; Foster and Boose, 1992). Timing is obviously different, with background canopy disturbances occurring continuously whereas catastrophic events occur in a pulsed and infrequent manner (Oldeman, 1989).

The general assumption is that release, sprouting, and ingrowth of gap-edge trees dominate in small gaps, while recruitment becomes more prevalent in large gaps (Dunn et al., 1983; Brokaw, 1985a,b; Denslow, 1987; Raich and Christensen, 1989; Whitmore, 1989; Everham and Brokaw, 1996) in both disturbance types. Similarly, predictions and data from forests dominated by background canopy gaps (Hartshorn, 1978; Denslow, 1980; Putz and Appanah, 1987; Uhl et al., 1988a; Brokaw, 1985b; Ashton, 1981; Jans et al., 1993) and from forests damaged by catastrophic wind

events (Weaver, 1986; Runkle, 1990; Walker, 1991; Bellingham et al., 1994; Richards, 1996) suggest that it is the frequency of large gaps and severely damaged patches that should determine the relative abundance of shade-intolerant species in a forest. Where background canopy disturbance dominates in the tropics, shade-tolerant species comprise by far the largest group (Clark and Clark, 1987; Whitmore, 1989; Welden et al., 1991; Lieberman et al., 1995). Few authors have found (Whitmore, 1974) or predict (Richards, 1996) a dominance by shade-intolerant species in forests damaged frequently by catastrophic wind disturbances. This may be owing to the finding that most catastrophic wind events cause only minor to moderate damage (Everham and Brokaw, 1996).

Even where gap sizes are large, relatively poor recruitment responses have been shown to occur (Uhl et al., 1988a; Boucher et al., 1994; Vandermeer et al., 1995) owing to lack of propagules and post-dispersal phenomena. In a large blow-down in the Venezuelan Amazon in which uprooting predominated, Uhl et al. (1988a) ascribed a lack of pioneer response to a lack of seed sources, which, in turn, may be due to poor regeneration of these species in the prevailing small gaps (see also Peterson and Carson, 1996). Putz and Appanah (1987) have suggested, however, that a lack of propagules should not be expected to be more strongly associated with forests damaged by catastrophic wind events (Putz and Appanah, 1987). Long intervals between events in forests whose disturbance regimes are dominated by catastrophic winds would tend to reduce the relative abundance of both adults and seed pools of short-lived pioneers (Noble and Slatyer, 1980). In cyclonic storm disturbance, lack of a recruitment response may be due to propagule limitation related to defoliation and branch damage of canopy trees (Lindo, 1968) and to the lack of seed dispersers in heavily damaged areas (Ackerman et al., 1991; Yih et al., 1991).

Even where propagules are present, recruitment may be reduced in catastrophic wind disturbances by a lack of disturbed and litter-free soil (Guzmán-Grajales and Walker, 1991; see review in Everham and Brokaw, 1996) and by rapid vegetative recovery that would compete with new seedlings (Everham and Brokaw, 1996). Similarly, both lack of litter-free soil in forests where uprooting is uncommon (e.g., Putz and Appanah, 1987) and competition from established individuals (Kennedy and Swaine, 1992) have been related to reduced recruitment in background canopy

disturbances. Lack of disturbed soil in catastrophic wind disturbances, even where mortality and structural damage rates are high, may not be as generally important as previously suggested (Everham and Brokaw, 1996): the proportion of uprooting among fallen trees ranges from 15% to 88% in tropical forests hit by catastrophic winds (Everham and Brokaw, 1996) while similar rates of uprooting (15%–90%) are reported for tree-falls in forests dominated by a background canopy disturbance regime (Table 8.3).

In this section, we have provided a series of predictions (Table 8.5) regarding changes in species composition and recovery pathways following canopy wind disturbance. No clear patterns emerge, because there have not been enough long-term studies of tropical forests to elicit broad geographic patterns or determine whether or not predictions, such as those that we provide, adequately describe recovery processes following background and catastrophic wind disturbances. A general model that might be useful in designing future investigations to test these and other predictions comes from succession research on prairie pothole wetlands in the United States (van der Valk, 1981). Prairie pothole wetlands occur over a broad range of hydrogeomorphic settings in which water quality (fresh or saline) and disturbances, both natural (wet and dry cycles) and anthropogenic (agriculture, fire), play important roles in determining the status of vegetation at any moment in time. Typically, vegetation undergoes dramatic changes in response to short- and long-term changes in water levels. Van der Valk based his model on "a Gleasonian approach" to understanding vegetation change at the ecosystem level, based on the ecological characteristics of individual species. He suggested that species or groups of species with similar life-history traits respond similarly to disturbance, whether of natural or anthropogenic origin. In applying this conceptual approach to tropical forests, the first step would be to characterize the disturbance regime of the forest. Once the disturbance regime was adequately characterized, the responses of individual species (or groups of species such as shade-tolerant and shade-intolerant) to the range of disturbances would be evaluated. In prairie pothole wetlands, for example, the interactions between water levels and germination characteristics of seeds of species in the soil seed bank were useful in predicting vegetation responses. In tropical forests, the soil seed bank appears to be less important, but species responses over the range of sizes of wind disturbances (e.g., ingrowth in small

canopy gaps, and sprouting in larger openings) appears to be most important. Ongoing long-term research in the Luquillo Experimental Forest in Puerto Rico (Zimmerman et al., 1996) should provide the types of data that will be required to test predictions such as those that we have provided in Table 8.5.

Ecosystem-level responses

Ecosystem-level processes (e.g., rates of decomposition, rates of nutrient uptake and release, primary production) should be influenced by wind-generated disturbances, especially in larger disturbances where changes in the physical structure of ecosystems are greater. Many changes in ecosystem-level processes are mediated through alterations of microclimate, changes in site water balance, and additions of nutrients and carbon associated with the destruction of biomass (Frangi and Lugo, 1991; Lodge and McDowell, 1991; Sanford et al., 1991; Lugo and Scatena, 1996; Scatena et al., 1996).

Microclimate modifications primarily involve increases and changes in the quantity and quality of light (Raich, 1989; Brown, 1996) and associated variables such as soil and air temperatures and relative humidity (Brown, 1993). Reductions in leaf biomass, and destruction of branches and boles increase amounts of photosynthetically active radiation (Bellingham et al., 1996), decrease fine-root biomass in the disturbance site (Parrotta and Lodge, 1991; Silver et al., 1996), and increase soil moisture owing to decreased evapotranspiration (Vitousek and Denslow, 1986). The degree of change in microclimatic variables following canopy disturbance is related to disturbance size (Chazdon and Fetcher, 1984; Canham et al., 1990; Bellingham et al., 1996), but there is often considerable spatial variation within the disturbance site (Brown, 1993). The microclimate changes as vegetation and the ecosystem recover from disturbance. Bellingham et al. (1996) found that photosynthetically active radiation increased with the severity of hurricane damage (i.e., amount of defoliation) but that light levels had returned to almost pre-hurricane levels within 33 months. Fernández and Fetcher (1991) found similar results in Puerto Rico 14 months after Hurricane Hugo. Increased light levels in single tree-fall gaps also decrease with time, but the causes of the changes would be different from those measured in hurricane-damaged forests because of differences in ecosystem recovery responses

(e.g., ingrowth versus sprouting in the understory: Bellingham et al., 1996).

There have been few studies of root biomass, root turnover, and root growth in gaps. Silver et al. (1996) found that root biomass in the Luquillo Experimental Forest (Puerto Rico) was only beginning to recover six years after Hurricane Hugo; though most of the soil nutrient pools had returned to pre-hurricane levels.

Wind-generated disturbances of all sizes significantly increase the necromass of fallen leaves, branches, trunks and upturned roots (Frangi and Lugo, 1991; Harmon et al., 1994; Smith et al., 1994). Not only does the amount of dead biomass increase in hurricane-impacted forests (Harmon et al., 1994), but the standing stocks of nutrients associated with the dead biomass increase tremendously because of the relatively high nutrient content of the leaves and wood brought down by the disturbance (Tanner et al., 1991). Frangi and Lugo (1991) found that the amounts of nitrogen, phosphorus, potassium, calcium, and magnesium in aboveground necromass had increased by 19%, 18%, 17%, 23%, and 16% respectively, 7 months after Hurricane Hugo. Whigham et al. (1991) measured an increase of approximately 50% in coarse woody debris in a dry tropical forest following Hurricane Gilbert. Standing stocks of calcium, potassium, magnesium, and nitrogen increased between 22% and 36% and phosphorus and magnesium increased by more than 55%. The amount of leaf material deposited by Hurricane Gilbert was 29–98% higher than the total annual amounts of leaf litter-fall measured for the four years prior to the hurricane (Whigham et al., 1991). The concentrations and total amounts of nutrients in leaf litter-fall associated with Hurricane Gilbert were in many instances 100–300% higher than they had been in the four previous non-hurricane years (Table 8.6).

Release of nutrients through leaching and decomposition of leaves and wood would potentially increase nutrient availability, as well as losses of nutrients to groundwater and surface water, and to the atmosphere by gas emission. There have been, however, few studies in which nutrient cycling has been examined at the ecosystem level in tropical and subtropical forests following disturbances similar to those caused by wind damage (Parker, 1985; Vitousek and Denslow, 1986; Uhl et al., 1988a; Lodge and McDowell, 1991; Walker, 1999). Hartshorn (1978), Whitmore (1978) and Orians (1982) each predicted that soil properties would change following canopy disturbance, and that tree uprooting in single tree-fall gaps would also change

the characteristics of exposed soils (Schaetzl et al., 1989). Vitousek and Denslow (1986) found higher soil moisture in tree-fall gaps, but no significant increase in soil nutrients between gap and non-gap habitats, even though soils associated with uprooted trees had lower nitrogen, phosphorus and carbon, and higher rates of nitrogen mineralization. Parker (1985) found similar results in disturbed and undisturbed areas in the same forest type as that studied by Vitousek and Denslow. Uhl et al. (1988a) found no evidence to support the hypothesis "that treefall gaps might represent zones of high nutrient leakage" in humid tropical forests in Venezuela.

There is some evidence for increased nutrient availability in larger wind-disturbed areas (Lodge and McDowell, 1991) but not as much as occurs in response to forest clear-cutting (Steudler et al., 1991). In addition, many of the changes in nutrient cycling in response to large-scale disturbances such as hurricanes appear to have little long-term impact on ecosystem function.

Table 8.6
Biomass and nutrients (totals and concentrations) in leaf litter-fall for Hurricane Gilbert compared to the range of values measured in the 4 years prior to the hurricane[1]

Leaf litter	Percent. increase[2]
Biomass	29–98
Phosphorus	
Total	133–250
Concentration	60–166
Potassium	
Total	92–189
Concentration	143–382
Calcium	
Total	43–133
Concentration	8–17
Magnesium	
Total	33–100
Concentration	0–(–6)
Manganese	
Total	50–200
Concentration	2–11

[1] Data compiled from Whigham et al. (1991).
[2] Percent increase $= 100 \cdot (x_1 - x_0)/x_0$: where x_0 is the mass or concentration before the hurricane, and x_1 during it.

As indicated earlier, many of the ecosystem responses related to nutrient cycling can be ascribed to large inputs of coarse woody debris and the release of nutrients through leaching and decomposition (Frangi and Lugo, 1991; Harmon et al., 1994; Smith et al., 1994). In this context, the Luquillo Experimental Forest in Puerto Rico has been the most intensively studied site (Zimmerman et al., 1996). Sanford et al. (1991) used simulation modeling to predict that an initial decrease in nitrogen mineralization would be followed by higher rates following hurricane damage. Their predictions with respect to nitrogen dynamics were verified by Lodge et al. (1991), who measured elevated soil ammonium concentrations and higher rates of nitrification 17 and 7 months, respectively, after Hurricane Hugo, and increased mineralization was later suggested by increased nitrate levels in stream water. Sanford et al. (1991) also predicted that a period of phosphorus immobilization after the hurricane would be followed in about two years by an increase in phosphorus availability. Soil phosphorus availability was not measured at the Luquillo site following Hurricane Hugo, but Lodge and McDowell (1991) used results from a long-term fertilization study at Luquillo to suggest that responses to increased amounts of phosphorus occur, but only after several years of fertilizer addition. This conclusion is supported by long-term studies of phosphorus addition to a tropical dry forest in the Yucatan (Whigham and Lynch, 1998). There was no detectable response in tree growth, leaf litter-fall biomass and nutrients to four years (1984–1988) of phosphorus fertilization of the forest (Whigham et al., 1998). One year after Hurricane Gilbert (1988), phosphorus concentrations in leaf litter-fall were higher in each of four years after the hurricane than they had been during four pre-hurricane years. It is unclear, however, whether the increased nutrient levels in leaf litter-fall were due to increased phosphorus availability following four years of fertilization and/or to responses to Hurricane Gilbert.

Reduced fine-root biomass and added labile carbon in disturbed sites (Parrotta and Lodge, 1991) seem to influence the rates of emission of gases containing nitrogen and carbon. Steudler et al. (1991) consistently found lower rates of loss of carbon dioxide, decreased rates of emission of methane, and higher rates of nitrous oxide production in hurricane-disturbed areas than in undisturbed sites. All these trends are consistent with the hypothesis that lower oxygen levels in the soil alter microbially-mediated processes such as denitrification, methanogenesis, and soil respiration.

We know of no data in which disturbance sites have been monitored until there is no evidence of the past disturbance. The studies of Bruenig (1989) and Whitmore (1989) suggest, however, that tropical and subtropical forests are very dynamic and that few areas remain in equilibrium for long periods of time. Zimmerman et al. (1996) provided a conceptual view of temporal patterns of recovery following catastrophic disturbance. Several authors have noted that it is possible to identify large-scale disturbance sites decades after the event occurred (e.g., Richards, 1996). Even though there have been few long-term studies of ecosystem-level processes in single tree-fall gaps or in areas impacted by blow-downs or hurricanes, the responses that have been measured are consistent enough to suggest that the impacts last for periods from a few months up to three years, and that ecosystem recovery occurs rapidly (Whigham and Lynch, 1998). We believe that large-scale and long-term impacts to wind damaged forests, particularly those damaged by hurricanes, would only occur following massive destruction of biomass by fires. Harmon et al. (1994) examined several sites in the Yucatan Peninsula, and found that sites that had been impacted by the hurricane and by fire had the highest amounts of coarse woody debris, and they estimated that it would take between 30 and 150 years to return to pre-hurricane levels.

CONCLUSIONS

There is ample evidence that wind influences tropical forests, and that the loss of biomass that results directly or indirectly from wind occurs over a range of scales. In this chapter we have chosen to divide the continuum of wind disturbances into background disturbances that result in the death of one or a few trees, and catastrophic events that open larger areas of forest (e.g., wind-throws and damage caused by hurricanes). The division that we have made is, of course, arbitrary, and was done primarily to separate wind disturbances into those that received the most scientific attention (background disturbances) from those that have not been adequately studied (catastrophic disturbances). One obvious conclusion is that there is still little known about the distribution of and long-term responses to catastrophic wind disturbances, which appear to be

widespread. Except for a series of recent studies of hurricanes (see articles in *Biotropica, 23*, 1991 and 28, 1996), most of the information that has been compiled about recovery from catastrophic events has been anecdotal or primarily qualitative. Recovery from catastrophic wind events can, however, be quite rapid even after extensive damage (Whigham and Lynch, 1998). With the advent of a more complete coverage of tropical areas using satellites and of improved techniques for evaluating satellite images, it should now be possible to evaluate more adequately the distribution and frequency of occurrence of catastrophic wind disturbances in tropical forests and monitor recovery from them.

We focussed our discussion on elements of wind disturbance regimes that have important effects on species, community and ecosystem responses. The following general conclusions are offered:

(1) Gap sizes should be largest where there is an abundance of large trees and a low rate of standing mortality, where vines are abundant, and where wind knocks down gap-edge trees.

(2) Forests of small stature (dry forests, high-altitude forests, and nutrient-poor forests) should have the smallest gaps, while forests on slightly seasonal sites with adequate soil nutrient levels should have the largest gaps, because the trees are large.

(3) Rates of gap formation should be highest where tree architecture is least vulnerable to wind, there is poor anchorage, and standing mortality rates are low, and in otherwise calm regions where gusty winds are most frequent.

(4) Soil disturbance should be greatest where uprooting rates are highest. This should occur where anchorage is poor owing to shallow rooting and unstable soils and parent material, and where overall rates of gap formation are highest.

(5) Wind is an important cause of background canopy disturbance, and appears to be the primary cause in some, although not all, forests not frequently affected by catastrophic wind and other major disturbances.

(6) High rates of background canopy disturbance, as with major disturbance, should lead to a reduction in the susceptibility of the forest to damage, because when a large or vulnerable tree is felled, it is replaced by a younger individual that is less likely to be prone to damage.

(7) The long-term impacts of catastrophic wind disturbances are poorly understood, especially ecosystem-level responses, but recent longer-term studies in the Caribbean are showing a wide range of responses at species, community, and ecosystem scales.

(8) Wind disturbances may be less important in parts of the Paleotropics, but many more studies are needed to verify this conclusion.

(9) There is a need for long-term studies of species, community, and ecosystem recovery from wind disturbances. Most studies, to date, have focussed on the effects of wind disturbances more than on the recovery.

(10) The effects of catastrophic winds, because of their long-sustained winds with speeds that are hard to predict, often cannot be predicted from what is known of the factors that influence background canopy-gap disturbance regimes.

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