# Forest Damage and Recovery from Catastrophic Wind

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# I. Abstract

The literature on the effects of catastrophic wind disturbance (windstorms, gales, cyclones, hurricanes, tornadoes) on forest vegetation is reviewed to examine factors controlling the severity of damage and the dynamics of recovery.

Wind damage has been quantified in a variety of ways that lead to differing conclusions regarding severity of disturbance. Measuring damage as structural loss (percent stems damaged) and as compositional loss (percent stems dead) is suggested as a standard for quantifying severity. Catastrophic wind produces a range of gaps from the size caused by individual treefalls to much larger areas. The spatial pattern of damage is influenced by both biotic and abiotic factors. Biotic factors that influence severity of damage include stem size, species, stand conditions (canopy structure, density), and the presence of pathogens. Abiotic factors that influence severity of damage include the intensity of the wind, previous disturbance, topography, and soil characteristics.

Recovery from catastrophic wind disturbance follows one of four paths: regrowth, recruitment, release, or repression. The path of recovery for a given site is controlled both by the severity of disturbance and by environmental gradients of resources. Recovery is influenced also by frequency of wind disturbance, which varies across geographical regions.

To develop robust theories regarding catastrophic wind disturbance, the relative roles of different abiotic and biotic factors in controlling the patterns of severity of damage must be determined. These patterns of severity and environmental gradients must then be tied to long-term dynamics of recovery.

## Resumen

La literatura sobre los efectos de disturbios catastróficos del viento (tormentas, ventarrones, ciclones, huracánes, tornados) sobre la vegetación de bosque es revisada para examinar los factores que controlan la severidad del daño y la dinámica de recuperación.

El daño del viento puede ser cuantificado en varias formas, lo cual conlleva a diferir en las conclusiones en cuanto a la severidad del disturbio. Medir daños como la pérdida estructural (por ciento de tallos dañados) y la pérdida composicional (porcentaje de tallos muertos) son normas sugeridas para cuantificar la severidad. Los vientos catastróficos producen una extensión de aperturas de gran tamaño causados por árboles caídos sobre muchas otras áreas mayores. El patrón espacial de daño es influenciado por factores abióticos y bióticos. Factores bióticos que influyen severamente al daño pueden ser tamaño del tallo, especie, condición de tolerancia (estructura del dosel, densidad), y la presencia de patogénos. Factores abióticos que influyen severamente sobre el daño incluyen la intensidad del viento, disturbios anteriores, topografía, y las características del suelo.

La recuperación de las catástrofes causados por el viento siguen uno de cuatro patrones: crecimiento, reclutaje, liberar o reprimir. La trayectoria de recuperación para un lugar es controlado por ambos: por lo severo del disturbio y por los gradientes ambientales del recurso. La recuperación es influenciada también por la frecuencia del disturbio por viento, el cual varia sobre el globo.

Para desarrollar una fuerte teoría en cuanto a disturbios catastróficos por viento, los roles relativos de los factores abióticos y bióticos en el control de modelos de severidad de daño tienen que ser determinados. Estos modelos de severidad y gradientes ambientales tienen que ser enlazados para una dinámica de recobro a largo plazo.

## РЕФЕРАТ

Обзор литературы о воздействии катастрофических ветров (штормов, циклонов, ураганов, смерчей) на лесную растительность с целью выявления факторов, влияющих на величину ущерба и на динамику рекомпенсации.

Ущерб от ветра оценивается различными методами, приводящими к разным выводам. Измерение ущерба как структурного воздействия (процент поврежденных стволов) и как композиционного воздействия (процент погибших стволов) предложено в качестве стандарта. Катастрофический ветер образует серию проплешин, размер которых колеблется в широком диапазоне. Пространственная конфигурация ущерба находится под воздействием как биотических, так и абиотических факторов. Биотические факторы величины ущерба включают: размер ствола, особенности особи, условия древостоя (структура и плотность листвы) и присутствие патогенов. Абиотические факторы величины ущерба включают интенсивность ветра,

предшествующие атмосферные возмущения, топографию и характеристики почвы.

Рекомпенсация после катастрофического ветрового воздействия следует по одному из четырех путей: спонтанное возобновление, спонтанное замещение другими древесными особями, подавление нижних ярусов древостоя (нуждающееся в их "высвобождении" от листвы верхнего яруса), нашествие сорняковой растительности. Какой из путей рекомпенсации возобладает, зависит от масштаба атмосферного возмущения и от целого ряда средовых градиентов. Рекомпенсация также зависит от глобально изменчивой частоты ветровых возмущений.

Для создания продуктивных теорий измерения ветрового ущерба необходима оценка различных биотических и абиотических факторов, влияющих на величину и конфигурацию ущерба. Последняя, а также средовые градиенты должны быть увязаны с долгосрочной динамикой рекомпенсации.

> "The oldest voice in the world is the wind. When you see it fitfully turning the blades of a mill lazily to draw water, you think of it as an unreliable servant of man. But in truth it is one of our masters, obedient only to the lord sun and the whirling of the great globe itself."
>
> —Donald Culross Peattie

## II. Introduction

Catastrophic winds, including cyclonic storms, tornadoes, gales, and severe windstorms, impact forests around the globe in both temperate and tropical regions. Tree species differences, tree age or size, silvicultural treatment, topography, edaphic characteristics, and previous disturbance may all influence the spatial patterns and severity of damage and recovery from catastrophic wind. Although the influence of these factors is increasingly understood for chronic wind effects, particularly in forest plantations, there is little evidence that these relationships hold for less frequent catastrophic winds. Catastrophic winds have been observed and quantified for centuries, but few clear generalizations about their impacts have been drawn. Improved understanding of these impacts is required, not only because the need for conservation and ecosystem management increases, but also because both the frequency and the intensity of such storms may increase, according to some meteorologists and global climate change models (Dunn & Miller, 1960; Emanuel, 1987; Gray, 1990; Wendland, 1977).

In this review we attempt to answer seven questions: 1) How should catastrophic wind intensity be quantified? 2) How should catastrophic wind effects be quantified? 3) Is catastrophic wind damage homogeneous, or are there spatial patterns of damage, and can these patterns be predicted? 4) How do biotic factors (e.g., tree size, species, and stand differences) influence damage? 5) How do abiotic factors (e.g., topography, soil, and previous disturbance) influence damage? 6) Can any generalizations be drawn regarding the dynamics of recovery from catastrophic winds? 7) Are there consistent differences between tropical and temperate forests in terms of wind disturbance and response?

Before presenting our own more extensive review, we shall briefly summarize the findings of nine previous papers comparing impacts of different storms on different forests (Andersen, 1954; Brokaw & Walker, 1991; Everham, 1995; Glitzenstein & Harcombe, 1988; Liegel, 1984; Lugo et al., 1983; Peterson & Pickett, 1991; Smith, 1946; Tanner et al., 1991). In addition, *Biotropica* and *Journal of Coastal Research* both had special issues in 1991 dealing with hurricane impacts, *BioScience* had a special section on Hurricane Andrew (Pimm et al., 1994), and Grace and Coutts (1995) published a collection of papers on the impacts of wind on forests.

Liegel (1984) reported assessments of hurricane impacts on 11 conifer plantations. He found the following: 1) more damage at higher elevations, 2) an increase in some types of wind damage with increasing annual rainfall, 3) more damage in thinned than in unthinned stands, 4) more uprooted than snapped stems, and 5) no clear differences between damage to conifers and broadleaf trees. He stressed the need to assess hurricane damage in order to develop models for predicting damage risk. Glitzenstein and Harcombe (1988) compared the impacts of a tornado, a large blowdown associated with a severe thunderstorm (Dunn et al., 1983), and a hurricane (Lugo et al., 1983) on six temperate and tropical broadleaf forests. They found that 1) damage was positively correlated with average stem size in a stand, 2) the size of the area affected and the severity of disturbance were comparable for all three catastrophic wind events, 3) mortality tends to be low, 4) trees severely damaged often recover, and 5) the effects of catastrophic wind disturbance probably never approach the severity of catastrophic fire. Peterson and Pickett (1991) compared 16 studies of wind disturbance and identified a trend toward more uprooting under wetter conditions. Smith (1946) described the different types of wind disturbance that affect New England. He found that each type has characteristic wind directions that should result in predictable patterns of protected and damaged patches on the landscape. He also reported that 1) local topography influences wind flow, 2) edaphic characteristics control root growth and therefore susceptibility to wind damage, and 3) silvicultural treatment (mixed-age management and thinning) affects wind resistance. Andersen (1954) reviewed the history of gale damage to Scotland (16 storms) and the literature on chronic and acute wind stress. He concluded that 1) topography influences wind and damage, 2) damage increases with tree height, 3) species differ in response, 4) rooting depth influences resistance, and 5) the juxtaposition of different silvicultural treatments can control damage. Brokaw and Walker (1991) presented a summary of damage reported for hurricanes impacting 14 tropical and temperate conifer and broadleaf forests. They found the following: 1) amount of stem breakage as opposed to uprooting varied among forests, sometimes correlated with stem size; 2) in some cases there is a bimodal distribution of damage versus stem diameter, large trees being more likely to be directly damaged by the wind and small trees more likely to be indirectly damaged; 3) previous mechanical damage to trees may increase subsequent wind damage; 4) no clear relationship exists between damage of conifers versus that of broadleaf plants, or monocots versus dicots; 5) species differ in impacts, but no clear generalizations exist such as correlations with successional class; 6) there is no clear correlation between topographic exposure and severity of damage; and 7) although structural damage is high, mortality is generally low. Lugo et al. (1983) compared hurricanes to other natural disturbances. They proposed that

hurricanes have a greater impact than either earthquakes or landslides, because of higher frequencies and larger areas affected. Yet they also predicted faster recovery from hurricane effects, because of adaptations to these frequent disturbances. Tanner et al. (1991), in a summary of impacts of hurricanes on forest ecosystems in the Caribbean, stated that the effects on ecosystems depend on four things: 1) hurricane intensity (including rainfall), 2) storm size and movement, 3) topography, and 4) susceptibility of the system to damage.

An overall conclusion from reviewing these papers is that generalizations are lacking. A barrier to comparing impacts of wind events is the lack of standard measures for storm intensity (Lugo et al., 1983). Another impediment to generalizations concerning impacts of catastrophic winds is a failure to standardize measures of impacts. Ackerman et al. (1991), reporting the results of a conference on ecological effects of hurricanes, mention measures of damage gradients as one missing research tool. Thus we review both results and methodological issues, and we recommend methods that we feel will provide comparative results. In particular, we develop further Everham's (1995) suggestion that quantifying wind disturbance and expressing damage as both percent mortality and percent basal area damaged will facilitate comparisons among systems.

## III. Literature Review

We reviewed 119 papers reporting the impacts of 100 storms in 20 countries and in 21 states in the United States. Table I is a summary of the storms, locations, and references, with indications of the efforts in each study to quantify the storm intensity or damage. The table is organized chronologically by storm event. In several cases, more than one paper reports on the same storm in the same forest. All were included whenever there are differences in plot location, sampling methodology, or analysis. For our review we have converted all measurements to metric equivalents.

### A. STORM INTENSITY

As mentioned above, our first question in assembling this review was, How should catastrophic wind intensity be quantified? Among the papers we reviewed, 101 included some description of storm intensity, usually either maximum wind gusts or average wind speed. Figure 1 represents the ranges of wind speed for each of four types of catastrophic wind events: windstorms, gales, hurricanes, and tornadoes (see literature cited for Table I). Several authors, however, mention that the critical factor in wind disturbance is gustiness; pulses of wind can cause more damage than a steady wind (Conrad, 1945; Cremer et al., 1977, 1982; Moss, 1940; Smith, 1946; Steven, 1953b; Webb, 1986; Wyman, 1954b). Therefore, the actual stress perceived at the point of assessment of damage is difficult to quantify. Few papers indicate the distance from the study site to the site where wind was measured and/or distance from the eye of the storm (Oliver & Mayhead, 1974). Francis and Gillespie (1993) propose that storms that increase quickly to maximum wind speed may result in more damage, as the trees do not defoliate first.

Lugo et al. (1983) suggest that duration of hurricane winds and wind speed would be a minimum standard for comparison and that this might help separate differences in damage due to ecosystem response from those due to variations in the intensity of the "stressor." However, wind intensity of particular storms may vary significantly over scales of kilometers (Boose et al., 1994; Canham, 1978), and the lack of detailed local meteorological data has made comparisons difficult (Tanner et al., 1991). Scatena and

### Table I

Catastrophic wind events

| Year | Storm | Location | Citation | Storm intensity | Quantify damage |
|------|-------|----------|----------|-----------------|-----------------|
| 1635 | Hurricane | New England, USA | Perley, 1891 | Yes | No |
| 1703 | Gale | Britain | Andersen, 1954 | No | Yes |
| 1788 | Gale | New England, USA | Perley, 1891 | Yes | No |
| 1815 | Hurricane | USA | Darling, 1842 | Yes | Yes |
| | | | Perley, 1891 | Yes | Yes |
| | | | Moss, 1940 | No | No |
| | | MA, USA | Oliver & Stephens, 1977 | No | Yes |
| 1821 | Hurricane | New England, USA | Redfield, 1831 | Yes | No |
| 1826 | Gale | Scotland | Andersen, 1954 | No | Yes |
| 1838 | Gale | Britain | Andersen, 1954 | No | No |
| 1860 | Gale | Scotland | Andersen, 1954 | Yes | No |
| 1868 | Gale | Scotland | Andersen, 1954 | No | No |
| 1879 | Gale | Scotland | Andersen, 1954 | No | Yes |
| 1880 | Windstorm | OR, WA, USA | Decker et al., 1962 | Yes | No |
| 1882 | Gale | Scotland | Andersen, 1954 | Yes | Yes |
| 1883 | Gale | Scotland | Andersen, 1954 | No | Yes |
| 1883 | Angin Besar | Malaysia | Wyatt-Smith, 1954 | No | No |
| | | | Browne, 1949 | No | No |
| 1884 | Gale | Scotland | Andersen, 1954 | Yes | Yes |
| 1893 | Gale | Britain | Andersen, 1954 | Yes | Yes |
| 1894 | Gale | Britain | Andersen, 1954 | Yes | Yes |
| 1911 | Gale | Scotland | Andersen, 1954 | Yes | Yes |
| 1913 | Windstorm | OR, USA | Weidman, 1920a | No | Yes |
| 1914 | Windstorm | OR, USA | Smith & Weitknecht, 1915 | Yes | Yes |
| | | | Weidman, 1920a, 1920b | No | Yes |
| 1916 | Windstorm | Ireland | Gallagher, 1974 | No | No |
| 1916 | Windstorm | NY, USA | Behre, 1921 | No | Yes |
| 1918 | Windstorm | OR, USA | Weidman, 1920b | No | Yes |
| 1920 | Windstorm | OR, USA | Weidman, 1920b | Yes | Yes |
| | | | Decker et al., 1962 | Yes | Yes |
| 1927 | Gale | Scotland | Andersen, 1954 | Yes | No |
| 1928 | San Felipe | Puerto Rico | Bates, 1930 | Yes | No |
| | | | Weaver, 1989, 1986 | Yes | No |
| 1931 | San Nicolas | Puerto Rico | Weaver, 1986 | Yes | No |
| 1932 | San Cipriano | Puerto Rico | Weaver, 1989, 1986 | Yes | No |
| 1934 | Windstorm | MN, USA | Hansen, 1937 | Yes | Yes |
| 1935 | Hurricane | FL, USA | Craighead & Gilbert, 1962 | Yes | No |
| 1936 | Cyclone | New Zealand | Shaw, 1983 | No | No |
| 1936 | Windstrom | Ireland | Gallagher, 1974 | No | No |
| 1937 | Gale | Britain | Andersen, 1954 | Yes | No |
| 1938 | Windstorm | Ireland | Gallagher, 1974 | No | No |
| 1938 | Hurricane | MA, CT, USA | Curtis, 1943 | No | No |
| | | NH, USA | Peart et al., 1992 | No | Yes |

**Table I** (continued)

Catastrophic wind events

| Year | Storm | Location | Citation | Storm intensity | Quantify damage |
|---|---|---|---|---|---|
| | | MA, USA | Rowlands, 1941 | Yes | Yes |
| | | | Spurr, 1956 | Yes | Yes |
| | | | Foster, 1988a, 1988b | Yes | Yes |
| | | | Foster & Boose, 1992 | Yes | Yes |
| | | New England, USA | Brooks, 1938, 1939a, 1939b, 1939c | Yes | Yes |
| | | | Butler, 1938 | Yes | Yes |
| | | | Cheston, 1940 | Yes | Yes |
| | | | Clapp, 1938 | No | Yes |
| | | | Felt, 1939 | No | No |
| | | | Meyer & Plusin, 1945 | No | Yes |
| | | | Bromley, 1939 | Yes | No |
| | | | Butler, 1938 | No | Yes |
| | | | Felt, 1939 | No | Yes |
| | | | Moss, 1940 | Yes | No |
| | | | Patric, 1974 | Yes | Yes |
| 1940 | Windstorm | Ireland | Gallagher, 1974 | No | No |
| 1943 | Windstorm | Ireland | Gallagher, 1974 | No | No |
| 1944 | Windstorm | Ireland | Gallagher, 1974 | No | No |
| 1944 | Hurricane | New England, USA | Conrad, 1945 | No | No |
| | | | Smith, 1946 | Yes | Yes |
| 1945 | Cyclones | Mauritius | King, 1945 | Yes | Yes |
| 1948 | Gale | New Zealand | Irvine, 1970 | Yes | No |
| 1949 | Windstorm | WI, MI, USA | Stoeckeler & Arbogast, 1955 | Yes | Yes |
| 1950 | Windstorm | NJ, USA | Reiners & Reiners, 1965 | No | Yes |
| | | | Eynon, 1951 | No | Yes |
| 1951 | Gale | Scotland | Andersen, 1954 | Yes | Yes |
| 1951 | Windstorm | OR, USA | Decker et al., 1962 | Yes | Yes |
| 1953 | Gale | Scotland | Andersen, 1954 | Yes | Yes |
| | | | Steven, 1953b | Yes | Yes |
| 1954 | Hazel | VA, USA | Trousdell, 1955 | Yes | Yes |
| 1954 | Carol | MA, USA | Wyman, 1954a | Yes | Yes |
| | | New England | Wyman, 1954b | No | No |
| 1955 | Windstorm | Ireland | Gallagher, 1974 | Yes | Yes |
| 1956 | Agnes | Australia | Webb, 1958 | Yes | No |
| 1956 | Betsy | Puerto Rico | Wadsworth & Englerth, 1959 | Yes | Yes |
| 1957 | Audrey | TX, USA | Nelson & Stanley, 1959 | Yes | Yes |
| 1957 | Gale | Ireland | Cruickshank et al., 1962 | Yes | Yes |
| | | | Gallagher, 1974 | Yes | Yes |
| 1959 | Cyclone | New Zealand | Shaw, 1983 | Yes | No |
| | | | Conway, 1959 | Yes | Yes |
| 1959 | Gale | Ireland | Cruickshank et al., 1962 | Yes | Yes |
| | | | Simpson, 1965 | No | Yes |

| Year | Storm | Location | Citation | Storm intensity | Quantify damage |
|---|---|---|---|---|---|
| 1960 | Donna | FL, USA | Craighead & Gilbert, 1962 | Yes | Yes |
| | | VA, NC, USA | Trousell et al., 1965 | Yes | Yes |
| 1960 | Alix, Carol | Mauritius | Sauer, 1962 | Yes | Yes |
| 1961 | Hurricanes | Western Samoa | Wood, 1970 | Yes | Yes |
| 1961 | Hattie | Belize | Wolffsohn, 1967 | Yes | Yes |
| 1961 | Hurricane | Ireland | Cruickshank et al., 1962 | Yes | Yes |
| | | | Gallagher, 1974 | Yes | Yes |
| 1962 | Hurricane | CA, USA | Boe, 1965 | Yes | Yes |
| | | WA, USA | Wiley, 1965 | Yes | Yes |
| | | OR, USA | Decker et al., 1962 | Yes | Yes |
| 1963 | Tornado | IN, USA | Webster, 1963 | No | No |
| 1965 | Betsy | MS, USA | Gunter & Eleuterius, 1971 | No | No |
| 1966 | Hurricane | Western Samoa | Wood, 1970 | Yes | Yes |
| 1967 | Annie | Soloman Islands | Whitmore, 1974, 1989 | Yes | Yes |
| 1968 | Gale | Scotland | Holtam, 1971 | Yes | Yes |
| 1968 | Gale | New Zealand | Irvine, 1970 | Yes | Yes |
| 1968 | Giselle | New Zealand | Shaw, 1983 | Yes | No |
| 1969 | Windstorm | Rwanda | Spinage & Guinness, 1971 | No | Yes |
| 1969 | Camille | MS, USA | Touliatos & Roth, 1971 | Yes | Yes |
| | | | Gunter & Eleuterius, 1971 | Yes | Yes |
| | | | Van Hooser & Hedlund, 1969 | No | Yes |
| | | | Nonnemacher, 1970 | Yes | Yes |
| 1973 | Windstorm | CO, USA | Veblen et al., 1989 | Yes | Yes |
| 1973 | Gale | Britain | Oliver & Mayhead, 1974 | Yes | No |
| 1974 | Windstorm | Ireland | Gallagher, 1974 | Yes | Yes |
| 1974 | Windstorm | Australia | Cremer et al., 1977 | Yes | Yes |
| 1975 | Tornado | MI, USA | Brewer & Merritt, 1978 | No | No |
| 1975 | Gale | New Zealand | Wilson, 1976 | Yes | Yes |
| 1975 | Allison | New Zealand | Shaw, 1983 | Yes | No |
| 1975 | Eliose | FL, USA | Wilkinson et al., 1978 | Yes | Yes |
| 1977 | Windstorm | WI, USA | Dunn et al., 1983 | Yes | Yes |
| 1977 | Windstorm | South Africa | Versfeld, 1980 | Yes | Yes |
| 1978 | Cyclone | Sri Lanka | Dittus, 1985 | Yes | Yes |
| 1979 | David | Dominica | Lugo et al., 1983 | Yes | Yes |
| 1979 | David Frederic | Puerto Rico | Liegel, 1982, 1984 | Yes | Yes |
| 1980 | Allen | Jamaica | Thompson, 1983 | Yes | Yes |
| 1981 | Windstorm | OR, USA | Greene et al., 1992 | No | Yes |
| 1982 | Windstorm | MN, USA | Webb, 1986, 1988, 1989 | No | Yes |
| 1982 | Bernie | New Zealand | Shaw, 1983 | Yes | Yes |
| 1983 | Tornado | TX, USA | Glitzenstein & Harcombe, 1988 | Yes | Yes |
| 1983 | Tornado | NY, USA | Pickering, 1986 | No | Yes |
| 1985 | Tornado | PA, USA | Peterson & Pickett, 1991 | Yes | Yes |

**Table I** *(continued)*

Catastrophic wind events

| Year | Storm | Location | Citation | Storm intensity | Quantify damage |
|---|---|---|---|---|---|
| 1985 | Kate | GA, USA | Engstrom & Evans, 1990 | Yes | Yes |
| 1986 | Winifred | Australia | Applegate & Bragg, 1992 | Yes | Yes |
| | | | Turton, 1992 | Yes | Yes |
| | | | Hopkins & Graham, 1987 | Yes | No |
| 1987 | Windstorm | Britain | Allen, 1992 | Yes | Yes |
| 1988 | Bola | New Zealand | Ogden et al., 1991 | No | Yes |
| 1988 | Gilbert | Jamaica | Bellingham et al., 1992 | Yes | Yes |
| | | | Bellingham, 1991 | Yes | Yes |
| | | | Wunderle et al., 1992 | Yes | Yes |
| | | | Barker & Miller, 1990 | Yes | Yes |
| 1988 | Gilbert | Mexico | Wigham et al., 1991 | No | Yes |
| 1988 | Joan | Nicaragua | Boucher et al., 1990 | Yes | Yes |
| | | | Boucher, 1990; Yih et al., 1991 | Yes | Yes |
| 1989 | Hugo | SC, USA | Putz & Sharitz, 1991 | Yes | Yes |
| | | | Sheffield & Thompson, 1992 | Yes | Yes |
| | | | Gresham et al., 1991 | Yes | Yes |
| | | | Hook et al., 1991 | Yes | Yes |
| 1989 | Hugo | Virgin Islands | Reilly, 1991 | Yes | Yes |
| | | Puerto Rico | Walker et al., 1992; Walker, 1991 | Yes | Yes |
| | | | Basnet, 1990; Basnet et al., 1992 | Yes | Yes |
| | | | Frangi & Lugo, 1991 | Yes | Yes |
| | | | Brokaw & Grear, 1991 | Yes | Yes |
| | | | You & Petty, 1991 | No | Yes |
| | | | Fernandez & Fetcher, 1991 | No | Yes |
| | | | Lodge et al., 1991 | No | Yes |
| | | | Scatena et al., 1993 | No | Yes |
| | | | Scatena & Lugo, in press | No | Yes |
| | | | Dallmeier et al., 1991 | No | Yes |
| | | | Zimmerman et al., 1994 | No | Yes |
| 1990 | Windstorm | Britain | Allen, 1992 | Yes | Yes |
| 1992 | Andrew | FL, USA | Ogden, 1992 | Yes | No |
| | | | Pimm et al., 1994 | Yes | Yes |
| | | | Smith et al., 1994 | No | Yes |
| | | | Loope et al., 1994 | No | Yes |

Larsen (1991) developed three indices of storm intensity: 1) maximum sustained wind and storm duration, 2) maximum sustained wind and proximity to the storm, and 3) rainfall totals (as percentage of annual average). Each of these indices represents a different view of hurricane impact: total storm energy, impact at a specific point, and relative rainfall, respectively.
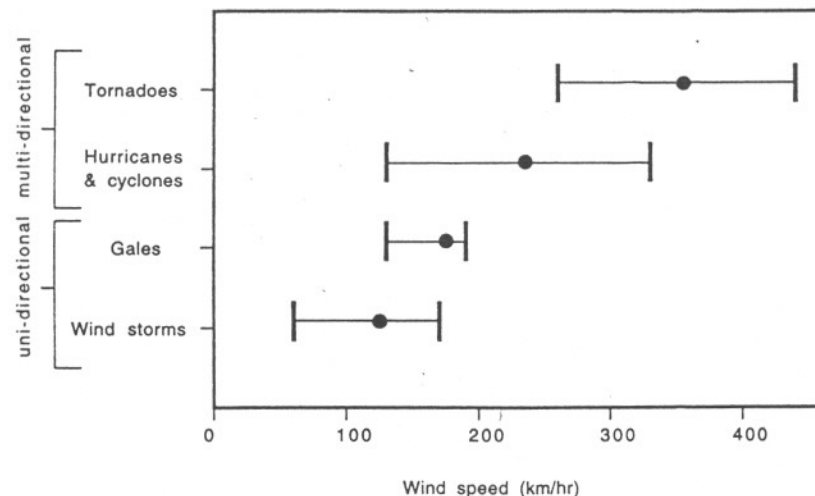


**Fig. 1.** Intensity of catastrophic wind events. References from Table I. Average for all reported intensities for each category plotted as solid circles, with vertical bars representing the maximum and minimum reported values.

### B. QUANTIFYING DAMAGE

Our second question was, How should catastrophic wind damage be quantified? There is little consistency in the methodologies used to quantify damage and assess recovery. Sampling plots vary from 2.5 m² (litterfall studies) to 16 ha and include circular plots, rectilinear plots, gridded plots, and transects. Minimum stem diameters range from 2 to 20 cm dbh. The delay in sampling after the storm varies from ten days to thirteen years (not including analysis of historical storm data). The greatest variation of methodology is in the parameters used to quantify damage. For example, of the 48 papers reviewed in Everham (1995) that included quantification of damage, 28 different schemes or methodologies were used, including such difficult-to-convert measures as "trees/chain of perimeter" (Alexander, 1964, 1967). Clearly, there are no standards for assessing impacts of catastrophic winds. One obvious explanation is that few researchers design experiments that anticipate naturally occurring catastrophic events. Instead, they capitalize on studies established before the disturbance or on surveys afterward (Lugo et al., 1983; Tanner et al., 1991).

Efforts to quantify damage can be classified into six types: 1) stem damage, 2) branch damage, 3) canopy damage, 4) mortality, 5) volume or mass changes, and 6) classification categories (using one or more of the above to set arbitrary damage categories of high, low, etc.). These types are not mutually exclusive. Many authors used more than one to describe the damage of catastrophic wind, but none reported damage in all six categories. Table II includes a summary of the different damage quantification methods reviewed. The variation in quantification techniques increases the difficulty of developing generalizations.

**Table II**

Summary of damage quantification

| Forest | Snap | Uproot | Branch | Canopy | Dead | Loss | Citation |
|---|---|---|---|---|---|---|---|
| Temperate hardwood | — | — | — | 20 | — | — | Peart et al., 1992[d] |
| Temperate hardwood | — | — | — | — | — | 20 | Steel, 1989[b] |
| Temperate hardwood | 4.6 | 16.8 | — | — | — | 21.4 | Reiners & Reiners, 1965[a,b] |
| Temperate conifer | 2.1 | 3.6 | 0.07 | — | 5.6 | — | Webb 1989, 1988[a] |
| Temperate conifer | — | — | — | — | 15.3 | 7.4 | Greene et al., 1992 |
| Temperate conifer | —6.1— | | — | — | — | 8.8 | Trousdell, 1955 |
| Temperate conifer | —13.2— | | — | — | — | — | Weidman, 1920a[b] |
| Temperate conifer | — | — | — | — | — | 17.5 | Smith & Weitknecht, 1915 |
| Temperate conifer | —28— | | — | — | — | 28 | Hansen, 1937b |
| Temperate conifer | 5.2 | 25.3 | — | — | — | 30.5 | Boe, 1965 |
| Temperate conifer | — | — | — | 57 | — | 66 | Veblen et al., 1989 |
| Temperate conifer | —67— | | — | — | — | 80 | Hook et al., 1991 |
| Temperate conifer | —97— | | — | — | — | — | Gunter & Eleuterius, 1971 |
| Temperate conifer | 33 | 66 | — | 99 | 93 | — | Peterson & Pickett, 1991 |
| Temperate mixed | 0.4 | 0.1 | 0.02 | — | 0.3 | — | Webb, 1989, 1988a |
| Temperate mixed | — | — | — | — | — | 2 | Ogden et al., 1991 |
| Temperate mixed | —3.2— | | — | — | — | — | Stoeckler & Arbogast, 1955 |
| Temperate mixed | —5— | | — | — | — | — | Behre, 1921 |
| Temperate mixed | 15 | — | — | — | — | — | Gallagher, 1974 |
| Temperate mixed | —24— | | — | — | — | — | Cruinkshank et al., 1962 |
| Temperate mixed | — | — | — | — | — | 24 | Oliver & Stephens, 1977[d] |
| Temperate mixed | — | — | 25 | — | — | 28 | Sheffield & Thompson, 1992[b] |
| Temperate mixed | — | — | — | — | — | 44 | Oliver & Stephens, 1977d |
| Temperate mixed | 17.3 | 14.3 | — | — | — | 48.7 | Putz & Sharitz, 1991 |
| Temperate mixed | —66— | | — | — | — | 50 | Spurr, 1956[c] |
| Temperate mixed | —54— | | — | 65 | 29 | 55 | Glitzenstein & Harcombe, 1988[b] |
| Temperate mixed | —52— | | — | — | — | — | Foster & Boose, 1992[b] |
| Temperate mixed | —89— | | — | — | — | — | Hook et al., 1991 |
| Temperate mixed | —53— | | — | — | — | 91 | Pickering, 1986 |
| Temperate mixed | —44— | | — | — | 30.7 | 94 | Foster, 1988b[b] |
| Temperate mixed | —70— | | — | — | — | — | Gunter & Eleuterius, 1971 |

**Table II** *(continued)*

Summary of damage quantification

| Forest | Snap | Uproot | Branch | Canopy | Dead | Loss | Citation |
|---|---|---|---|---|---|---|---|
| Temperate mixed | —89— | | — | — | — | 94 | Dunn et al., 1983 |
| Temperate coastal | —11— | | — | 27 | — | — | Gresham et al., 1991 |
| Temperate swamp | 6.5 | 3.8 | — | — | — | 19.0 | Putz & Sharitz, 1991 |
| Temperate pine plant | —7.1— | | — | — | — | 7.1 | Cremer et al., 1977[a] |
| Temperate pine plant | 1.7 | 6.9 | — | — | — | 7.1 | Versfeld, 1980[a] |
| Temperate pine plant | — | — | — | — | — | 7.5 | Simpson, 1965 |
| Temperate mixed plant | —32— | | — | — | — | — | Wilson, 1976[b] |
| Subtropical mixed | — | — | — | 70 | — | — | Craighead & Gilbert, 1962 |
| Subtropical pine | — | — | — | — | 5.5 | — | Wilkinson et al., 1978 |
| Subtropical pine | —31— | | — | 100 | — | — | Loope et al., 1994[c] |
| Subtropical hardwood | —25— | | — | 100 | — | — | Loope et al., 1994c |
| Tropical mixed plant | 38.7 | 8.4 | — | — | — | 47.1 | Thompson, 1983b |
| Tropical pine plant | — | — | — | — | — | 23 | Wunderle et al., 1992[a] |
| Tropical pine plant | —37.5— | | — | — | 7.5 | 36 | Liegel, 1982, 1984 |
| Tropical pine plant | —65— | | — | — | — | — | King, 1945[b] |
| Tropical plantation | — | — | — | — | 25 | — | Sauer, 1962 |
| Tropical pine forest | —44— | | — | — | 58 | — | Boucher, 1990 |
| Tropical wet | 8.5 | 5.8 | — | 14.1 | 8.1 | 20 | Bellingham, 1991[b] |
| Tropical wet | 2 | 2.5 | — | 29 | 1 | 10 | Frangi & Lugo, 1991 |
| Tropical wet | 11 | 9 | 13 | 56 | 7 | — | Walker, 1991[b] |
| Tropical wet | 7.5 | 6.9 | — | — | 9 | 16.7 | Zimmerman et al., 1994 |
| Tropical wet | 17 | 16.5 | 30.5 | 78 | — | — | Walker et al., 1992 |
| Tropical wet | —30— | | — | — | — | — | Wadsworth & Englerth, 1959[b] |
| Tropical wet | 8.2 | 30 | — | — | 25 | — | Dallmeier et al., 1991 |
| Tropical wet | — | — | — | — | — | 20.8 | Wunderle et al., 1992[a,b] |
| Tropical wet | —36.9— | | — | 15 | — | — | Whitmore, 1974, 1989[b] |
| Tropical wet | —37— | | — | — | — | 32 | Applegate & Bragg, 1992[b] |
| Tropical wet | 6 | 43 | 34 | 99 | — | 41 | Basnet et al., 1992 |
| Tropical wet | 12.3 | 43 | — | 23 | 7 | — | Bellingham et al., 1992 |
| Tropical wet | — | — | — | — | — | 50 | Scatena et al., 1993 |
| Tropical wet | 24 | 33.5 | — | — | 2 | 57.5 | Lugo et al., 1983[a,b] |
| Tropical wet | —75— | | — | — | 13 | — | Boucher, 1990 |
| Tropical wet | —80— | | — | 82 | — | — | Yih et al., 1991b |

**Table II** *(continued)*

Summary of damage quantification

| Forest | Snap | Uproot | Branch | Canopy | Dead | Loss | Citation |
|---|---|---|---|---|---|---|---|
| Tropical wet | —80— | | — | — | 23 | — | Boucher, 1989 |
| Tropical moist | — 9— | | — | — | — | — | Reilly, 1991a,b |
| Tropical mangrove | — | — | — | — | 40 | — | Craighead & Gilbert, 1962[a] |
| Tropical mangrove | — | — | — | — | — | 40 | Wunderle et al., 1992[a,b] |
| Tropical seasonal | — | — | — | — | — | 90 | Wolffsohn, 1967 |
| Tropical dry | 8 | 2 | — | — | 1 | 15 | Lugo et al., 1983[a] |
| Tropical dry | — | — | — | — | — | 8.5 | Wunderle et al., 1992[a,b] |
| Tropical dry | — | 32 | — | 33 | 40 | — | Dittus, 1985 |
| Tropical dry | 11.5 | 4 | 77 | 100 | 9.7 | — | Whigham et al., 1991 |

— = not reported and could not be determined; [a] not reported directly, calculated from data; [b] values averaged for more than one site; [c] estimated; [d] reconstructed data.

## 1. Stem Damage

Stem damage is most commonly reported as percent of downed trees, referred to as windthrow, blowdown, windfall, or windblow. These terms are ambiguous and do not distinguish between stem breakage and uprooting (Schaetzl et al., 1989b). Secondarily, these types of damage are often differentiated as uprooting, breakage, and bending or leaning. Most authors use actual counts from established plots, but aerial surveys and area estimates are reported also (Wilson, 1976). These numbers may be given as raw counts (Versfeld, 1980) without pre-disturbance stem numbers or densities, or as percentages. Researchers vary in their inclusion of leaning or bent stems to include. Wilkinson et al. (1978) used twelve categories of stem lean, four categories of stem damage, and four categories of root exposure, in addition to categories relating to crown damage. Gresham et al. (1991) set eight categories from undamaged stems to downed stems. Scatena and Lugo (In press) used three main categories: little damage, standing damage, and down damage; but the standing category had nine subcategories and the prone category had five. Brewer and Linnartz (1973) suggest that a 45° lean from vertical is a critical point for survival [*Pinus taeda* (L.) stems with less lean had greater than 50% survival].

## 2. Branch Damage

Branch damage is quantified either by counting branches damaged or by assignment to arbitrarily defined categories, and it varies based on the size of the branches assessed. Many researchers set no clear size categories and subjectively grade branch damage. Moreover, when these clearly defined categories are applied to standing damaged trees, the assessment of branch diameters from the ground is subjective. Different minimum branch sizes, unquantified branch sizes, and categorization of damage all make it difficult to compare branch damage values.

## 3. Canopy Damage

Canopy damage may be quantified directly from estimates of structure loss or defoliation or may be determined indirectly using techniques to measure structure or changes in light levels. Both Whitmore (1989) and Glitzenstein and Harcombe (1988) attempted to determine directly the percent canopy change for an entire study area. Whitmore (1989) scored each plot as gap, building, or mature, and was then able to determine the percent of the area in gaps. Glitzenstein and Harcombe (1988) used aerial photographs to determine the percent cover after a tornado. Frangi and Lugo (1991) scored each stem for percent defoliated. More typically, researchers establish several categories for scoring canopy damage on each stem. This categorization of canopy damage makes it difficult to determine an overall average for the disturbed site.

Canopy change has been assessed indirectly by measuring changes in light levels. Turton (1992) used hemispheric photography to determine the percent change in available light at the forest floor. Veblen et al. (1989), Fernandez and Fetcher (1991), and Walker et al. (1992) all measured light levels after wind disturbance; only the latter team used a site established before the storm and was able to quantify changes. Whitmore (1989) used photographs to assess canopy damage and monitor recovery of specific trees. No effort was made to determine an average for the area of study. Applegate and Bragg (1992) also used photographs to monitor recovery of the canopy, but no attempt was made to quantify these changes. Changes in canopy structure have been measured more directly by estimating vegetation cover at different heights above ground to produce vegetation profiles (Brokaw & Grear, 1991; Wunderle et al., 1992). Measures both of light levels and of vegetation profiles promise to give clearer averages of canopy changes, if measurements are made before and after the disturbance.

## 4. Mortality

Mortality measurements pose a number of problems. Mortality is often assumed to be the same as blowdown, which may be reasonable for some coniferous forests but is not for many broadleaf forests, particularly in the tropics, where percent resprouted stems may be as high as 64.8% of dicot stems (Zimmerman et al., 1994), 87% of snapped stems (Boucher, 1990), or 56% of all trees (Bellingham et al., 1992). No clear relationship exists between damage and mortality.

When and how mortality is assessed influences the values found. For example, post-disturbance mortality appears to be elevated for months to years after catastrophic wind (Bellingham, 1991; Craighead & Gilbert, 1962; Dittus, 1985; Putz & Chan, 1986; Sauer, 1962; Smith et al., 1994; Veblen et al., 1989; Wiley, 1965), invalidating immediate post-disturbance estimates. Shaw (1983) reports that "overmature" trees may survive a storm but rapidly decline and die from even minor damage. Webster (1963) found increased windfall and mortality in subsequent months, for trees that were damaged by a tornado. Walker (1995) suggests that "mortality estimates made before trees begin to sprout after a hurricane may be too high.... Estimates made during the intermediate period of vigorous sprouting may be too low if damaged trees continue to die." Often, assessment of storm-associated mortality can be obscured by standing dead trees that died

before the storm event. Most researchers appear to determine subjectively whether a stem was previously dead or was killed by the storm.

Thirty-three of the papers reviewed by Everham (1995) that quantified damage did not include measures of mortality. This leads to a potential misunderstanding of the impacts of catastrophic wind damage; for example, O'Brien et al. (1992) ran computer simulations of hurricane damage with 100% mortality, although hurricane mortality never reaches that level. Mortality should be tracked for several years after catastrophic wind events to determine the extent of elevated mortality.

### 5. Volume or Mass Changes

Volume losses are typically reported by foresters concerned with timber yield. Often, estimates of volume lost are reported without corresponding estimates of undamaged timber or conversion to percent loss. Biomass, or related measures such as basal area, are often measured or estimated by ecologists interested in energy or nutrient flows. Again, undamaged biomass, estimates of pre-disturbance levels, and totals from undisturbed areas are generally not reported. Sheffield and Thompson (1992) included a detailed assessment of the impacts of Hurricane Hugo on forests in South Carolina. Their assessment is based on volume losses but includes pre-hurricane levels, pre-hurricane mortality, hurricane mortality, non-lethal hurricane damage, and an elaborate post-hurricane risk assessment that is forest- and age-class specific and includes consideration of crown loss, root damage, stem damage, and salt burn.

### 6. Classification Categories

Five of the papers reviewed by Everham (1995), and five other papers (Hook et al., 1991; Shaw, 1983; Smith et al., 1994; Touliatos & Roth, 1971; Wiley, 1965), included an overall damage categorization that could be used for comparing spatial patterns of damage. As might be expected, no two categorizations were the same. These schemes use three to five categories of percentages of types of stem damage. Although this type of categorization may facilitate analysis of spatial patterns, unless overall average values of damage are given, comparisons among sites and events are difficult.

### 7. Summary of Damage Quantification

Apparent severity of damage from catastrophic wind can vary depending on how damage is measured, which, in turn, reflects the different goals of researchers. In addition, different methodologies may influence results even when the same measure is used. Measurements of damage severity are sensitive to species distributions and to stem size. Species differences are most pronounced when differences in types of stem damage or in stem and branch damage are considered. These inconsistencies make it difficult to develop generalizations about catastrophic wind disturbance; any standard for quantifying damage should minimize these influences. Therefore, a summary damage parameter that incorporates all types of stem damage would tend to minimize the species effects. One approach to eliminating the problem of using different minimum stem sizes would be reporting data at a variety of stem sizes from the smallest stems up. Comparisons could then be made using the larger stem classes, common to more studies. Another approach would be to use a damage parameter that is less sensitive to change in minimum stem size. For example, basal area calculations minimize the effect of small stems and therefore vary little with changes in the

minimum stem size. Pickett and White (1985) suggest either biomass destroyed or individuals killed as possible measures of disturbance effects.

A single general measure of structural damage, such as basal area lost, may not be adequate to describe changes to a forest and, in particular, predict the path of recovery. Boucher et al. (1990) reported an inconsistency between damage and recovery from Hurricane Joan in Nicaragua: "Damage to pine forests was considerably less than to rain forests," but "long-term prospects for [the recovery of] rain forest areas ... [are] brighter." In the rain forest, 75% of the stems were broken or uprooted compared to 44% of the stems in the pine forest, but mortality in the pine forest was 58% compared to only 13% in the rain forest. The rain forest was more greatly affected only if damage is quantified by percent stems lost. But in terms of mortality, the rain forest was less affected and its more rapid recovery is predictable.

The effects of a given catastrophic wind event might best be expressed as a combination of a general measure of structural damage (percent basal area or percent stems lost) and a measure of potential compositional change (percent mortality). Figure 2 diagrams this concept with a comparison of 20 disturbed forests. The points on this graph are located using percent mortality and percent stem damage or basal area lost. Several trends are evident: 1) mortality tends to be concentrated at the lower end of the gradient, 2) structural damage is distributed throughout the gradient, and 3) the region of gradient space defined by high mortality and low structural damage rarely exists. The maximum reported hurricane mortality is for a pine forest in Nicaragua (Boucher et al., 1990; "11" in Fig. 2). The highest structural damage attributed to a hurricane is 94% for the 1938 storm in New England (Foster, 1988b; based on estimated basal areas before and after the hurricane; "5" in Fig. 2). The highest reported structural and compositional damage both occur in a tornado-impacted temperate forest in Pennsylvania (Peterson & Pickett, 1991; "20" in Fig. 2).

To examine adaptations to wind, we must be able to standardize how we examine damage. Three recommendations can be made to facilitate comparisons. First, data reported with separate categories for size classes, vegetative types (conifer, broadleaf; early or late successional), and damage classifications would facilitate comparisons of the impacts of wind. Second, effort should be made to quantify undamaged trees or to provide estimates of pre-disturbance forest composition. Neustein (1971) states that "all surveys which did not include undamaged crops are basically weak." Finally, a standard for all researchers reporting average values for their study sites of both structural damage and mortality should help us to compare events and develop general hypotheses about catastrophic wind disturbance.

### C. PATTERN OF DAMAGE

Our third question was, Is catastrophic wind damage homogeneous, or are there patterns of damage, and can these patterns be predicted? Walker et al. (1992), Foster and Boose (1992), and Boose et al. (1994) all mention variation in damage over the landscape either due to proximity to the eye of cyclonic storms or due to shifts in wind direction as the storm passes. At smaller scales, researchers in a variety of forests have noted variation in damage: Putz and Sharitz (1991) for hurricane effects in South Carolina, Bellingham et al. (1992) for hurricane damage in Jamaica, Foster (1988b) and Conrad (1945) for hurricane damage in Massachusetts, Webb (1958) for cyclone damage in Queensland, Shaw (1983) for cyclone damage in New Zealand, Wiley (1965) for hurricane damage in Washington, Browne (1949) for cyclone damage in Malaysia, Steven (1953b) for gale
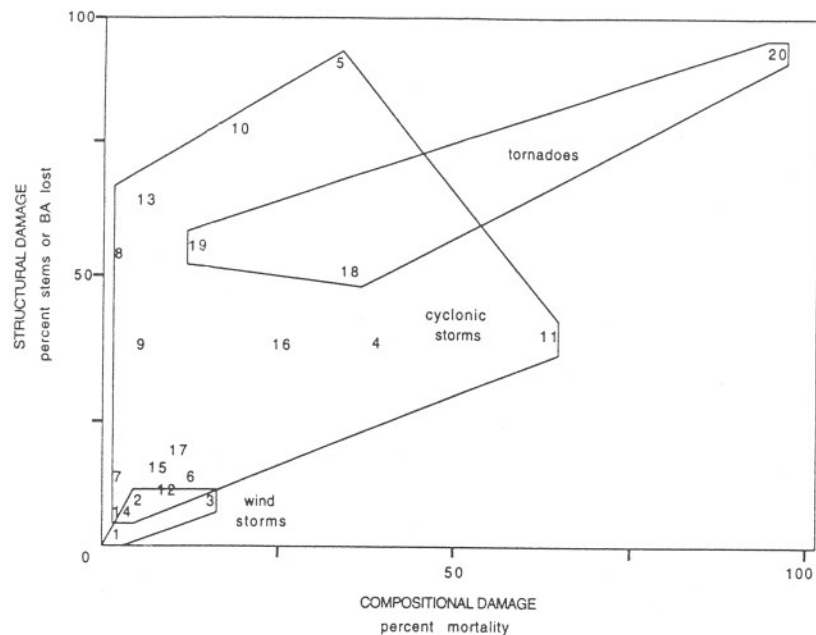
**Fig. 2.** Gradient space for severity of catastrophic wind events. Structural damage is quantified as percent basal area damaged or percent stems damaged. Compositional damage is quantified as percent stems killed. 1, 2: Webb, 1988; 3: Greene et al., 1992; 4: Dittus, 1985; 5: Foster, 1988b; 6: Whigham et al., 1991; 7, 8: Lugo et al., 1983; 9: Liegel, 1984; 10, 11: Boucher, 1989, 1990; 12, 13: Bellingham et al., 1992; 14: Frangi & Lugo, 1991; 15: Walker, 1991; 16: Dallmeier et al., 1991; 17: Zimmerman et al., 1994; 18, 19: Glitzenstein & Harcombe, 1988; 20: Peterson & Pickett, 1991.

damage in Scotland, Stoeckeler and Arbogast (1955) for windstorm damage in Wisconsin, Furley and Newey (1979) for hurricane damage in Belize, Glitzenstein and Harcombe (1988) for tornado damage in Texas, and Weaver (1989) for hurricane-damaged recovering forests in Puerto Rico. Canham (1978) stated that successively more intense winds would tend to topple more successively resistant stems until the whole canopy is opened. However, there is no evidence of homogeneity of damage increasing with increasing intensity of wind.

Minimum gap size caused by wind disturbance varies, but this variation is partly an artifact of methodology. Lorimer (1977) used surveyors' records to quantify historical blowdown patches as small as 25 ha, but proposed that damage may have been much more spotty but not recorded by surveyors. Canham (1978) also used surveyors' data to document windstorm gaps from 0.65 to 3785 ha with a median of 32.4 ha. Ruth and Yoder (1953) reported windstorm damage in gaps down to 0.5 ha. Foster and Boose (1992), using aerial photos, found patches of hurricane damage of 0.04 (their arbitrarily set minimum size) to 35 ha, with most less than 2 ha. Foster (1988b) reported hurricane blowdown as "highly irregular" in size and shape, with gaps as small as 30 m². Webb

(1986) found gaps of 20 to 269 m² in a pine–fir stand, and smaller gaps in a pine–maple stand, following a severe windstorm. Baldwin (1940) found patches "devoid of trees" up to 0.2 ha following the 1938 hurricane. Thus catastrophic windstorms can create damaged patches in a great range of sizes. As Foster (1988b) observed, although there is generally uniform action of wind, local gusts and turbulence produced some otherwise inexplicable patterns of damage and survival.

### D. BIOTIC AND ABIOTIC INFLUENCES ON DAMAGE

Foster and Boose (1992) state that a "relatively small number of variables can be used to explain the damage" in their uncomplicated terrain. These factors can be divided into two groups: biotic and abiotic. Because catastrophic wind research principally involves post-disturbance surveys not coupled with pre-disturbance data, it is difficult to separate biotic and abiotic factors and determine their relative roles in influencing damage, the subject of our fourth question.

#### 1. Biotic Factors

Biotic factors that may influence the severity of wind on forests have been identified for decades; they include: a) stem size, b) stand conditions, c) species differences, and d) tree pathogens (e.g., rot, fungus, and insect infestation) (Bromley, 1939; Busby, 1965; Day, 1950; Hubert, 1918; Smith, 1946; Stoeckeler & Arbogast, 1955).

#### a. Stem Size

Most researchers have found a positive correlation between stem size and catastrophic wind damage. An increased risk for wind damage to larger trees has been observed by the following researchers in their respective areas: Smith and Weitknecht (1915) for windstorm damage in Oregon; Behre (1921) for windstorm damage in New York; Brewer and Merritt (1978) for windstorm and possibly tornado damage in Michigan; Clapp (1938), Rowlands (1941), Curtis (1943), and Foster and Boose (1992) for hurricane damage in New England; King (1945) for cyclone damage in Mauritius; Lines (1953) and Andersen (1954) for gale damage in Scotland; Wadsworth and Englerth (1959) for hurricane damage in Puerto Rico; Neustein (1968) for severe windstorm damage in Scotland; Spinage and Guinness (1971) for windstorm damage in Rwanda; Whitmore (1974) for some species damaged by cyclones in the Solomon Islands; Dunn et al. (1983) for a windstorm in Wisconsin; Harcombe and Marks (1983) for windstorm damage in Texas; Dittus (1985) for cyclone damage in Sri Lanka; and Glitzenstein and Harcombe (1988) for tornado damage in Texas. Some studies report increasing damage with size up to some maximum, where damage stabilizes regardless of further increases in size. Damage ceased to increase above 30 m in height for pine plantations in Australia (Cremer et al., 1977, 1982). Scots pine damage leveled off above the 18 m tall size class, although it continued to increase for broadleaf species in Scotland (Andersen, 1954). Damage ceased to increase in stems above 35 cm dbh for softwoods in South Carolina (Sheffield & Thompson, 1992).

Three studies suggest the possibility of a negative correlation between size and damage. Boucher (1990) reported highest survival in the largest trees, after a hurricane in a rain forest in Nicaragua; yet in Boucher et al. (1990) both damage and mortality showed a unimodal response, with the greatest damage in the medium-size tree class. Alexander (1964) found more damage in understory trees when examining the wind damage to clear cuts in Colorado, but this may have been a unique response to the stand

conditions and thinning history. Cremer et al. (1977), examining the impacts of a windstorm on pine plantations in Australia, reported 15% windthrow in stands 30–35 m, 13% windthrow in stands 35–40 m, and only 9% windthrow in the tallest stands of 40–45 m. However, these tallest stands had the longest history of thinning and may have been more preconditioned to wind. It is possible that the tallest trees were actually more resistant in many of the studies that indicated a positive correlation between tree size and damage, but sample sizes of the largest categories tend to be small and are often pooled over a large range. The actual relationship between tree size and damage may be more complex than a simple linear correlation.

Most studies indicate a unimodal distribution of damage relative to stem size, with the smallest trees sheltered from the wind and the largest trees preconditioned to "weather the storm." Bromley (1939) found that the youngest and the oldest trees survived the 1938 New England hurricane best, while trees 30–100 years old were damaged the most. Peterson and Pickett (1991) found the most uprooting at intermediate (30–40 cm dbh) stem sizes. Both Webb (1958) and Applegate and Bragg (1992) found cyclone damage to a rain forest in Queensland to be concentrated in the intermediate-size stems (10–20 cm dbh, in the former; and to the intermediate canopy layer, with an emergent layer surviving, in the latter). Boe (1965), studying the impact of a hurricane on redwood stands in Northern California, found higher percent damage in intermediate size classes (30–60 cm dbh). Neustein (1971) found gale damage in Scotland increased in trees with stems up to 12 m tall, but then the rate of damage dropped off. Dittus (1985) reported that the highest percentage felled occurred in the canopy layer (0–90%), with lower percentages in both the emergent (10–70%) and the subcanopy layers (0–75%). In Nicaragua, both Boucher (1989) and Yih et al. (1991) reported damage and mortality concentrated in stems of 15–45 cm dbh. Putz and Sharitz (1991) described Hurricane Hugo damage in South Carolina as most severe in the non-dominant trees, with the largest trees receiving crown damage but not snapping or uprooting. Their data for bottomland forest stand shows a peak of damage in the middle (40–80 cm) diameter size class if the two types of stem damage are combined, as is indicated also by some results of a wider survey of hurricane impacts in South Carolina (Sheffield & Thompson, 1992). Dallmeier et al. (1991), studying the impact of Hurricane Hugo in Puerto Rico, found no relationship between stem damage and stem size, but did find correlation between higher crown damage and intermediate stem sizes of 20–30 cm dbh. Frangi and Lugo's (1991) assessment of hurricane damage in Puerto Rico clearly shows a unimodal response, with the greatest damage in the class 12–14 m tall, while the largest size class (24–26 m) suffered mostly defoliation and branch loss. Sauer (1962) found that young (<3 years) and old (>25 years) *Casuarina equisetifolia* L. were relatively less damaged. Glitzenstein and Harcombe (1988: fig. 10) compare five studies based on the average stem diameter and the percent basal area lost. The trend appears to be a positive linear relationship, but if the point for the downburst in Wisconsin is considered an outlier, given its extreme intensity (253 km/hr), the graph could easily be viewed as unimodal. It appears there is ample evidence to support the hypothesis that the largest trees are better able to withstand some catastrophic winds, resulting in a unimodal response curve of stem size versus damage (Fig. 3). But this preconditioning of the largest stems may be obscured by small sample sizes in some studies, and may be unimportant under the most intense wind disturbance.

Especially strong winds may obscure a difference in resistance of different-sized stems (Andersen, 1954; Hook et al., 1991; Mergen, 1954; Wilkinson et al., 1978). The impact of Hurricane Allen on forests in Jamaica is a good example. Where less than 50% of the



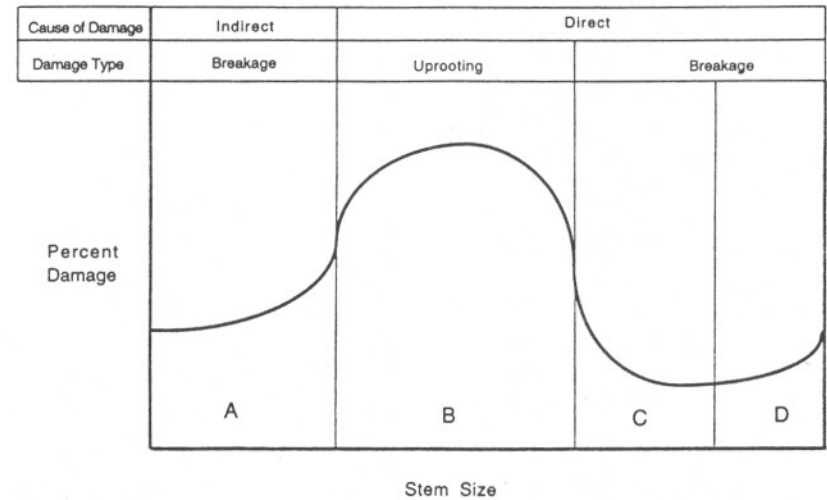| Cause of Damage | Indirect | Direct | | |
|---|---|---|---|---|
| Damage Type | Breakage | Uprooting | | Breakage |

Fig. 3. Proposed relationship between stem size and severity of damage, damage type, and cause of damage, in a mixed-age forest. A: Small stems protected from the wind but damaged indirectly by other falling stems and branches. B: Greatest damage in intermediate size classes exposed to the direct impact of the wind, but not yet preconditioned. Higher proportion of stems uprooted. C: Larger stems that are exposed to the wind but have been preconditioned and previously thinned by wind. Higher proportion of snapped stems. D: Overmature trees may increase in damage due to presence of pathogens.

stems were damaged, the remaining stems were larger than average, possibly indicating the survival of the largest stems. If the damage was greater than 50%, the surviving stems were smaller than average, possibly reflecting the removal of the largest stems and a downward shift in average stem size (Thompson, 1983). Depending on sample size and the size categories used in the analysis, very different conclusions might be drawn.

Four studies in three areas indicate a bimodal relationship between size and damage. Baker (1915) found that large trees (203–254 cm dbh) tended to be damaged more directly by wind during storms in Washington, while small stems were more affected by falling trees and branches. Thus the intermediate stem sizes were less damaged, although Baker did note that the very largest stems (>254 cm dbh) were relatively windfirm. Webb (1989) found size related to wind damage but not to mortality in her Minnesota study. The largest stems were damaged directly by the wind and the smaller stems indirectly. The intermediate-size stems were presumably more sheltered from the wind but large enough to avoid the larger falling stems. However, only the counts of damaged trees per size category are reported, not percentages, so it is difficult to determine the actual distribution of damage. Both Scatena and Lugo (in press) and Basnet et al. (1992) found that an intermediate size class (20–25 m in height, 50–60 cm in diameter, respectively) was the class least damaged in a Puerto Rican forest following Hurricane Hugo. Scatena and Lugo used six size categories of 5 m each (from 0–5 to >25) and found percent damaged stems (from smallest to largest) of 32, 21, 30, 43, 19, and 37 (differences not significant). There was not a clear bimodal distribution, and if the six categories are collapsed into three of

10 m each, the percent damaged are 24, 33, and 26, with the greatest damage in the intermediate size class of 10–20 m height. Basnet's data included fewer than five stems greater than 60 cm, making conclusions about the distribution of damage suspect.

A number of researchers have found no significant relationship between stem size and wind damage. Lugo et al. (1983) found a size relationship with types of hurricane damage but no clear trend for overall stem damage or mortality; however, in their study no sample size in categories above 50 cm dbh exceeded ten stems. Wilkinson et al. (1978) found no relationship of hurricane damage to height or diameter, but this was in a 25-year-old slash pine plantation with presumably little variation in either size parameter. Qinghong and Hytteborn (1991) found no size difference in windstorm damage, but observed that the trees may not have been large enough to exhibit differences. Putz and Sharitz (1991) reported "no clear relationships between types of damage and tree size" for hurricane effects in South Carolina, but used a minimum stem size of 20 cm and only three categories: 20–40, 40–80, and >80 cm. As mentioned above, their data may suggest highest percent damage among intermediate-size stems. Alexander (1967) found no size difference in windstorm damage, but sampled only the perimeters of clear cuts where damage would presumably not vary closely with size. Zimmerman et al. (1994) found no overall trend toward the relationship between damage and size, but some species showed relationships between size and specific types of damage, most often an increase in damage to larger branches.

A lack of clear trends in size versus damage, within and among studies, may be explained by several factors: 1) the difficulty of isolating differences in height that covary with other species-specific morphological differences; 2) variation in the relationship between height (more readily related to exposure) and diameter (more commonly measured), particularly in the largest diameter classes; 3) confounding of direct with indirect (stems hit by others) wind impacts; 4) complications caused by different measures of damage; and 5) variations in minimum, maximum, and categories of size.

Both Curtis (1943) and Pickering (1986) point out that a problem in correlating damage with stem diameter is that the form of the crown can greatly influence exposure to the wind. Deep crowns (distributed along the stem) may resist damage better than shallow crowns (concentrated at the top) (Boe, 1965; Pickering, 1986). Curtis (1943) refers to shallow-crowned trees as having a "high point" and also mentions crown density as positively correlated to wind damage, and the suppleness of the stem as negatively correlated to damage. Both crown form and crown density, at least in part, are independent of diameter. Curtis provides several figures to illustrate these morphological differences and provides data suggesting that species differences in damage actually relate to differences in crown development. King (1986) discusses increased exposure with increased height, but points out that the largest-diameter tree may gain additional diameter without growing taller. Cremer et al. (1982) suggests this change in height:diameter ratio in the largest trees increases their resistance to wind. Stem taper, related to stem flexibility and subsequently to damage (Cremer et al., 1982; Petty & Swain, 1985), is also not distinguished by a simple diameter measure.

Webb (1986) estimated that indirect causes account for 71% and 86% of the damage in two forest stands struck by a severe windstorm. With as many as two-thirds of the stem damage caused by other falling trees, the size of neighboring trees potentially will be better correlated to damage than size of a damaged tree itself (Smith & Weitknecht, 1915; and see Applegate & Bragg, 1992; Baker, 1915; Basnet, 1990; Dittus, 1985; Falinski,

1978; Frangi & Lugo, 1991; Greene et al., 1992; Harcombe & Marks, 1983; Ogden et al., 1991; Reilly, 1991; Reiners & Reiners, 1965).

Size may also influence the type of damage. Larger trees can be more subject to windthrow and smaller trees to stem snapping (Healey, 1990; Lugo et al., 1983; Thompson, 1983). This could be due to the difference between direct wind impacts on larger stems and indirect impacts on smaller ones (Figure 3). Bellingham et al. (1992) and Walker et al. (1992), however, found no differences in type of damage based on stem size. Putz et al. (1983) found higher numbers (percent of stems not reported) uprooted in medium-sized stems. Peterson and Pickett (1991) found that the largest stems in a tornado disturbance were more likely to be snapped than uprooted.

These complications have resulted in different interpretations of the relationship of stem size to damage: 1) no relationship, 2) a positive linear relationship, or 3) a more complex relationship. Determining relationships between diameter and damage has been complicated by methodological differences. All 16 studies in Table III used different minimum or maximum stem size, or intervals of stem sizes to examine size and damage relationships.

### b. Stand Conditions

There are several aspects of stand condition or history that may influence the severity of catastrophic wind damage: 1) even-age vs. mixed ages, 2) single species vs. mixed species, 3) maturity, 4) density relative to thinning history, and 5) juxtaposition with other disturbances or contrasting silvicultural treatments.

Many authors have noted increased damage in even-age stands; however, the impact due to stand structure is difficult to separate from impacts due to stand age, thinning history, and species composition in these usually single-species stands. This distinction is important, since it is hypothesized that the lower and more uniform canopy height (lacking emergents) of some wind-impacted forests makes them less susceptible to catastrophic wind (Brown et al., 1983; Odum, 1970; Webb, 1958).

Clapp (1938) found that mixed-age stands lost all big trees, while even-age stands were blown down entirely. Others have found mixed, irregular-shaped canopies to be more stable (Andersen, 1954; Boe, 1965; Jensen, 1941; Ruth & Yoder, 1953). An uneven-aged canopy exposes the largest trees to chronic winds and may precondition them to acute wind stress (Smith, 1946). Cline (1939) found young even-aged conifer stands susceptible to the wind. However, Clapp (1938), Boe (1965), and Peart et al. (1992) found the youngest stands to be wind resistant. The difference may be in definitions of "young." Curtis (1943) found increased damage in older, dense, even-age stands, but concluded "uneven forests in themselves are not more windfirm than even aged [stands]." Thompson (1983) also found greater damage in even-age plantations, but this damage varied with the species. Plantations of *Pinus caribea* Morelet and *Eucalyptus* spp. were seriously windthrown, whereas plantations of *Hibiscus elatus* Sw. were only debranched. Natural forests, which were both mixed-age and multi-species, were less damaged and suffered less mortality (58% versus 13%) than any plantations. Wadsworth and Englerth (1959) found spotty damage to individual trees in mixed-species, mixed-age stands, high or no damage in mixed-species, even-age stands, and high damage in even-age plantations. There appears to be less preconditioning to wind in dense even-age stands, making them more susceptible once the canopy is opened, but this effect may be either amplified or mitigated by species composition.

### Table III

Comparison of quantifications of stem size

| Citation | Minimum stem size (cm) | Category interval (cm) | Maximum stem size (cm) | Damaged related to size |
|---|---|---|---|---|
| Baker, 1915 | 25 | 25 | 305 | Yes |
| Hansen, 1937 | 2.5 | 2.5 | 25 | Yes |
| Boe, 1965 | 25 | 25 | 229 | Yes |
| Reiners & Reiners, 1965 | 15 | 18 | >86 | Yes |
| Brewer & Merritt, 1978 | 25 | 25 | >76 | Yes |
| Harcombe & Marks, 1983 | 4.5 | 20 | >40 | Yes |
| Glitzenstein & Harcombe, 1988 | 4.5 | 5 | 60 | Yes |
| Peterson & Pickett, 1991 | 10 | 10 | 90 | Yes |
| Putz & Sharitz, 1991 | 20 | 40 | >80 | Yes |
| Yih et al., 1991 | 5 | 15 | >46 | Yes |
| Reilly, 1991 | 5 | 2 | 100 | Yes |
| Basnet et al., 1992 | 2.5 | 10 | 70 | Yes |
| Dallmeier et al., 1991 | 10 | 5 | >55 | Yes |
| Qinghong & Hytteborn, 1991 | 10 | 10 | 70 | Yes |
| Sheffield & Thompson, 1992 | 15 | 5 | >129.5 | Yes |
| Zimmerman et al., 1994 | 10 | 5, 10 | >100 | No |

Differences in susceptibility of multi- compared to single-species stands are confounded by the fact that often single-species stands are also even-age plantations, and there is little consistency in reports. Bellingham (1991) found higher damage in pine plantations (80% blowdown) than in mixed species stands (20% blowdown). Trousdell et al. (1965) also reported more damage to natural stands than to single-species plantations (age of plantations not given). Lugo et al. (1983) found native species-rich climax associations to be less damaged than less diverse palm brakes; however, these forest types differ in stand structure, and the palm brake plots were closer to the path of the hurricane and presumably exposed to more intense winds. Clapp (1938) found no difference in mixed stands relative to pure stands. Cheston (1940) found more damage in mixed pine–hardwood stands than in pure hardwood stands, since the pines were selectively damaged. Andersen (1954) recommends mixing in windfirm species to decrease wind damage in plantations. In any case, higher species diversity increases the likelihood that some of the species will be relatively more wind-resistant. This could minimize damage where the alternative is unchecked damage in pure stands of susceptible species.

Many researchers report a positive correlation between stand age and damage, and many of the biotic factors—e.g., stem size, species differences, and presence of pathogens—are associated with changes in the age of the stand. King (1986) found higher damage in mature stands than in smaller, denser stands of second growth. Steven (1953b) found damage concentrated in middle-age and older forests. As reported above, although Cline (1939) found young, even-age conifer stands susceptible to the wind, others report less damage in younger stands or in young, dense, second-growth vegetation (Clapp, 1938; Cruickshank et al., 1962; Boe, 1965; Foster, 1988b; Touliatos & Roth, 1971; Trousdell, 1955; Wadsworth & Englerth, 1959). Canham (1978), found old growth blown

down but not younger stands. Sheffield and Thompson (1992) recorded higher damage for older stands, and Curtis (1943) reported the same for old, dense, even-age stands in which canopies tended to be concentrated high on the stem and root development was poor. Both Andersen (1954) and Foster (1988a) found ages at which the damage leveled off, not increasing with age. Andersen (1954) found that stand-level damage leveled off at ages with average stem height of 60 feet, though species within the stand were affected differently. He also reported on several studies in Europe where no relationship was found between age and windfirmness. Foster (1998a) found increasing damage with age up to 30 years. Others report decreases in damage with the oldest stems, and therefore the highest damage in stands of an intermediate age (Bromley, 1939; King, 1945; Wiley, 1965). This may be due to the response noted above for stem size: the oldest stands have more stems that have survived previous storms and are now preconditioned to resist damage. Bromley (1939) found the most damage in stands 30–100 years old. Younger stands were not exposed to the wind, and older stands had developed deeper, stronger root systems. In the case of King (1945), the young plantations had 30–60% damage, the medium-age stands 100%, and the oldest 90%, but the stands also differed in species composition. A relationship between stand age and damage may be due not to age per se but to age-related stand characteristics such as number of large trees, structural complexity, density, and species composition, all of which are influenced by stand management.

More wind damage is reported in thinned stands (Bromley, 1939; Liegel, 1984; Nelson & Stanley, 1959; Ruth & Yoder, 1953; Wadsworth & Englerth, 1959; Wilson, 1976). Thinning increases wind flow in the canopy and removes the support of surrounding trees. Yet others report that the most heavily damaged forests were the least logged (Merrens & Peart, 1992; Peart et al., 1992; Trousdell, 1955), perhaps because they contained more old, susceptible trees. Curtis (1943) likewise stated that old, dense stands were more susceptible to wind damage. These conflicting reports might be resolved if the timing of thinning was included in the analysis. What appears critical about stand density is the temporal proximity of thinning to subsequent wind exposure. In many cases, stands are highly susceptible to wind damage immediately after thinning but with further development can become more resistant. Alexander (1964) reports that stands growing in less dense conditions, as opposed to thinned, are more stable (see also Cremer et al., 1982).

Versfeld (1980) suspected that delayed thinning had increased damage in some stands. Andersen (1954) reviewed five studies on the effect of thinning on subsequent damage but found increased damage only when the stand was "recently" thinned (also see Foster, 1988a; Touliatos & Roth, 1971). Wadsworth and Englerth (1959) reported more damage to thinned stands—in their case, thinned less than two years before a hurricane. Cremer et al. (1977), studying the impact of catastrophic wind on plantations in Australia, had records of thinning history of each stand. Stands that were thinned less than five years before the disturbance had 22% windthrow. Stands thinned less recently had only 0.2% windthrow. In addition, unthinned stands downwind of clearcuts had 38% windthrow, but if these downwind stands were thinned less than six months before, the damage was 88%.

Over time a thinned canopy fills in and the remaining stems thicken, reducing wind damage. Cremer et al. (1977, 1982) suggest that five years is required to recover from thinning, which is supported by Weidman's (1920a) results that two-thirds or more of the damage occurred in the first five to six years after thinning. In one plot, 94% of wind damage in the fifteen years after thinning occurred in the first five years (Weidman, 1920a). Mergen (1954) states that stem growth and preconditioning to wind are more rapid in young stems, so that stand recovery time may vary with stand age.

Thinning increases stand wind resistance when weaker stems are culled. Boe (1965) found less damage in shelterwoods where 75% of the co-dominants were removed, presumably because the strongest stems were left, while many of the weaker stems had been removed. However, Nelson and Stanley (1959) found greater damage in stands that had been selectively cut to remove the diseased and poor-risk trees, but this thinning occurred less than a year before a hurricane. In another case of thinning less than a year before wind disturbance, Hansen (1937) found decreased damage and proposed that the most susceptible stems had been removed. Of course winds may remove weaker stems selectively, resulting in decreased damage over time (Alexander, 1967; Ruth & Yoder, 1953).

Natural treefall gaps and clearcuts may increase stand susceptibility when greater canopy roughness leads to further blowdown. Openings may result from harvesting or from tree death due to insects, pathogens, or wind (Andersen, 1954). Greene et al. (1992) proposed a positive feedback from disturbance to blowdown to account for a continued decline in biomass after disturbance. Young and Hubbell (1991) showed that trees along edges of existing gaps in a Panamanian forest were more likely to fall than other trees. Cremer et al. (1977) found that damage increased below clearcuts (38%) as compared to non-isolated stands (0.2%). Others reported that subsequent storms will extend prior openings in canopies (Mergen, 1954; Neustein, 1968). Cruickshank et al. (1962) explain this effect as increased turbulence caused by the previous gaps or clearcuts. They found increasing damage over the course of three storms and proposed that each storm made the stand more vulnerable (though the intensity of the storms also increased). Cremer et al. (1977) state they found no evidence of patches of downed trees progressing from a weak point in the canopy, but Baker (1915) found clusters of damaged trees that he explained as one tree falling, opening the canopy, and weakening the roots of neighboring trees; this process was later referred to as the "domino effect" by Canham (1978). Shaw (1983) reported that canopy gaps increased the likelihood of damage. Foster (1988b) reported that damage was increased by past logging and agricultural activities that create abrupt changes in stand height and density (DeWalle, 1983; Somerville, 1980). In one case where higher damage was detected in relatively unthinned stands, those stands were on the edges of clearcuts (Boe, 1965).

## c. Species

Many studies have reported differences among tree species in susceptibility to wind damage. Table IV summarizes the reported resistance to catastrophic wind for 242 species in 61 families. Resistance to wind disturbance was classified as low, intermediate, or high. Species were assigned to these three categories: 1) by the researcher, 2) by division into three equal-sized groups, in cases where species' resistances were ranked in a list, or 3) according to naturally occurring clusters of damage severity in cases where species specific damage data were presented. We arbitrarily divided the intensity of disturbance into low (<160 km/hr) and high (>160 km/hr) categories. Of the 42 papers reporting species' specific damage resistance, 21 were from tropical sites and 21 from temperate, 33 followed high-intensity disturbance, and 9 followed lower-intensity disturbance. Distinct trends are apparent neither for individual families nor for increasing intensity of wind for a given species.

Species may differ in type of damage suffered, mortality following damage, or resprouting after damage. A number of researchers have reported species differences in stem breakage versus uprooting (Greene et al., 1992; Hook et al., 1991; Liegel, 1982;

**Table IV**

Species resistance to catastrophic wind

| Taxon* | Region† | Level of resistance‡ To storms of lower intensity | To storms of higher intensity |
|---|---|---|---|
| **Aceraceae** | | | |
| Acer rubrum | Temperate | 1[gg]  3[nn] | 1[n]  2[cc]  1[ii] |
|  | Temperate | | 1[b]  2[r]  1[f] |
|  | Temperate | | 2[bb]  1[ff]  1[u] |
| Acer saccharum | Temperate | 3[nn]  3[gg] | 3[f] |
| **Agavaceae** | | | |
| Beaucarnea pliabilis | Tropical | | 3[oo] |
| **Alangiaceae** | | | |
| Alangium salviifolium | Tropical | | 1[m] |
| **Anacardiaceae** | | | |
| Campnosperma brevipetiolata | Tropical | | 1[pp] |
| Lannea coromandelica | Tropical | | 3[m] |
| **Annonaceae** | | | |
| Polyalthia spp. | Tropical | | 3[m] |
| **Aquifoliaceae** | | | |
| Ilex opaca | Temperate | | 2[p] |
| Ilex vomitoria | Temperate | | 2[p]  3[p] |
| **Araliaceae** | | | |
| Dendropanax arboreus | Tropical | | 1[ss] |
| Schefflera morototoni | Tropical | | 2[uu]  1[ll] |
| **Arecaceae** | | | |
| Palms | Tropical | | 3[b]  3[ss]  3[o] |
| Palms | Temperate | | 3[ii]  3[u] |
| Coccothrinax argentata | Temperate | | 3[x] |
| Cocos nucifera | Tropical | | 3[dd] |
|  | Temperate | | 1[h] |
| Licuala ramsay | Tropical | | 3[b] |
| Paurotis wrightii | Temperate | | 1[h] |
| Prestoea montana | Tropical | | 3[ee]  3[uu]  2[mm] |
|  | Tropical | | 3[k]  1[d]  3[ll] |
| Roystonea elata | Temperate | | 3[x] |
| Roystonea regia | Temperate | | 3[h] |
| Sabal palmetto | Temperate | | 3[h] |
| Thrinax parviflora | Temperate | | 3[h] |
| Thrinax radiata | Temperate | | 3[x] |
| **Betulaceae** | | | |
| Betula spp. | Temperate | 1[a] | |
| Betula alleghaniensis | Temperate | 3[gg] | |
| Betula populifolia | Temperate | | 1[c] |
| Betula papyrifera | Temperate | 1[nn]  3[nn] | 1[n]  1[cc] |
| Betula nigra | Temperate | | 3[p] |
| Carpinus caroliniana | Temperate | 3[nn] | 2[p]  1[r] |
| Ostrya virginiana | Temperate | 3[nn] | |
| **Bignoniaceae** | | | |
| Stereospermum personatum | Tropical | | 1[m] |
| Tabebuia heterophylla | Tropical | 3[kk] | 3[uu]  2[ll] |
| Tabebuia pallida | Tropical | | 2[v] |

## Table IV (continued)
### Species resistance to catastrophic wind

| Taxon* | Region† | Level of resistance‡ To storms of lower intensity | To storms of higher intensity |
|---|---|---|---|
| **Bombacaceae** | | | |
| Montezuma speciosissima | Tropical | 3[kk] | |
| Ochroma pyramidale | Tropical | 1[kk] | 3[o] |
| **Boraginaceae** | | | |
| Cordia spp. | Tropical | | 1[m] 2[m] |
| Cordia alliodora | Tropical | 3[kk] | |
| Cordia borinquensis | Tropical | | 3[ll] |
| Cordia sulcata | Tropical | | 3[uu] |
| **Burseraceae** | | | |
| Bursera simaruba | Tropical | 3[kk] 2[kk] | 3[oo] 2[x] |
| Dacryodes excelsa | Tropical | | 3[ee] 3[y] 3[uu] |
| | Tropical | | 2[k] 2[mm] 3[d] |
| | Tropical | | 3[ll] |
| Tetragastris balsamifera | Tropical | | 3[uu] |
| **Casuarinaceae** | | | |
| Casuarina spp. | Tropical | 1[kk] | |
| Casuarina equisetifolia | Tropical | | 2[v] 1[dd] 1[o] |
| Casuarina glauca | Temperate | | 1[x] |
| **Celastraceae** | | | |
| Elaeodendron glaucum | Tropical | | 2[m] |
| **Chrysobalanaceae** | | | |
| Hirtella rugosa | Tropical | | 3[ll] |
| Maranthes corymbosa | Tropical | | 2[pp] |
| **Combretaceae** | | | |
| Buchenavia capitata | Tropical | | 3[uu] 3[ll] |
| Laguncularia racemosa | Tropical | 1[kk] | |
| Terminalia arjuna | Tropical | | 1[v] |
| Terminalia calamansanai | Tropical | | 3[pp] |
| Terminalia catappa | Tropical | 1[rr] | 3[dd] |
| Terminalia richii | Tropical | 1[rr] | |
| **Cornaceae** | | | |
| Cornus florida | Temperate | | 1[ii] 2[p] 2[u] |
| **Cunoniaceae** | | | |
| Schizomeria serrata | Tropical | | 3[pp] |
| **Cupressaceae** | | | |
| Cupressus lusitanica | Tropical | 1[kk] | |
| Thuja occidentalis | Temperate | 2[gg] | |
| **Cyrillaceae** | | | |
| Cyrilla racemiflora | Temperate | | 3[p] |
| **Dilleniaceae** | | | |
| Dillenia salmonensis | Tropical | | 2[pp] |
| **Dipterocarpaceae** | | | |
| Dipterocarpus lowii | Tropical | | 3[g] |

## Table IV (continued)
### Species resistance to catastrophic wind

| Taxon* | Region† | Level of resistance‡ To storms of lower intensity | To storms of higher intensity |
|---|---|---|---|
| **Ebenaceae** | | | |
| Diospyros montana | Tropical | | 2[m] |
| Diospyros ovalifolia | Tropical | | 1[m] |
| Maba buxifolia | Tropical | | 2[m] |
| **Elaeocarpaceae** | | | |
| Elaeocarpus sphaericus | Tropical | | 2[pp] |
| Sloanea berteriana | Tropical | | 3[uu] 1[mm] 2[k] |
| | Tropical | | 2[d] 2[ll] |
| **Euphorbiaceae** | | | |
| Alchornea latifolia | Tropical | | 3[uu] 1[ll] |
| Alchorneopsis portoricensis | Tropical | | 1[d] 1[ll] |
| Amanoa caribaea | Tropical | | 2[y] |
| Bridelia retusa | Tropical | | 2[m] |
| Croton poecilanthus | Tropical | | 2[uu] 3[ll] |
| Drypetes glauca | Tropical | | 3[uu] 3[ll] |
| Drypetes lateriflora | Tropical | | 2[oo] |
| Drypetes sepiaria | Tropical | | 3[m] 2[m] |
| Endospermum medullosum | Tropical | | 3[pp] |
| Gymnanthes lucida | Tropical | | 3[oo] |
| Hyeronima clusioides | Tropical | 1[kk] | |
| Richeria grandis | Tropical | | 1[y] |
| Sapium laurocerasus | Tropical | | 2[uu] 2[ll] |
| Securinega samoana | Tropical | 2[rr] | |
| **Fagaceae** | | | |
| Fagus grandifolia | Temperate | | 1[aa] 3[f] |
| Fagus sylvatica | Temperate | 2[a] 1[i] | |
| Quercus spp. | Temperate | 3[a] 2[i] | 3[f] |
| Quercus alba | Temperate | | 3[n] 3[cc] 3[ff] |
| | Temperate | | 3[r] 2[ff] |
| Quercus borealis | Temperate | | 2[n] |
| Quercus falcata | Temperate | | 1[p] 2[r] 2[bb] |
| | Temperate | | 1[ff] |
| Quercus laurifolia | Temperate | | 3[r] |
| Quercus nigra | Temperate | | 1[p] 2[p] 2[u] |
| Quercus rubra | Temperate | 1[gg] 3[nn] | 2[cc] |
| Quercus velutina | Temperate | | 3[n] 3[cc] |
| Quercus virginiana | Temperate | | 3[h] 3[ii] 2[q] |
| | Temperate | | 1[x] |
| **Flacourtiaceae** | | | |
| Casearia arborea | Tropical | | 2[uu] 1[d] 2[ll] |
| Casearia sylvestris | Tropical | | 3[uu] |
| Homalium racemosum | Tropical | | 3[uu] |
| **Guttiferae** | | | |
| Calophyllum brasiliense | Tropical | 3[kk] | |
| Calophyllum kajewskii | Tropical | | 1[pp] |
| Calophyllum vitiense | Tropical | | 3[pp] |
| Clusia rosea | Tropical | | 1[o] |

**Table IV** (continued)

Species resistance to catastrophic wind

| Taxon* | Region† | Level of resistance‡ | |
| --- | --- | --- | --- |
| | | To storms of lower intensity | To storms of higher intensity |
| **Guttiferae** (continued) | | | |
| Garcinia spicata | Tropical | | $2^m$ |
| Symphonia globulifera | Tropical | | $2^y$ |
| **Hamamelidaceae** | | | |
| Liquidambar styraciflua | Temperate | | $3^{ff}$ $2^p$ $3^p$ $3^u$ |
| | Temperate | | $3^{ii}$ $2^{bb}$ $2^{ff}$ |
| **Juglandaceae** | | | |
| Carya spp. | Temperate | | $3^n$ $3^{cc}$ $3^r$ |
| Carya aquatica | Temperate | | $2^{bb}$ |
| Carya illinoinensis | Temperate | | $1^{ii}$ |
| **Lauraceae** | | | |
| Alseodaphine semicarpifolia | Tropical | | $1^m$ |
| Cinnamomum camphora | Tropical | | $3^v$ |
| Nectandra coriacea | Tropical | $1^{kk}$ | |
| Ocotea leucoxylon | Tropical | | $3^{uu}$ $1^d$ |
| **Leguminosae** | | | |
| Albizia falcata | Tropical | $1^{rr}$ | |
| Albizia lebbek | Tropical | | $1^v$ |
| Andira inermis | Tropical | $3^{kk}$ | |
| Bauhinia racemosa | Tropical | | $3^m$ |
| Cassia fistula | Tropical | | $2^m$ |
| Cassia roxburghii | Tropical | | $3^m$ $2^m$ |
| Cassia siamea | Tropical | $3^{rr}$ | |
| Dipteryx panamensis | Tropical | | $3^e$ |
| Erythrina poeppigiana | Tropical | $1^{kk}$ | |
| Hymenaea courbaril | Tropical | $1^{kk}$ | |
| Inga laurina | Tropical | | $2^{uu}$ $1^k$ $2^d$ |
| | Tropical | | $2^{ll}$ |
| Inga vera | Tropical | $1^{kk}$ | |
| Intsia bijuga | Tropical | $2^{rr}$ | |
| Leucaena pulverulenta | Temperate | | $2^u$ |
| Lysiloma bahamensis | Tropical | | $3^h$ |
| Lysiloma latisiliqua | Temperate | | $2^x$ |
| Ormosia krugii | Tropical | | $2^{uu}$ $1^{ll}$ |
| Pterocarpus marsupium | Tropical | | $1^v$ |
| Robinia pseudoacacia | Temperate | | $1^f$ |
| Sabinea florida | Tropical | $2^{kk}$ | |
| Tamarindus indica | Tropical | | $1^v$ $2^m$ |
| **Loganiaceae** | | | |
| Strychnos potatorum | Tropical | | $3^m$ |
| **Magnoliaceae** | | | |
| Liriodendron tulipifera | Temperate | | $1^r$ $1^{ff}$ |
| Magnolia glauca | Temperate | | $2^p$ $2^r$ |
| Magnolia grandifolia | Temperate | | $2^u$ |
| Magnolia virginiana | Temperate | | $2^u$ |
| **Malipighiaceae** | | | |
| Byrsonima crispa | Tropical | | $1^{ss}$ |
| Byrsonima spicata | Tropical | | $3^{uu}$ |

**Table IV** (continued)

Species resistance to catastrophic wind

| Taxon* | Region† | Level of resistance‡ | |
| --- | --- | --- | --- |
| | | To storms of lower intensity | To storms of higher intensity |
| **Malvaceae** | | | |
| Hibiscus elatus | Tropical | $1^{kk}$ | $2^{hh}$ |
| **Melastomataceae** | | | |
| Calycogonium squamulosum | Tropical | | $2^{ll}$ |
| Miconia tetrandra | Tropical | | $1^{uu}$ $2^{ll}$ |
| Tetrazygia elaeagnoides | Tropical | $1^{kk}$ | |
| **Meliaceae** | | | |
| Aglaia roxburghiana | Tropical | | $1^m$ |
| Cedrela odorata | Tropical | $1^{rr}$ | |
| Guarea guidonia | Tropical | | $3^{ee}$ $3^{uu}$ $1^k$ |
| | Tropical | | $2^d$ |
| Guarea kunthiana | Tropical | | $3^{ss}$ |
| Guarea trichiliodes | Tropical | $1^{kk}$ | |
| Khaya nyasica | Tropical | | $1^d$ |
| Swietenia macrophylla | Tropical | $1^{kk}$ $3^{rr}$ | $1^d$ |
| Swietenia mahagoni | Tropical | $3^{kk}$ $3^{rr}$ | $1^v$ |
| Walsura piscidia | Tropical | | $1^m$ |
| **Moraceae** | | | |
| Brosimum alicastrum | Tropical | | $1^{oo}$ |
| Brosimum guianensis | Tropical | | $3^{ss}$ |
| Cecropia schreberiana | Tropical | | $1^{uu}$ $3^o$ |
| Ficus amplissima | Tropical | | $3^m$ |
| Ficus aurea | Tropical | | $3^h$ |
| Ficus benghalensis | Tropical | | $1^v$ $3^{dd}$ $3^m$ |
| Ficus microcarpa | Tropical | | $2^m$ |
| Ficus mollis | Tropical | | $3^m$ |
| Ficus racemosa | Tropical | | $2^m$ |
| Ficus religiosa | Tropical | | $3^m$ |
| **Myrsinaceae** | | | |
| Ardisia obovata | Tropical | $1^{kk}$ | |
| **Myrtaceae** | | | |
| Eucalyptus delegatensis | Tropical | | $2^{qq}$ |
| Eucalyptus globulus | Tropical | | $2^{qq}$ |
| Eucalyptus robusta | Tropical | $1^{kk}$ | $1^{hh}$ $1^v$ |
| Eucalyptus saligna | Tropical | | $1^{hh}$ |
| Eucalyptus umbellata | Tropical | | $3^{dd}$ |
| Eugenia spp. | Tropical | $3^{kk}$ | |
| Myrcianthes fragrans | Tropical | | $3^{oo}$ |
| Otoba novagranatensis | Tropical | | $1^{tt}$ |
| Syzygium cumini | Tropical | | $3^m$ |
| **Nyssaceae** | | | |
| Nyssa aquatica | Temperate | | $3^q$ $3^{bb}$ |
| Nyssa sylvatica | Temperate | | $3^{ff}$ $3^{ii}$ $3^p$ |
| | Temperate | | $2^{ff}$ |
| **Oleaceae** | | | |
| Chionanthus domingensis | Tropical | | $1^{uu}$ |
| Fraxinus spp. | Temperate | $2^i$ | |
| Fraxinus americana | Temperate | $3^{gg}$ | $2^n$ $2^{cc}$ |

### Table IV (continued)
Species resistance to catastrophic wind

| Taxon* | Region† | Level of resistance‡ | |
|---|---|---|---|
| | | To storms of lower intensity | To storms of higher intensity |
| Oleaceae (continued) | | | |
| Fraxinus excelsior | Temperate | 2^a | |
| Fraxinus pennsylvanica | Temperate | | 3^r 3^f 1^bb |
| Pinaceae | | | |
| Abies amabilis | Temperate | 2^a | |
| Abies balsamea | Temperate | 1^gg 2^nn | |
| Larix spp. | Temperate | | 3^qq |
| Larix decidua | Temperate | 3^a 1^l | |
| Larix leptolepis | Temperate | 1^i 1^l | |
| Picea abies | Temperate | 2^a 3^i 1^i | |
| | Temperate | 1^l | |
| Picea glauca | Temperate | 2^gg 1^nn | |
| Picea sitchensis | Temperate | 3^gg 1^i 1^l | |
| Pinus banksiana | Temperate | 1^gg | |
| Pinus caribea | Tropical | 2^w | 1^v 1^hh 1^u |
| Pinus echinata | Temperate | | 1^p 3^ff |
| Pinus elliotti | Temperate | 3^a | 1^z 2^ff |
| Pinus lambertiana | Temperate | | 2^qq |
| Pinus muricata | Temperate | | 2^qq |
| Pinus nigra | Temperate | 1^l | 1^qq |
| Pinus oocarpa | Tropical | 1^w | |
| Pinus palustris | Temperate | | 1^p 2^ff 2^qq |
| Pinus patula | Tropical | | 1^hh |
| Pinus ponderosa | Temperate | 1^s | 1^qq |
| Pinus radiata | Temperate | 1^t 1^jj | 1^qq |
| Pinus resinosa | Temperate | 2^gg 3^nn | 2^j 1^f |
| Pinus serotina | Temperate | | 2^ff |
| Pinus sinensis | Tropical | | 3^v |
| Pinus strobus | Temperate | 2^gg 3^nn 2^nn | 3^j 1^n 1^cc |
| | Temperate | | 2^qq 1^f |
| Pinus sylvestris | Temperate | 2^a | 1^j |
| Pinus taeda | Temperate | | 1^ii 1^p 1^r |
| | Temperate | | 1^bb 2^ff |
| | Tropical | | 2^v |
| Pinus virginiana | Temperate | 1^s | |
| Pseudotsuga menziesii | Temperate | 1^a 3^t 3^gg | 3^qq |
| Pseudotsuga taxifolia | Temperate | 1^i 1^l | |
| Tsuga canadensis | Temperate | | 3^n 1^aa |
| Tsuga heterophylla | Temperate | 3^gg 1^gg | |
| Platanaceae | | | |
| Platanus occidentalis | Temperate | 3^a 2^i | 3^f 1^bb 2^u |
| Polygonaceae | | | |
| Coccoloba diversifolia | Tropical | 3^kk | 3^oo |
| Rhamnaceae | | | |
| Colubrina arborescens | Tropical | 1^kk | |
| Rhizophoraceae | | | |
| Rhizophora mangle | Tropical | 3^kk | |

### Table IV (continued)
Species resistance to catastrophic wind

| Taxon* | Region† | Level of resistance‡ | |
|---|---|---|---|
| | | To storms of lower intensity | To storms of higher intensity |
| Rubiaceae | | | |
| Adina cordifolia | Tropical | | 1^m |
| Guettarda valenzuelana | Tropical | | 3^uu |
| Ixora arborea | Tropical | | 2^m |
| Laugeria racemosa | Tropical | 3^kk | |
| Mitragyna parvifolia | Tropical | | 2^m |
| Rutaceae | | | |
| Chloroxylon swietenia | Tropical | | 1^m |
| Salicaceae | | | |
| Populus spp. | Temperate | | 1^f |
| Populus deltoides | Temperate | | 1^cc 1^ii |
| Populus grandidentata | Temperate | 2^nn 3^nn | |
| Populus heterophylla | Temperate | | 1^bb |
| Populus tremuloides | Temperate | 2^nn 1^nn | |
| Salix spp. | Temperate | | 1^f |
| Sapindaceae | | | |
| Glenniea unijuga | Tropical | | 2^m |
| Lepisanthes tetraphylla | Tropical | | 3^m 2^m |
| Matayba domingensis | Tropical | | 3^uu 3^ll |
| Pometia pinnata | Tropical | 1^rr | 1^pp |
| Sapindus emarginatus | Tropical | | 3^m |
| Sapindus saponaria | Tropical | | 3^oo |
| Schleichera oleosa | Tropical | | 2^m |
| Talisia olivaeformis | Tropical | | 3^oo |
| Sapotaceae | | | |
| Bumelia salicifolia | Temperate | 3^kk | 2^x |
| Dipholis salicifolia | Tropical | 3^kk | |
| Manilkara bidentata | Tropical | 3^kk | 3^uu 2^mm 1^d |
| | Tropical | | 2^ll 3^tt |
| Manilkara hexandra | Tropical | | 3^m 2^m |
| Manilkara zapota | Tropical | | 2^oo |
| Micropholis chrysophylloides | Tropical | | 3^ll |
| Pouteria multiflora | Tropical | 1^kk | |
| Sideroxylon foetidissimum | Tropical | | 3^h |
| Sterculiaceae | | | |
| Sterculia caribaea | Tropical | | 2^y |
| Sterculia foetida | Tropical | | 2^m |
| Symplocaceae | | | |
| Symplocos tinctoria | Temperate | | 1^p |
| Taxodiaceae | | | |
| Taxodium spp. | Temperate | | 1^z 3^h |
| Taxodium distichum | Temperate | | 3^ii 2^q 3^z |
| | Temperate | | 3^bb 3^x |
| Tiliaceae | | | |
| Grewia polygama | Tropical | | 1^m 2^m |
| Tilia americana | Temperate | 3^gg | |

### Table IV (continued)

Species resistance to catastrophic wind

| Taxon* | Region† | Level of resistance‡ | |
| | | To storms of lower intensity | To storms of higher intensity |
|---|---|---|---|
| Ulmaceace | | | |
| *Holoptelea integrifolia* | Tropical | | 1[m] |
| *Ulmus alata* | Temperate | | 3[p] |
| *Ulmus americana* | Temperate | 3[gg] | 3[r]  3[f]  2[bb] |
| Verbenaceae | | | |
| *Gmelina arborea* | Tropical | 2[rr] | |
| *Gmelina moluccana* | Tropical | | 3[pp] |
| *Petitia domingensis* | Tropical | 3[kk] | |
| *Premna tomentosa* | Tropical | | 3[m]  2[m] |
| *Tectona grandis* | Tropical | 1[kk] | |
| *Vitex pinnata* | Tropical | | 2[m] |
| Vochysiaceae | | | |
| *Vochysia ferruginea* | Tropical | | 1[e] |

* Nomenclature follows Abeywickrama, 1973; Allan, 1961; Elias, 1980; Hooker, 1973; Little et al., 1974; Long & Lakela, 1971; Seymour, 1980.

† Designated on the basis of study site.

‡ 1 = high levels of wind damage; 2 = intermediate levels of wind damage; 3 = low levels of wind damage.

[a] Andersen, 1954; [b] Applegate & Bragg, 1992; [c] Baldwin, 1940; [d] Basnet et al., 1992; [e] Boucher, 1989, 1990; [f] Bromley, 1939; [g] Browne, 1949; [h] Craighead & Gilbert, 1962; [i] Cruickshank et al., 1962; [j] Curtis, 1943; [k] Dallmeier et al., 1991; [l] Day, 1950; [m] Dittus, 1985; [n] Foster, 1988a; [o] Francis & Gillespie, 1993; [p] Glitzenstein & Harcombe, 1988; [q] Gresham et al., 1991; [r] Hook et al., 1991; [s] Hubert, 1918; [t] Irvine, 1970; [u] Kerr, 1973; [v] King, 1945; [w] Liegel, 1982; [x] Loope et al., 1994; [y] Lugo et al., 1983; [z] Ogden, 1992; [aa] Peterson & Pickett, 1991; [bb] Putz & Sharitz, 1991; [cc] Rowlands, 1941; [dd] Sauer, 1962; [ee] Scatena & Lugo, in press; [ff] Sheffield & Thompson, 1992; [gg] Stoeckeler & Arbogast, 1955; [hh] Thompson, 1983; [ii] Touliatos & Roth, 1971; [jj] Versfeld, 1980; [kk] Wadsworth & Englerth, 1959; [ll] Walker, 1991; [mm] Walker et al., 1992; [nn] Webb, 1986, 1989; [oo] Whigham et al., 1991; [pp] Whitmore, 1974; [qq] Wilson, 1976; [rr] Wood, 1970; [ss] Yih et al., 1991; [tt] You & Petty, 1991; [uu] Zimmerman et al., 1994.

Nonnemacher, 1970; Peterson & Pickett, 1991; Putz et al., 1983; Stoeckeler & Arbogast, 1955; Touliatos & Roth, 1971; Van Hooser & Hedlund, 1969; Veblen, 1986; Wadsworth & Englerth, 1959; Webb, 1988; Zimmerman et al., 1994). Others have examined differences in mortality (Glitzenstein & Harcombe, 1988; Harcombe & Marks, 1983; Putz et al., 1983; Sauer, 1962; Webb, 1986, 1989). Species differences in post-disturbance sprouting are often reported (Bellingham et al., 1994; Glitzenstein & Harcombe, 1988; Peterson & Pickett, 1991; Pickering, 1986; Putz & Brokaw, 1989; Walker et al., 1992; Zimmerman et al., 1994).

Differences among species in either severity or type of damage often can be related to morphological differences such as 1) strength of wood, 2) tree geometry, including shape of the bole or shape and size of crown, and 3) extent and depth of roots (Touliatos & Roth, 1971; Webb, 1986). Mergen (1954) and Wilson and Archer (1979) review stress, damage, and tree morphology.

Numerous authors have linked damaged levels to wood strength or density. Curtis (1943) found that the bending force required for hardwoods is greater than twice that required for white pine (*Pinus stobus* L.). Weaver (1989) found that higher specific gravity

is associated with less breakage and uprooting. Hook et al. (1991) concluded that the strong wood of *Quercus virginiana* Mill. resulted in lost branches only and little windthrow. Walker et al. (1992) found less snapping with higher-density wood, and Van Hooser and Hedlund (1969) reported more snapping in pines and more uprooting in the denser broadleaf species. But Peterson and Pickett (1991) found no differences in proportion of uprooted to snapped trees among species that differed greatly in modulus of rupture. However, the intensity of tornado winds in the latter case may have obscured differences related to morphology that are important in less intense disturbances. Others have found a negative correlation between wood strength and mortality (Putz et al., 1983; Webb, 1989; Zimmerman et al., 1994). Putz et al. (1983) found that species with shorter, thicker stems and denser wood tend to uproot rather than to snap, whereas species with low-density wood tend to have higher mortality.

Some authors have linked damage levels to crown and root characteristics. Foster (1988a) reported that species with full crowns and shallow roots are more susceptible than those with a vertical distribution of canopy, flexible branches, and a tapering shape. Cremer et al. (1977) found that sway, and therefore windthrow, increases with slender stems and wind drag of the crown. However, Andersen (1954) reported that slender, whippy stems survived gale damage, whereas full-crowned trees were blown down. The tendency for dense-crowned trees to be damaged and open-foliage crowns to be spared has been noted also (Kerr, 1973; Smith & Weitknecht, 1915; Touliatos & Roth, 1971). As mentioned previously, Curtis (1943) diagrammed several crown types. He found that the pattern of damage in the conifers he studied was related to crown development—specifically, greater crown development leads to higher damage. Putz et al. (1983) suggest that the presence of buttresses should lead to more snapped than uprooted stems, but they found no effect on damage or the frequency of uprooting (see also Walker et al., 1992). Basnet et al. (1992) attribute the resistance of *Dacryodes excelsa* Vahl to the presence of root grafts in this species. Lateral root development, in particular on the leeward side of the stem, can preventing uprooting (Day, 1960; Mergen, 1954; Smith, 1946), but Steinbrenner and Gessel (1956) reported that windward-side root development explained damage patterns.

Two possible broad trends in species' susceptibility to catastrophic wind damage must be discussed: 1) susceptibility to damage being greater for conifers than for broadleaf species (Cline, 1939; Curtis, 1943; Foster, 1988a; Stoeckeler & Arbogast, 1955) and 2) susceptibility of pioneer species being greater than that of late successional species (King, 1986; Putz et al., 1983; Webb, 1986; Zimmerman et al., 1994). The first trend may actually be a manifestation of the second, as conifers play an early role in the secondary succession of many temperate forests. A third possible trend, increased damage to exotic species, has been documented by King (1945) and Wadsworth and Englerth (1959). This relationship is difficult to isolate, as exotic species tend to be in plantations that may be more susceptible to wind for independent reasons.

Cline (1939) reported pure conifer stands blown down like "fields of grain," whereas hardwoods withstood the wind. In mixed stands, conifers tend to be windthrown selectively (Meyer & Plusnin, 1945). Spurr (1956) found 93% of softwood stands blown down, 57% of mixed stands, and only 38% of hardwood stands. Ottenheimer (1992) reported 88% damage in white pine stands and 28% in mixed hardwood stands. King (1945) found increased resistance in endemic hardwoods relative to pines and exotic hardwoods. When hardwood trees drop their leaves in the temperate zone, cold-season wind drag is reduced, and these species may be less susceptible than evergreen conifers to wind damage and especially to uprooting where frozen soil provides strong root anchorage (Moore, 1988).

Neustein (1971) observed that hardwoods and the deciduous conifer larch (*Larix decidua* Miller), were less affected by a gale because they were leafless at the time of the storm.

Mortality tends to be higher in early successional species (Webb, 1986; Zimmerman et al., 1994); thus differences in susceptibility among broadleaf species may be due to their successional class. The susceptibility of pioneer species may be due to their fast growth of weak wood and to exposed positions in the canopy (Nelson et al., 1994; Veblen et al., 1989; Webb, 1989; Whitmore, 1974). Many fast-growing broadleaf pioneer species achieve dominant, and therefore exposed, positions (Foster, 1988a; Ottenheimer, 1992; Veblen et al., 1989; Whitmore, 1974). As mentioned, fast growth and weak wood of pioneers is also associated with higher mortality (Putz et al., 1983; Webb, 1989; Zimmerman et al., 1994). King (1986), comparing two broadleaf species, found that the later successional species (*Acer saccharum* Marsh.) was more resistant than the shade-intolerant one (*Populus tremuloides* Michaux). Early successional species also exhibit less sprouting ability (Putz & Brokaw, 1989; Walker et al., 1992; Zimmerman et al., 1994).

Not all researchers report these trends. Lindo (1968) estimated that native pines were more resistant than native hardwoods to hurricane damage in Belize. Cruickshank et al. (1962) found broadleaf species more impacted than conifers when a hurricane struck Ireland. Andersen (1954) states that hardwoods and softwoods are equally at risk when in full leaf. Boucher et al. (1990) reported higher percentage withthrow in broadleaf rain forest than in pine stands in Nicaragua, though actual mortality was greater in pine stands. Walker (1991) did not find successional status a good predictor of damage over a wide range of species. Francis and Gillespie (1993) found that the pioneer species *Ochroma lagopus* Sw. and *Cecropia peltata* L. suffer only minor structural damage, because they shed their few large leaves early in the hurricane.

Several researchers have reported no differences in damage among species. In these studies there may in fact have been no differences attributable simply to species identity, but differences may have been hidden by the measure of damage used or confounded with co-varying differences in size or exposure. Dittus (1985) reported no differences in species-rank abundances before and after cyclone disturbance, but did find five species "significantly" reduced. Dallmeier et al. (1991) found uniform thinning (mortality) without regard to species, but they did detect species differences in the type of crown damage. Clapp (1938) reported that species differences were actually differences in aspect and exposure, that hardwoods and softwoods blew down equally when equally exposed. Baker (1915), Webb (1988), and Glitzenstein and Harcombe (1988) all state that the species differences they observed were actually differences in size of the different species. Webb (1988) found no differences among species for large stems, which tended to be snapped and killed, while some species with only small stems differed in damage and survival.

Species differences can be obscured by other factors. Schaetzl et al. (1989a) state: "Species that appear to be windfirm in one site context may be highly prone to uprooting elsewhere"; and Webb (1986) states that "within a species, one population may be susceptible to damage while another is resistant." Foster (1988a) explains these population differences as being related to variation in shoot to root form, soil characteristics, historical factors, and chance. Thus, differences in populations of a given species can be the result of differences in exposure due to topography or differences in root growth reflecting soil conditions (Andersen, 1954; Clapp, 1938).

From this wealth of studies on differences among species in susceptibility to wind damage we can make some generalizations: 1) species differences do exist and can be explained by canopy architecture, wood density, bole shape, rooting patterns, and susceptibility to infection; 2) softwoods (shade-intolerant pioneer species and some conifers) tend to be affected more heavily than hardwoods; and 3) species differences can be obscured by differences in exposure, edaphic conditions, silvicultural treatment, or wind intensity experienced by different populations of a species.

### d. Pathogens

A final biotic factor that influences damage is the presence of insect infestation or fungus or other pathogens. The presence of these wood-weakening agents varies among species and with age, and therefore may affect correlations between these latter factors and damage (Wilson, 1976). Bromley (1939) found that the presence of fungus and insect infestation increased hurricane damage to trees in New England. Hubert (1918), reporting on a survey of 90 windfall areas, found 18 percent of the sites to have fungi as the principal secondary cause of damage. Windstorm damage in Wisconsin was associated with the presence of rots and cankers; 75% of the broken stems had internal rot (Stoeckeler & Arbogast, 1955). Trousdell (1955) also found hurricane damage associated with heart rot in trees in Virginia. Qinghong and Hytteborn (1991) found increased breakage associated with fungal infections and proposed that windstorms tended not to kill trees unless they were already weakened by fungus or insects. Ruth and Yoder (1953) found that the presence of root rot increased tree susceptibility to wind damage in Oregon. Alexander (1964) also found that the presence of root and butt rots increased wind damage in conifers in Colorado. Thompson (1983) observed that 50% of the stumps examined after hurricane disturbance in Jamaica were infected and possibly weakened by fungi. In Washington state, Wiley (1965) found 40% of the stems damaged by a windstorm had either stem or root rot. Webb (1988) reported that wood-rotting fungi promoted breakage of some stems, and root-rotting fungi may have stimulated uprooting of others hit by a windstorm in Minnesota. Putz and Sharitz (1991) found hurricane damage in South Carolina to be correlated to previous mechanical damage that may have led to fungal infection (see also Hubert, 1918). Interestingly, the majority of these studies involve wind impacts in temperate regions. It is unclear whether pathogens are less of a contributory influence in the tropics, or whether tropical forest researchershave failed to investigate this possibility.

### e. Summary of Biotic Effects

We draw several conclusions about the influence of biotic factors on wind damage: 1) there is generally a unimodal relationship between stem size and susceptibility to direct wind damage (this is obscured when smaller stems, damaged by falling trees, are included in the analysis); 2) damage is related to canopy evenness, age of the stand (particularly resistance in the youngest even-aged stands), recent thinning, and proximity of canopy openings, but diversity of species does not increase overall resistance of a stand; 3) there are species differences in susceptibility to different types of damage, subsequent mortality, and ability to sprout following damage; some conifers and early successional species are particularly susceptible to severe stem damage and mortality, but these susceptible species are not necessarily more likely to sprout; and 4) weakening from pathogens has increased damage in temperate forests struck by catastrophic winds. However, any of

these trends may be obscured by the highest intensity of wind disturbances, or by conflicting and confounding interactions among biotic and abiotic factors.

### 2. Abiotic Factors

Various abiotic factors have been examined for their influence on severity of wind damage to forests, including 1) storm intensity, timing, and associated precipitation, 2) topographic features, 3) edaphic conditions, and 4) disturbance history.

### a. Storm Intensity

Storm intensity is the most obvious abiotic factor that influences severity of damage. The most commonly reported measures of wind intensity are either maximum sustained wind or maximum gusts. As mentioned earlier, Lugo et al. (1983) suggested duration and maximum wind speed as measures of intensity of disturbance. Scatena and Larsen (1991) suggested the additional measures of proximity to the storm and total rainfall. The perceived intensity of wind also may be a function of direction. There is a distinction between destructive winds that come from the same direction as prevailing winds, and those from different directions, for which the biota may not be preconditioned (Alexander & Buell, 1955; Boe, 1965; O'Cinneide, 1975; Qinghong & Hytteborn, 1991). Also, wind direction changes during a cyclonic storm, while the storm may be gaining or losing intensity (Boose et al., 1994).

The impact of a catastrophic wind disturbance may depend partly on timing. During the cold season in temperate climates, deciduous trees will be less susceptible to uprooting, due both to reduced wind drag after dropping leaves and, in the more polar latitudes, to stronger anchorage in frozen soils (Mayer, 1989).

Precipitation is another aspect of storm intensity that influences damage (Day, 1950). The 1938 hurricane in New England caused an abnormally high percent of damage as uprooting (87–100%) as opposed to stem snapping (Brake & Post, 1941; Bromley, 1939; Curtis, 1943; Foster, 1988a), perhaps due to the quantity of rain (15–35 cm) that fell with the storm (Brooks, 1939c). Trousdell et al. (1965) thought the same mechanism accounted for their values of over 99% uprooting in Virginia and North Carolina from a hurricane (see also Moore, 1988). Versfeld (1980), studying the impact of two windstorms at the same site in South Africa, found both a lower proportion of uprooting and a lower overall damage level for the storm preceded by drier conditions. However, Versfeld (1980) ignored the possibility that the decreased overall damage could be due to the removal of the most windthrow-prone individuals; the wetter windstorm occurred only three months before the second, drier windstorm. Cremer et al. (1977) also supported their assessment that damage was amplified by saturated soils during a windstorm in Australia by comparing a subsequent storm at the same site and of similar severity that occurred two years later under drier conditions. Again, damage was less in the second, drier, storm.

### b. Topography

Many researchers have examined the role of topographic features in increasing or decreasing exposure to wind, or affecting wind direction, and thus influencing the severity of wind disturbance. Changes in wind direction over a landscape can be examined by mapping directions of treefalls (Boe, 1965; Boose et al., 1994; Cremer et al., 1977; Dallmeier et al., 1991; Falinski, 1978; Glitzenstein & Harcombe, 1988). One would naturally expect damage to be highest on ridges and windward slopes and least in valleys

and leeward slopes. In a study of 159 windthrow areas, Neustein (1971) found 45% on windward slopes, 32% on ridges, 6% on lee slopes, and 7% on flats. But the ensuing discussion will show that the relationship between topography and wind damage can be complex, insofar as wind sometimes causing greater damage in valleys and on lee slopes. Exposure is a complex relationship of aspect, slope, topographic position, and landscape position (Foster & Boose, 1992), while damage itself can reflect topographic correlates of species characteristics. Table V summarizes the reported interactions between topographic features and damage.

Many observers have reported increased damage on windward slopes and ridges (Alexander, 1964; Curtis, 1943; Liegel, 1984; Neustein, 1968, 1971; Ruth & Yoder, 1953; Smith, 1946; Stoeckeler & Arbogast, 1955; Webb, 1958). And numerous others have observed the expected decreased damage in sheltered valleys or on lee slopes (Andersen, 1954; Webb, 1958; Liegel, 1984; Wunderle et al., 1992). But Bellingham et al. (1992) found decreased damage on ridge tops affected by a hurricane in Jamaica. They suggested that the ridge top canopy was more streamlined and that chronic winds in these exposed positions selected for the more wind-resistant species. Lugo and Scatena (1993), and Basnet et al. (1992), all investigating the same watershed in Puerto Rico, report less damage and mortality on ridge tops and upland valleys. They proposed that this difference was due to 1) the predominance of wind-resistant species on ridge tops, at least one of which (*Dacryodes excelsa* Vahl) exhibits root grafting; 2) drier soil conditions on ridge tops that lead to more developed root systems; and 3) increased damage in exposure valleys due to trees dropping down the slope. The results of two studies indicated that slope alone does not explain damage and recorded increased damage where slope gradient changes rapidly (Ruth & Yoder, 1953; Alexander, 1964).

Valleys may provide protection from catastrophic wind (Table V) but also may amplify disturbance. Liegel (1984) found trees leaning or blown down like "spokes in a wheel," in protected valley sites. Many others report increased damage in valleys, and saddles between ridges, where the wind is constricted and accelerated (Alexander, 1967; Andersen, 1954; Brennan, 1991; Brooks, 1938; Chandler, 1968; Cremer et al., 1977; Curtis, 1943; Gloyne, 1968; Irvine, 1970; Lugo et al., 1983; Ruth & Yoder, 1953; Scatena & Lugo, in press; Smith, 1946; Weidman, 1920a). Reporting on earlier hurricane damage in Puerto Rico, Weaver (1986, 1989) noted increased damage in some valleys where saturated soils seemed to increase windthrow.

An interesting debate in the literature regards damage to lee slopes. As indicated in Table V, increased damage on lee slopes were reported by Smith and Weitknecht (1915) for windstorm damage in Oregon, by Boe (1965) for windstorm damage in California, by Alexander (1967) for windstorm damage in Colorado, by Irvine (1970) for windstorm damage in New Zealand, by O'Cinneide (1975) for gale damage in Ireland, and by Brooks (1939a) for the 1938 hurricane in New England. However, Clapp (1938) and Smith (1946) reported no lee slope damage for the 1938 hurricane in New England. Foster (1988b) reported little lee slope damage from the same storm, possibly because the 1938 hurricane came from the south and east and the prevailing winds are from the north and west. In this situation the lee slopes would be more preconditioned to chronic wind and possibly less susceptible to the hurricane winds. This does not explain the lack of lee side damage in Scotland for the gale of 1968, which came from the west as do most gales (Neustein, 1971). Brokaw and Grear (1991) and Boose et al. (1994) found that hurricane damage to high elevation (cloud forest) in Puerto Rico did not vary from windward to leeward slopes

### Table V

Interaction between topographic features and wind damage*

| Aspect | Ridges | Valley | Exposed slope | Lee slope | Percent slope | Gradient change | Citation |
|---|---|---|---|---|---|---|---|
| | | | | | | | **Temperate Forest** |
| | | | + | − | | | Conrad, 1945 |
| | | + − | + | + | | | Andersen, 1954 |
| | | | | | + | | Baker, 1915 |
| 0 | + | | | + | 0 | | Smith & Weitknecht, 1915 |
| | + | | | | | | Canham, 1978 |
| | | + | + | + | + | + | Alexander, 1964 |
| | | | + | | | | Stoeckeler & Arbogast, 1955 |
| | + | | + | | | | Neustein, 1968 |
| | + | + | | + | | + | Day, 1965 |
| | | | | + | | + | Alexander, 1967 |
| | | + | | | | | Brennan, 1991 |
| | | + | | | | | Chandler, 1968 |
| | | + | | | | | Weidman, 1920b |
| + | | | + | − | | | Clapp, 1938 |
| | + | + | | − | | | Smith, 1946 |
| | + | + | | + | | | Ruth & Yoder, 1953 |
| + | + | | + | − | | | Foster, 1988b |
| + | | | | | + | | Foster & Boose, 1992 |
| | + | | | + | | | Smith & Weitknecht, 1915 |
| | | | | + | | | O'Cinneide, 1975 |
| | | | | + | | | Boe, 1965 |
| | + | + | + | + − | + − | | Neustein, 1971 |
| | + | + | | | | | Smith, 1946 |
| | + | + | + | − | | | Curtis, 1943 |
| | | + | | + | | | Irvine, 1970 |
| | | | | + | | | Brooks, 1939a, 1939b |
| | | + | | | | | Brooks, 1938 |
| | + | + | | + | | | Shaw, 1983 |
| | | | | | | | **Tropical Forest** |
| | | − | | | − | | Wunderle et al., 1992 |
| | + | + − | | | | | Liegel, 1984 |
| + | + | + | | | | | Wadsworth & Englerth, 1959 |
| 0 | + | − | + | | | | Webb, 1958 |
| | − | + | | | | | Basnet et al., 1992 |
| | − | + | | | | | Scatena & Lugo, in press |
| | − | + | + | | | | Lugo & Scatena, 1993 |
| | + | − | | | | | Frangi & Lugo, 1991 |
| + | + | − | | | | | Boose et al., 1994 |
| | + | + | + | | | | Weaver, 1986 |
| | | + | | | | | Weaver, 1989 |
| | − | + | | | | | Bellingham et al., 1992 |
| | + | + | + | | | | Reilly, 1991 |
| | + | | | | | | Brokaw & Grear, 1991 |
| | + | | | | | | Frangi & Lugo, 1991 |

* +, increased damage; −, decreased damage; 0, no significant effect.

and suggested that, while the windward slopes were subjected to more intense winds, they were also preconditioned by chronic winds from the same direction.

O'Cinneide (1975) proposed that greater lee side damage was the result of 1) turbulent flow over the ridge, 2) soil differences on windward and lee slopes, 3) preconditioning on the windward side, and/or 4) winds from unusual directions (affecting trees not preconditioned to wind). Others propose that lee slope damage is influenced by the steepness of the slope. With steep enough slopes, the wind flows over the ridge and past the vegetation on the lee side. In modeling the exposure to hurricane winds, Boose et al. (1994) use an inflection angle of 6° (13%) for winds passing over a ridge. Ruth and Yoder (1953) found decreased damage with lee slopes of greater than 70%; Andersen (1954) found that lee slopes steeper than 8° (18%) were protected; and both Gloyne (1968) and Foster and Boose (1992) proposed that lee slopes of greater than 10% are protected. Boe (1965) noted that the presence of uncut timber on windward slopes tended to protect lee slopes. It is possible that these differences in protected lee slopes reflect differences in the intensity of the wind disturbance, but, of the above, only Andersen (1954) reports wind speed (144–160 km/hr).

Some studies reported no effect of topography on damage. Alexander and Buell (1955) found no difference in direction of treefalls related to different aspects and topographic positions, but they did not report whether total damage varied with different exposures. Canham (1978) reported little influence of topography on blowdowns, but his study involved reconstructing historical records of blowdowns. Variation in directions of individual storms, and the downward component of winds in thunderstorms (considered the primary source of severe blowdown), will obscure variation in exposure to wind. Canham (1978) did observe that "local topography figures in the pattern from any given storm," and local variations in exposure can account for small patches of blowdown. Smith and Weitknecht's (1915) detailed survey of over 640 ha struck by two windstorms in Oregon led them to conclude that local topography does not influence windthrow. However, no description of the topographic variation of the site is given, they only report summary data and conclusions, and no description of the directions of the two storms are given. Baker (1915) investigated 1400 ha in Washington and concluded that only very steep slopes had an impact on windthrow. Again, no detailed analysis of the data is presented, so it is difficult to determine what comparisons were made. Cremer et al. (1977) used aerial photographs to assess damage in over 70 km² in hilly terrain of Australia struck by a single windstorm and concluded "topographic features did not appear to be important." No analysis was presented, but Cremer et al. (1977) seemed to expect a simple association with ridge tops and windward exposure. They report "stands were thrown on both lee and windward slopes. In several places more throw occurred in the valley."

A last point regarding the influence of topography on wind and wind damage is that the relationships seem to become more complex, or less predictable, at finer spatial scales. The large-scale influence of topography is evident where the windward sides of mountains were more damaged than protected leeward sides (Boose et al., 1994; Browne, 1949; Lugo et al., 1983), but there is much less consistency in damage patterns at smaller scales of topography (Bellingham, 1991; Boose et al., 1994; Brokaw & Grear, 1991). Gloyne (1968) stated that wind is canalized by valleys at scales of tens of miles but that the ability of the wind to follow smaller-scale contours is a function of the degree of slope. Lawrence et al. (1991) proposed that large-scale variation in damage is controlled by landscape features and fine-scale variation is a function of individual response of stems. At fine

spatial scales, the interactions between landscape features, vegetation, and the moving air masses make the relationship between topography and wind damage more than simply a matter of exposure differences due to aspect.

### c. Soil Characteristics

Some apparent topographic associations with damage may actually reflect edaphic characteristics that co-vary with topography (Basnet, 1990; Furley & Newey, 1979; O'Cinneide, 1975), especially soil depth. Associations between edaphic conditions and damage severity seem to be indirectly biotic, the critical factor being the effects on root development and anchorage. Shallow soils, high water table, a shallow impermeable soil layer, or soil textures may all restrict root growth and increase susceptibility to damage. Neustein (1968) suggested that sites with high wind and turbulence, such as ridges, upper slopes, and shoulders, also have shallower soils. Valleys may have deeper soils but still be more affected by the wind, presumably because the soils are more saturated, limiting root development (Basnet et al., 1992; Scatena & Lugo, in press). Weaver (1989) reported more windthrow in valleys due to saturated soils; and Wunderle et al. (1992) found the most severe damage on a flood plain (also see Lugo et al., 1983; Reilly, 1991).

A number of researchers have reported associations between wind damage and soil characteristics independent of topography (Table VI). Damage may be higher for species with shallower root systems (Touliatos & Roth, 1971) due to shallow soil (Neustein, 1968, 1971) or high soil moisture (Sauer, 1962). Smith (1946) stated that damage is increased on moist, hard, or thin soils—any condition that prevents the deep penetration of tree roots. Smith and Weitknecht (1915) found decreased damage in medium and deep soils. Alexander (1964) found more damage on shallow soils with less drainage. Trousdell et al. (1965) found 51% damage on plots with a layer that restricts root growth and only 7% damage on plots without this restrictive layer. Liegel (1984) found increasing damage with higher average rainfall. Ruth and Yoder (1953) found damage associated with thin soils or high water tables. Both Bromley (1939) and Foster (1988a) found increasing damage with water-logged soil, associated with an impermeable soil layer, which resulted in shallow-rooted trees.

However, both Wadsworth and Englerth (1959) and Versfeld (1980) found little relation between soil depth and damage. In the former study, they found several cases contrasting with those reported above: heavy uprooting in deep soils in bottom lands (where soil depth was related to high soil moisture). They found breakage only in shallow soils on hills where the root systems were well anchored in rock. Putz and Sharitz (1991) observed an exception to the common relationship between soil moisture and damage: uprooting was uncommon in South Carolina sloughs during a hurricane. They proposed that resistance of these trees was due to a unique, well-developed root system adapted to wet soils. Stoeckeler and Arbogast (1955) found less damage on peat, and suggested that wet peat enabled trees to tilt downward in the wind and spring back afterward. Mayer (1989) found more uprooting when storms hit during warm periods and soil was wet, and more stem breakage when wind hit trees in frozen soils and anchorage was presumably firmer. Andersen (1954) observed looser soil and more uprooting during warm, wet winters.

The development of tree root systems is also influenced by soil texture (Andersen, 1954; Touliatos & Roth, 1971; Webb, 1958). Brewer and Merritt (1978) and Pickering (1986) report damage on clay soils; the latter observed that these soils are poorly drained and may cause higher root mortality. Trousdell et al. (1965) reported 30% damage on

### Table VI

Soil characteristics and catastrophic wind damage[†]

| Soil depth | Soil water | Soil texture | Hard pan | Root growth | Citation |
|---|---|---|---|---|---|
| | | | | | **Temperate Forest** |
| | | | | − | Felt, 1939 |
| | | * | + | | Trousell et al., 1965 |
| − | | | | − | Steven, 1953b |
| | | * | | | Brewer & Merritt, 1978 |
| − | | * | | − | Pickering, 1986 |
| | | * | | − | Mergen, 1954 |
| − | + | * | | − | Day, 1965 |
| − | + | * | + | − | Neustein, 1968, 1971 |
| | | | | − | Touliatos & Roth, 1971 |
| − | + | | + | − | Smith, 1946 |
| − | | | | | Smith & Weitknecht, 1915 |
| | + | | | | Alexander, 1964 |
| | + | | | | Liegel, 1984 |
| − | + | | | | Ruth & Yoder, 1953 |
| | + | | + | | Foster, 1988a |
| | + | | + | − | Bromley, 1939 |
| − | | | | − | Putz & Sharitz, 1991 |
| | + | * | + | | Andersen, 1954 |
| − | + | | + | − | Cremer et al., 1977 |
| 0 | | | | | Versfeld, 1980 |
| | | * | | − | Touliatos & Roth, 1971 |
| | + | | | | Hook et al., 1991 |
| − | | | | − | Stoeckeler & Arbogast, 1955 |
| − | + | | + | − | Day, 1950 |
| | | | + | | Brewer & Merritt, 1978 |
| | | | | | **Tropical Forest** |
| − | + | | | | Walker et al., 1992 |
| + | + | | | | Wadsworth & Englerth, 1959 |
| | + | | | | Sauer, 1962 |
| | + | | | − | Basnet et al., 1992 |
| | + | | | − | Scatena & Lugo, in press |
| | + | | | | Weaver, 1989 |
| | | * | | | Webb, 1958 |

[†] Indications of relationship: 0, no association; *, association exists; −, negative association; +, positive association.

coarse-textured soils and only 5% on medium to fine soils. Mergen (1954) found that soil texture affects the distribution of roots and soil consistency, influencing its anchoring capacity.

### d. Disturbance History

Previous disturbance may influence the severity of damage for a given intensity of disturbance. As mentioned above, previous disturbances—natural or anthropogenic—that open the canopy can increase turbulent air flow, resulting in a positive feedback to wind disturbance (Allen, 1992; Boe, 1965; Cremer et al., 1977; Cruickshank et al., 1962; DeWalle, 1983; Greene et al., 1992; Mergen, 1954; Neustein, 1968; Shaw, 1983;

Somerville, 1980; Veblen et al., 1989). Non-lethal damage associated with one windstorm may predispose trees to subsequent windthrow (Hubert, 1981; Putz & Sharitz, 1991; Webster, 1963), particularly when the later storm winds come from another direction (Trousdell, 1955). Over longer time spans, pioneer species that invade and grow to maturity following a disturbance may create a community that is relatively more susceptible to subsequent wind disturbance (Nelson et al., 1994; Veblen et al., 1989; Webb, 1989; Whitmore, 1974). However, Smith et al. (1994) hypothesize that gaps that existed before hurricane disturbance, possibly created by small lightning-strike fires, had lower vegetation that survived the hurricane disturbance.

Also in the case of successive disturbances by wind the feedback may not always be positive. Both Ruth and Yoder (1953) and Alexander (1967) found less damage over time with successive wind disturbances. In studying the effects of two windstorms in southeast Britain, Allen (1992) found that the second storm, though of equal or greater intensity, resulted in one-quarter the damage. Foster (1988b) found that recent severe disturbance (logging, agriculture, fires) may leave stands of young, dense second growth that are wind resistant.

## e. Miscellaneous Abiotic Effects

In addition to mortality and structural damage, other forms of damage associated with windstorms include salt stress from spray or high tides, causing loss of foliage (Applegate & Bragg, 1992; Chabreck & Palmisano, 1973; Gardner et al., 1991; Gunter & Eleuterius, 1971; Hook et al., 1991; Morgan et al., 1959; Moss, 1940; Sauer, 1962; Sheffield & Thompson, 1992; Wyman, 1954b); structural damage from waves (Chabreck & Palmisano, 1973; Graham, 1990; Gunter & Eleuterius, 1971; Morgan et al., 1959; Sauer, 1962; Stoneburner, 1978); sand, silt, and mud deposition (Bush, 1991; Craighead & Gilbert, 1962; Chabreck & Palmisano, 1973; Smith et al., 1994); and damage due to microclimate changes such as more light and wind, higher temperature, and less humidity (Applegate & Bragg, 1992; Fernandez & Fetcher, 1991; Loope et al., 1994; Turton, 1992).

## f. Summary of Abiotic Effects

Wind damage is related to intensity of wind and topographic exposure, but the variation in exposure over the landscape is complex, and may result in valleys or lee slopes being subjected to greater intensity of wind. Exceptions to the relationship between exposure and damage occur when those positions most exposed to catastrophic wind are also those most preconditioned by chronic wind. The relationship between soil and wind damage relates to root growth, which may be restricted by shallow soils, high water table, a shallow impermeable soil layer, or poor soil texture. Previous disturbances may influence subsequent wind damage by 1) increasing turbulence by opening the canopy, 2) selectively removing susceptible trees, and 3) changing the vegetation composition to more wind-resistant forms.

Both biotic and abiotic factors influence severity of wind disturbance. Variations in spatial patterns of damage may be difficult to interpret when 1) species respond differently to damage, 2) species distribution over the landscape also varies, or 3) species distributions are influenced by abiotic factors that also influence the severity of wind disturbance. Are the spatial patterns of damage driven by patterns of species distribution, or are differences in damage to species the result of their distribution in areas not equally exposed to wind? Since most studies of catastrophic wind are reactive rather than

proactive, and since—to date—no study sites have been designed to anticipate wind disturbance and separate the influence of various factors, it is difficult to answer this question. Some recent efforts by Borchard et al. (1992) to separate the species vs. environmental factors may help unravel this complex problem of the relative role of different factors determining the impact of catastrophic wind disturbance.

### E. DYNAMICS OF RECOVERY

So far, this paper has focused on the factors influencing the pattern of severity of catastrophic wind disturbance, but the more crucial issue is the response of the forest ecosystem to this disturbance. We examine the dynamics of recovery in terms of 1) comparisons with other disturbances, 2) paths of recovery and mechanisms that affect these paths, and 3) interactions with subsequent disturbance events.

### 1. Comparison to Other Disturbances

Catastrophic wind disturbance has been compared to a variety of other disturbances in terms of impact and implications for recovery. As mentioned above, Lugo et al. (1983) compared the impacts of a hurricane to an earthquake and a landslide and concluded that hurricanes are more damaging because they affect larger areas more often. However, their estimate of recovery time is much faster for hurricanes, indicating a fundamental difference in the nature of the disturbance or the path to recovery. Boucher (1990) suggested that a hurricane, a single discrete disturbance event, differs from anthropogenic disturbances such as logging, agriculture, and conversion to pasture, because these latter are of longer duration and involve repeated removals of vegetation. Veblen et al. (1989) proposed that wind disturbance is more similar to insect outbreaks than to fire disturbance, because fire affects the understory and bares mineral soil.

Ackerman et al. (1991) suggest that less severe hurricanes result only in defoliation and debranching, moderate intensity hurricanes cause damage comparable to background treefall gap dynamics, and more severe hurricanes may produce gaps of a much larger size. Each could result in a different array of microclimates and therefore a different dynamic of recovery. Dallmeier et al. (1991) state that post-hurricane forests "cannot be compared to a forest gap"; rather, they are more comparable to forests that have been uniformly thinned. Spurr (1956) also suggests that hurricane disturbance is similar to logging, then describes some interactions between the two that control the recovery process, involving substrate disturbance and damage to advanced regeneration that survives the wind disturbance, which would indicate some differences in their impacts. Merrens and Peart (1992) report recovery from hurricane disturbance to follow the same succession as follows clearcutting.

Treefall associated with catastrophic wind potentially differs from background tree mortality and gap creation in three ways: the gap size distribution, the nature of the damage, and the ability of the system to respond. It is inappropriate to make a clear distinction between background treefalls and those associated with catastrophic wind. It is more appropriate to visualize a gradient of disturbance from trees that die standing and create only small openings in the canopy, through larger gaps created by single trees falling and perhaps knocking down other trees, to groups of treefalls struck by intense winds and sometimes creating gaps with indistinct edges when surrounding vegetation is defoliated. Catastrophic disturbance can create the largest gaps as well as the relatively small, single treefall size (Allen, 1992; Foster, 1988a; Foster & Boose, 1992; Greene et al., 1992).

The studies presented in Table VII support the assumption that catastrophic wind disturbance creates a range of gap sizes, with three possible exceptions. In a study of tornado disturbance in Texas, Glitzenstein and Harcombe (1988) found no small gaps, but their goal was not to identify all gaps associated with the storm but to focus on two areas of discrete, severe blowdown. Nor did Lorimer (1977) find small gaps, but he was restricted to a 25 ha minimum gap size in his study of surveyor's records, because smaller gaps had not been recorded. Nelson et al. (1994) shows a minimum gap size of 30 ha because of the limited resolution of the remote-sensing technique used. Canham (1978) shows gaps down to 0.65 ha but also was limited by the resolution of his data; he estimates that the gaps actually ranged down to 0.004 ha. Foster and Boose's (1992) study of hurricane damage in Puerto Rico is probably the most comprehensive analysis of gap size distribution following catastrophic wind. Although they found gaps up to 37 ha, the distribution was strongly concentrated in the smaller size class, indicating that hurricane disturbance creates gaps of all sizes.

Along the gradient of gap sizes we should see shifts not only in scale but in type of damage, which differentially influence resulting microclimate and path of recovery. Trees that die in place and gradually disintegrate rarely involve uprooting (Foster, 1988a), do not form large root mounds, and should make relatively small gaps. However, Putz et al. (1983) found no difference in gap size caused by snapped trees compared to that caused by uprooted trees, although they were not examining catastrophic wind impacts. Individual treefalls not caused by catastrophic wind produce mostly coarse woody litter and are not surrounded by defoliated vegetation. Catastrophic wind disturbance knocks down trees and debranches and defoliates surrounding vegetation, increasing light levels dramatically (Fernandez & Fetcher, 1991; Turton, 1992; Veblen et al., 1989; Walker et al., 1992) and sometimes producing litterfall exceeding average yearly totals (Lodge et al., 1991; Whigham et al., 1991).

## 2. Spatial Influences on Recovery

Differing dynamics of recovery based on gap size are well established (Brokaw, 1985a, 1985b; Hartshorn, 1978; Runkle, 1981, 1984, 1985), regardless of the gap creation mechanism. Webb (1986) found that after catastrophic wind disturbance, trees grow into small gaps from the sides, but in large gaps shrubs and previously established seedlings reform the canopy. Dunn et al. (1983) reported that encroachment of surrounding vegetation and advanced growth closed small gaps, while pioneer species filled in only the larger gaps. Putz and Brokaw (1989) found this same pattern; in large gaps pioneer species are of increased importance. Sprouts grow faster initially but cannot compete with pioneer species over time. Ogden et al. (1991) state that it is the ratio between gap size (horizontal area) and canopy height that determines whether growth from below (of released under-story) or lateral growth from surrounding vegetation will fill the gap. High values of this ratio indicate large gaps where recovery from below also will include the establishment of new individuals and the gap is unlikely to fill in from the side. Even though vertical growth is twice that of lateral growth, the majority of the gaps in their study were closed by lateral growth (their largest gap, 315 m², was relatively small).

When catastrophic winds strike an area, the resources that promote recovery in background-level treefall gaps may be eliminated, and certain forms of subsequent disturbance are encouraged. If defoliation is extensive, fruits and seeds will also be blown down, regardless of their developmental maturity. Even though many species will flower in response to defoliation (see below), a temporal gap of seed availability is created.

### Table VII

| Area (ha) | | | | |
|---|---|---|---|---|
| Minimum | Maximum | Median or average | Wind intensity (km/hr) | Citation |
| — | 37 | 0.04 | 200 | Foster & Boose, 1992 |
| 0.025 | 5 | — | — | Allen, 1992 |
| — | 0.0315 | 0.0013 | — | Ogden et al., 1991 |
| 0.002 | 0.009 | 0.025 | 147 | Webb, 1989 |
| 0.002 | 0.027 | 0.035 | 147 | Webb, 1989 |
| 0.65 | 3786 | 32 | — | Canham, 1978 |
| 10.4 | 31.1 | — | 180–250 | Glitzenstein & Harcombe, 1988 |
| 25 | — | — | — | Lorimer, 1977 |
| 30 | 3370 | 30–100 | — | Nelson et al., 1994 |

Without a supply of mature fruit, the usual seed dispersers, if they survived the disturbance event, will themselves disperse to other less disturbed areas (Boucher, 1990; Yih et al., 1991). The entire system is less able to provide and disperse new plant propagules, and recovery must therefore depend on soil seed banks (if exposed from under the thick litter layer) or vegetative recovery. Large quantities of woody litter over the landscape increases both the possibility of catastrophic fire and the likelihood of insect population explosions.

### 3. Temporal Influences on Recovery

Estimates of recovery time after catastrophic wind vary tremendously, as the result of differences in quantification of recovery, frequencies of disturbance, and, possibly, variations in storm intensity. Unfortunately, recovery times have not been documented frequently enough to evaluate these interacting factors (Table VIII). Most authors suggest that the recovery process is "rapid and widespread" (Applegate & Bragg, 1992) since they observe new leaves within a few weeks (Craighead & Gilbert, 1962; Fernandez & Fetcher, 1991; Frangi & Lugo, 1991; Hopkins & Graham, 1987; Lugo et al., 1983; Pimm et al., 1994; Reilly, 1991; Walker et al., 1992; Webb, 1958; Whigham et al., 1991; Wunderle et al., 1992; You & Petty, 1991) or a few months (Applegate & Bragg, 1992; Bates, 1930; Bellingham, 1991; Bellingham et al., 1992; Dallmeier et al., 1991; Spurr, 1956; Walker, 1991; Yih et al., 1991).

Foster (1988b) suggests a 5–10-year reorganization period before the recovery mechanisms are fully operational. For example, Bates (1930) noted a two–month delay in refoliation following the 1928 hurricane in Puerto Rico. Silver (1992) found that fine root biomass continued to decline nine months after Hurricane Hugo in Puerto Rico. Moss (1940) found significant levels of salt still in the soil six months after the 1938 hurricane in New England. The reorganization period may include delayed mortality, recorded by several researchers after catastrophic wind. It would be interesting, if this reorganization period does occur, to compare the time required to reorganize with the frequency of catastrophic wind events in a given area.

Weaver (1989) proposes three stages in recovery after a hurricane: 1) colonization and growth—establishment and growth of pioneer species; 2) building—a shift from pioneer species to shade–intolerant species; and 3) maturity—shade-tolerant species reaching a self-sustaining steady state of standing biomass. Weaver's (1989) data indicates a shift from the first to the second stage starting at 20 years after the disturbance. Unfortunately,

**Table VIII**

Catastrophic wind recovery time

| Time (years) | Location | Disturbance | Citation |
|---|---|---|---|
| 0.92 | Australia | Cyclone | Turton, 1992 |
| 50[a] | Dominica | Hurricane | Lugo et al., 1983 |
| 30 | Dominica | Hurricane | Beard, 1948 |
| 2–6[a] | USA | Hurricane | Van Hooser & Hedlund, 1969 |
| 45 | Puerto Rico | Hurricane | Weaver, 1986 |
| 10s–100s[a] | Jamaica | Hurricane | Bellingham et al., 1992 |
| 30–100[a] | New England | Hurricane | Clapp, 1938 |
| 40 | New England | Hurricane | Peart et al., 1992 |
| 50 | New England | Hurricane | Merrens & Peart, 1992 |

[a] Predicted recovery time.

his data do not include the dynamics of the first decade following the hurricane, so a possible reorganization period was not evaluated.

Differences in measured recovery time partly are caused by differences in definitions and quantification of recovery. Turton (1992) states that light levels in the understory return to pre-cyclone levels after 11 months but does not state that recovery is complete. Van Hooser and Hedlund (1969) estimate that recovery time for the volume lost in a storm would be the same as "if growth were to continue at the same rate as before the storm," a condition they acknowledge as "highly unlikely." Beard (1948) seemed to rely on the visual appearance of forest structure to evaluate recovery. Peart et al. (1992) also described post-storm recovery based on the structure of the canopy, specifically gap structure. Merrens and Peart (1992) report slightly longer recovery time for the same storm when comparing standing biomass. Weaver (1986) quantified recovery based on stands reaching an apparent steady state in biomass. Bellingham et al. (1992) predicted recovery times from Hurricane Gilbert in Jamaica based on the path of recovery: centuries if pioneer species establish, decades if the recovery is through sprouting of surviving stems. To date, too few studies have actually documented the entire recovery process to draw any conclusions about factors that influence the time to recovery (Crow, 1980).

Frequent catastrophic wind disturbance has led a number of authors to rethink the concept of recovery. Webb (1958) states that the return time of cyclones to north Queensland is much shorter than the life span of trees and proposed that these forests never reach a climax state but are in a constant state of recovery. Others emphasize the role of allogenic influences, as opposed to autogenic compositional changes, in creating new age classes (Foster & Boose, 1992; Henry & Swan, 1974; Oliver & Stevens, 1977). Canham and Loucks (1984) propose that forests in Wisconsin may reach old growth, but not for long before they are again disturbed. Several workers propose that ecosystems in areas of high hurricane frequency will not recover to a steady state but are always in a state of disturbance and recovery (Basnet, 1990; Basnet et al., 1992; Boucher, 1990; Clark, 1990; Lugo et al., 1983; Lugo & Scatena, 1993; Putz & Chan, 1986). In this situation, the concept of "recovery time" is inappropriate.

As mentioned above, the majority of studies of catastrophic wind have quantified only the impacts and the immediate response. But several studies have examined forests in the latter stages of recovery, following, for example, the New England hurricane of 1938 (Foster, 1988a, 1988b; Foster & Boose, 1992; Merrens & Peart, 1992; Peart et al., 1992), a severe wind in Malaysia (Browne, 1949; Wyatt-Smith, 1954), and hurricanes in Puerto

Rico (Crow, 1980; Weaver, 1986, 1987, 1989). However, these studies all fail to document the critical first stage of the dynamics of recovery. Probably only Whitmore's (1974, 1989) plots in the Solomon Islands were established before a catastrophic wind disturbance and then followed for at least a decade thereafter. Several sites are now poised to follow recovery through several disturbance cycles on established plots, in Jamaica (Bellingham, 1991), Nicaragua (Boucher et al., 1990), Mexico (Whigham et al., 1991), and Puerto Rico (Dallmeier et al., 1991; Zimmerman et al., 1994).

### 4. Paths to Recovery

Recovery from catastrophic wind disturbance might be expected to follow one or more of four paths: regrowth, release, recruitment, or repression (Fig. 4). The critical question is, "Will the forests of 10–20 years' time be dominated by regrowth of damaged trees or will saplings and seedlings 'released' by disturbance play a significant role" (Sugden, 1992)? In other words, will there be a shift in the community structure during recovery? Both Oliver (1981) and Halpern (1988) stress the importance of disturbance severity in influencing response. As suggested in Figure 2, control of the path of recovery may be a function of both the type and severity of damage. Other factors may influence recovery, including edaphic characteristics, topography, response differences among species, and previous disturbance (Brokaw & Walker, 1991; Furley & Newey, 1979; Glitzenstein & Harcombe, 1983; Peterson & Pickett, 1991; Spurr, 1956; Tanner et al., 1991; Webb, 1986).

#### a. Regrowth

Regrowth refers to vegetative recovery of surviving stems. The prevalence of this type of recovery depends on the nature and extent of structural damage—e.g., uprooted vs. snapped stems—and on mortality. The importance of regrowth should decline as mortality increases. As most catastrophic wind disturbances cause low to moderate mortality, this recovery path may well be the most common. Of the 47 instances reported in Table IX, 66% include regrowth as one observed path to recovery; a higher percentage (85.2%, $n = 27$) is reported in tropical forests, as compared to temperate forests (40%, $n = 20$).

Boucher (1989) introduced the phrase "direct regeneration" to describe recovery through sprouting. This recovery path has been documented and referred to in a variety of ways: Sauer (1962) described it as "vegetative advance of adjacent survivors," Dunn et al. (1983) referred to "encroachment of canopy trees," Pickering (1986) used the phrase "sprout regeneration," Walker (1991) called it "direct species recovery," and Marks (1974) presented sprouting as one form of "reorganization response."

Regrowth can shift tree-community structure, through a differential ability of species to sprout (Bellingham et al., 1994; Walker et al., 1992; Zimmerman et al., 1994). Shade-tolerant species seem both to survive and to sprout at higher frequencies than pioneer species. Rather than result in a shift to shade-intolerant species, a catastrophic wind event may increase the dominance of established primary-forest trees (Dallmeier et al., 1991; Putz & Sharitz, 1991; Scatena & Lugo, in press; Wyatt-Smith, 1954).

Simple leaf loss may not be especially damaging. Craighead and Gilbert (1962) found that deciduous trees refoliated following hurricane disturbance late in the year and retained their leaves well past the normal time for leaf loss. Putz and Sharitz (1991) reported that defoliation in South Carolina by Hurricane Hugo was not particularly damaging to the deciduous trees since it occurred close to the usual time of leaf loss.
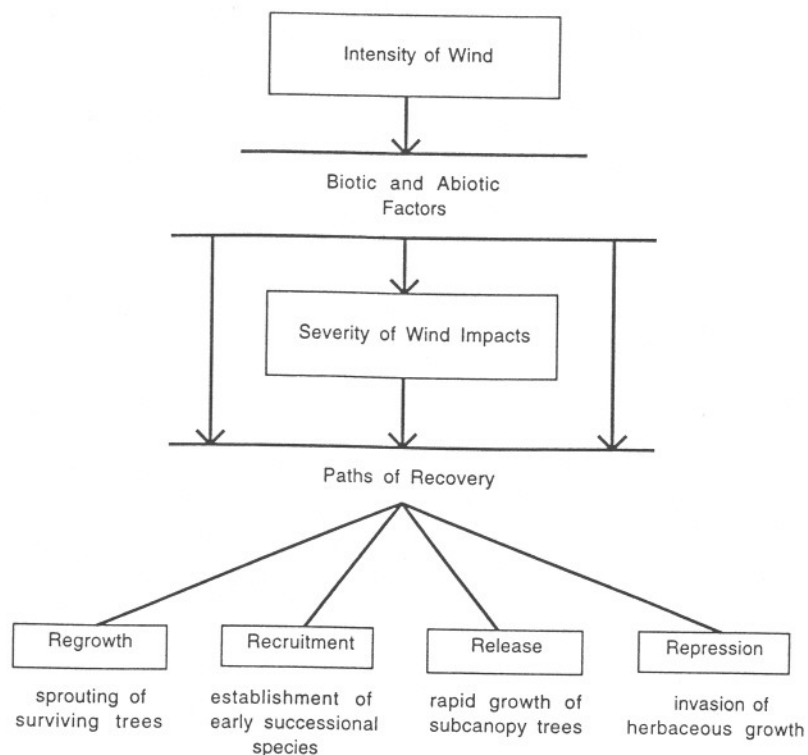
**Fig. 4.** Paths to recovery from catastrophic wind disturbance. Intensity of wind disturbance is filtered through biotic and abiotic factors which amplify or mitigate the severity of damage. The severity of damage, in conjunction with the abiotic and biotic factors, influences the path to recovery. See text for description of recovery paths.

### b. Recruitment

"Recruitment" refers to recovery of the forest through the establishment of seedlings of early successional species. This does not necessarily refer to classical models of secondary succession. Merrens and Peart (1992) suggest a "shortened" succession following the 1938 hurricane in New England, with shortlived pioneer species established briefly, immediately followed by the release of primary-forest species also established at the time of the hurricane. Foster (1988b) suggests that shade-intolerant species are established through canopy disturbance and then suppressed until released by the next disturbance.

Recruitment may occur in localized parts of a wind-affected forest, but it appears to be relatively rare as the principal path of recovery after catastrophic wind, possibly because of the generally low levels of mortality in this type of disturbance. Yih et al. (1991) noted the paucity of pioneer-species seedlings and suggested several possible

**Table IX**

Dynamics of recovery from wind disturbance

| Wind intensity (km/hr) | Mortality | Damage[a] | Sprouting | Rg | Rc | Rl | Rp | Citation |
|---|---|---|---|---|---|---|---|---|
| | | | | Path to recovery[b] | | | | |
| _Temperate Forest_ | | | | | | | | |
| | 15.3 | 7.4 | | | + | + | | Greene et al., 1992 |
| | | 91 | | + | + | + | + | Pickering, 1986 |
| 90 | | 7.1 | | | + | + | | Cremer et al., 1977 |
| 120 | | 60 | | | | + | | Peart et al., 1992 |
| 120 | | | | | + | | | Smith, 1946 |
| 120 | | | | | | + | | Henry & Swan, 1974 |
| 120 | | | | + | + | + | | Merrens & Peart, 1992 |
| 126 | 0.3 | 0.6 | | + | − | + | | Webb, 1986, 1988, 1989 |
| 126 | 5.6 | 6.4 | | | + | | | Webb, 1986, 1988, 1989 |
| 142 | | 66 | | | + | | | Veblen et al., 1989 |
| 155 | 19 | | | + | − | | | Putz & Sharitz, 1991 |
| 155 | | 48.7 | | + | − | | | Putz & Sharitz, 1991 |
| 140–180 | | 20 | | + | | | + | Craighead & Gilbert, 1962 |
| 200s | | | | | + | + | | Spurr, 1956 |
| 200 | 30.7 | 94 | | + | | + | | Foster, 1988a |
| 180–250 | 34 | 83 | 22 | | | + | | Glitzenstein & Harcombe, 1988 |
| 180–250 | 14 | 37 | 75 | | | + | | Glitzenstein & Harcombe, 1988 |
| 242 | | 31 | | | + | | + | Loope et al., 1994 |
| 253 | | 94 | | + | + | + | + | Dunn et al., 1983 |
| 430 | 93 | 99 | 24.9 | − | + | | | Peterson & Pickett, 1991 |
| _Tropical Forest_ | | | | | | | | |
| | | | | | | | + | Lindo, 1968 |
| | | | | + | + | | | Furley & Newey, 1979 |
| | | | | + | + | | | Weaver, 1989 |
| | | | | | + | | | Wyatt-Smith, 1954 |
| | | | | + | + | | + | Browne, 1949 |
| 120 | | 30 | | | | | + | Wadsworth & Englerth, 1959 |
| 147 | | | | + | | + | + | Webb, 1958 |
| 150 | | | | + | | | + | Wood, 1970 |
| 166 | 1 | 10 | 27.5 | + | | | | Frangi & Lugo, 1991 |
| 176 | | 32.8 | | + | | | + | Applegate & Bragg, 1992 |
| 184 | | 36.9 | | + | + | + | + | Whitmore, 1974 |
| 185 | 40 | 32 | | + | | | | Dittus, 1985 |
| 166–194 | | 50 | | + | | | | Scatena & Lugo, in press |
| 166–194 | 9 | 16.7 | 64.8 | + | + | | | Zimmerman et al., 1994 |
| 166–194 | 1 | 4.8 | 37.5 | + | + | + | | Frangi & Lugo, 1991 |
| 166–194 | 7 | 20 | | + | + | | | Walker, 1991 |
| 166–194 | | | | + | + | | | Fernandez & Fetcher, 1991 |

**Table IX** (*continued*)

Dynamics of recovery from wind disturbance

| Wind intensity (km/hr) | Mortality | Damage[a] | Sprouting | Rg | Rc | Rl | Rp | Citation |
|---|---|---|---|---|---|---|---|---|
| | | | | | | | | Path to recovery[b] |
| | | | **Tropical Forest** (*continued*) | | | | | |
| 166–194 | 4 | | 100 | + | | + | | You & Petty, 1991[d] |
| 166–194 | 25 | 38.2 | | + | | | | Dallmeier et al., 1991 |
| 240 | 25 | | | + | + | | + | Sauer, 1962 |
| 240 | | | | + | + | | | Bates, 1930 |
| 241 | 2 | 57.5 | | + | + | + | | Lugo et al., 1983 |
| 250 | 58 | 75 | 83.6 | + | + | | | Boucher, 1990 |
| 250 | 13 | 50 | 5 | + | | | | Boucher, 1990 |
| 255 | 7 | 55.3 | 56 | + | + | | | Bellingham et al., 1992 |
| 255 | 8.1 | 14.3 | 59.3 | + | | | | Bellingham, 1991 |
| 300 | 9.7[c] | 16.9 | | + | | | | Whigham et al., 1991 |

[a] Damage calculated as percent loss of biomass, volume, or stems. [b] Rg = regrowth; Rc = recruitment; Rl = release; Rp = repression. [c] Mortality before fire. [d] Single species studied.

causes: the lack of seed dispersers, thick litter, and inhibition by the root systems of surviving stems. However, the seedlings of shade-tolerant species were found, so the explanation may simply have been the rarity of mature pioneer trees in the area before the hurricane (Yih et al., 1991).

The dual-damage parameter presented in Figure 2 may help predict the severity of damage required for recruitment. Recruitment would be expected after at least low to moderate mortality and/or moderate to high structural damage. The thick litter layer associated with high levels of structural damage might restrict recruitment (Yih et al., 1991). Seedling numbers increased when litter was removed from experimental plots in a forest after hurricane disturbance (Guzman-Grajales & Walker, 1991). However, Pickering (1986) still found recruitment as the primary path to recovery (followed by release and regrowth) in a tornado-impacted forest with high structural damage (91%).

It is possible that the two-dimensional damage gradient space (Fig. 2) misses a critical factor that influences recruitment: disturbance of the substrate. Both Sauer (1962) and Stoneburner (1978) mention ocean waves exposing bare soil as a requirement for recruitment. Spurr (1956) found an association between post-hurricane salvage logging and invasion of pioneer species, which may be tied to soil disturbance. Following wind disturbance, fire bares the substrate and can stimulate establishment of pioneer species (Canham, 1978; Foster, 1988b; Furley & Newey, 1979; Putz & Sharitz, 1991; Smith, 1946; Veblen et al., 1989). Foster (1988b) suggests that the difference between the 1635 hurricane, when pines were established, and the 1938 hurricane, when they were not, was due to the fires that followed the former and not the latter. Snook (1993) hypothesized that much of the mahogany (*Swietenia macrophylla* King) in the Yucatan becomes established when fires follow hurricane damage. However, Whigham et al. (1991) reported on a fire that followed Hurricane Gilbert in the Yucatan and did not find significant recruitment of pioneer species.

### c. Release

"Release" refers to the rapid growth of suppressed subcanopy trees or saplings. These may be either the immature individuals of the dominant canopy species or the vanguard of a significant shift in species dominance. This type of recovery is triggered by both structural damage and mortality to the canopy trees. Spurr (1956) observed stands 10 years after hurricane disturbance and found the canopy to be dominated by species prevalent in the understory at the time of the hurricane. Only in places where the seedling or sapling density was low when the hurricane hit did recruitment of pioneer species predominate. Thus, the tendency for recovery to include the release of the understory, and a possible shift in community composition, is partly tied to stand history. Glitzenstein and Harcombe (1988) found a shift to dominance of shade-tolerant understory stems when the canopy had been dominated by large early-successional species that were removed by a tornado. Veblen et al. (1989) found that a windstorm in Colorado removed the pioneer species (*Pinus contorta* Dougl.) established after a fire and released the shade-tolerant fir and spruce from the understory.

### d. Repression

"Repression" refers to secondary succession that is suppressed by the establishment or growth of plants, often vines (Applegate & Bragg, 1992; Lindo, 1968; Wadsworth & Englerth, 1959; Webb, 1958; Whitmore, 1974; Wood, 1970), that restrict the regrowth or recruitment of trees; it also refers to succession that is suppressed by heavy litter. Former canopy vines may be blown to the ground but not killed and then are poised to dominate recovery. The lack of availability of tree seeds following extensive defoliation may allow dominance of herbs or shrubs that were not defoliated by the wind due to their protected position under the canopy. Some edaphic conditions, particularly drought that has followed many catastrophic wind disturbances (Applegate & Bragg, 1992; Holtam, 1971; Hopkins & Graham, 1987; Touliatos & Roth, 1971), may adversely affect survival of tree seedlings relative to herbaceous species. No investigation of this possibility has been reported.

Heavy structural damage is associated with both high light levels and heavy litter and therefore may encourage or, conversely, repress establishment of early-successional species (Putz & Sharitz, 1991; Whitmore, 1974). Whitmore (1974) suggested that indirect damage to seedlings and saplings that are crushed by falling debris may restrict recovery through release of previously suppressed plants. Yih et al. (1991) suggested that the thick layer of material knocked down by Hurricane Joan was one reason that establishment of pioneer species was so rare in Nicaragua. Canham (1978) suggested that pioneers seldom invade following wind disturbance unless fire, which removes litter, also occurs. Others have discussed the possible effects of wind disturbance and subsequent fire (Foster, 1988b; Furley & Newey, 1979; Loope et al., 1994; Smith, 1946; Snook, 1993; Veblen et al., 1989).

The occurrence of these four paths of recovery is presented in Table IX, but too few studies have followed the recovery process long enough for us to develop strong generalizations. For example, Boucher (1990) emphasized the predominance of regrowth (sprouting) in a rain forest in Nicaragua after a severe hurricane, but noted that mortality of sprouts, and additional delayed mortality of surviving trees, could still change the mode of recovery. Dallmeier et al. (1991) stated that "most previous studies of regeneration after disturbance do not help us to predict the path of succession" for a hurricane-disturbed

site in Puerto Rico. Peterson and Pickett (1991) stated the need for "information from other wind-disturbed forests before we can generalize on the relative contribution of seed banks, surviving seedlings and saplings, colonizing seeds and sprouts to post-disturbance forest structure and before we can relate these sources of regeneration to underlying environmental gradients and disturbance intensities." One point can be made: because of low mortality, the classical secondary succession stage of complete establishment of pioneer species may never follow wind disturbance.

## 5. Mechanisms of Recovery

A variety of species adaptations facilitate recovery from wind disturbance, including 1) resistance to wind damage, 2) ability to sprout, and 3) ability to flower and fruit quickly. The first, resistance to wind, has been covered in some detail above. Species differ in their susceptibility to damage; their tendency toward types of damage such as debranching, uprooting, or snapping; and their resulting mortalities. Dunn et al. (1983) state that few species have adaptations specifically for catastrophic disturbance, but "some specializations that allow species to coexist in non-equilibrium communities dominated by small scale disturbance also pre-adapt them to large-scale disturbance."

### a. Sprouting

A number of researchers have reported differences among species in sprouting ability (Bellingham et al., 1994; Glitzenstein & Harcombe, 1988; Peterson & Pickett, 1991; Putz & Brokaw, 1989; Walker et al., 1992; Zimmerman et al., 1994). Groups that seem to be poor at sprouting are pines (Boucher et al., 1990), palms (Frangi & Lugo, 1991), and pioneers (Putz & Brokaw, 1989; Webb, 1986; Zimmerman et al., 1994). Several workers have noted connections between sprouting, damage level, and tree size: a higher frequency of sprouting with broken stems than with uprooted stems (Putz et al., 1983), increased incidence of sprouting with more branch damage and with broken stems (Zimmerman et al., 1994), more sprouting with broken stems or complete defoliation (Bellingham et al., 1994). Bellingham et al. (1994) also found that larger undamaged stems and smaller damaged stems sprouted more. However, Harcombe and Marks (1983) determined that sprouting was not associated with higher damage; trees were either highly damaged and died or had low to moderate damage and sprouted. A generalization emerging (Table X; also see Glitzenstein & Harcombe, 1988) is that overall sprouting following catastrophic wind disturbance is positively correlated to available water.

Survival of sprouts varies across sites: 40.6% in gaps in Panama (Putz & Brokaw, 1989), 68% for a tornado-impacted forest in Pennsylvania (Peterson & Pickett, 1991), and 74% for gaps in Texas (Harcombe & Marks, 1983). This small sample of studies does not allow us to generalize about the environmental factors that influence sprout survival. But stems with sprouts survived better than stems without them in Bellingham et al.'s (1994) study of hurricane damage. Among sprouting stems in treefall gaps, Putz and Brokaw (1989) found lower survival in larger than smaller stems. Despite sometimes high mortality of sprouts and sprouting stems, sprouting may still play an important role in recovery. After 12 years of recovery in a Panamanian forest, sprouting was present in 38 of 46 gaps studied (Putz & Brokaw, 1989), whereas pioneer trees were restricted to larger treefall gaps. In the large gaps, sprouts grow faster initially but cannot out-compete pioneer species over time.

**Table X**

Sprouting response to catastrophic wind

| Sprouting (percent) | Moisture | Wind intensity (km/hr) | Region | Citation |
|---|---|---|---|---|
| 24 | Mesic | — | Temperate | Harcombe & Marks, 1983 |
| 22.4 | Mesic | 180–250 | Temperate | Glitzenstien & Harcombe, 1988 |
| 72.3 | Hydric | 180–250 | Temperate | Glitzenstein & Harcombe, 1988 |
| 24.9 | Mesic | 430 | Temperate | Peterson & Pickett, 1991 |
| 53 | Hydric | — | Tropical | Putz & Brokaw, 1989 |
| 59.3 | Hydric | 160–185 | Tropical | Bellingham, 1991 |
| 56 | Hydric | 160–185 | Tropical | Bellingham et al., 1992 |
| 61.4 | Hydric | 160–185 | Tropical | Bellingham et al., 1994 |
| 64.8 | Hydric | 166–194 | Tropical | Zimmerman et al., 1994 |
| 27.5 | Hydric | 166–194 | Tropical | Frangi & Lugo, 1991 |
| 83.6 | Hydric | 250 | Tropical | Boucher et al., 1990 |
| 5 | Hydric | 250 | Tropical | Boucher et al., 1990 |

### b. Flowering and Fruiting

Numerous researchers have noted unseasonal or abnormally intense flowering following catastrophic wind disturbance: a hurricane in Puerto Rico (Bates, 1930), a hurricane in Florida (Craighead & Gilbert, 1962), a hurricane in Dominica (Lugo et al., 1983), cyclones in Mauritius (King, 1945), and cyclones in Australia (Applegate & Bragg, 1992; Hopkins & Graham, 1987; Webb, 1958). All reported cases involved relatively intense disturbances. Either less intense wind disturbance does not elicit this response or researchers in those cases did not look for it. Defoliation is thought to stimulate the flowering response (King, 1945; Webb, 1958; Vaughan & Wiehe, 1937).

Increased flowering would produce more fruiting. In Puerto Rico, Walker and Neris (1993) found post-hurricane seedfall in gaps to be double that of pre-hurricane levels and found intact forest seedfall to be triple that of pre-hurricane levels. During their 20-month post-hurricane study they did not find an increase over time, and they reported that the spatial heterogeneity was greater than the temporal. Of course, immediately after a catastrophic storm that strips trees of flowers and fruits, one would expect reduced fruiting. Thus several workers have noted decreased fruit abundance immediately after catastrophic wind disturbance (Lynch, 1991; Synder & Synder, 1979; Wiley & Wunderle, 1994; Zamore, 1981). Immediately after a cyclone hit a Sri Lankan forest, fruiting and flowering was significantly less than before, but then fruiting seemingly increased (not significantly) in later years to a higher level than before the disturbance (Dittus, 1985).

### c. Damage Type

The form of stem damage, specifically uprooting vs. stem breakage, can influence the pathway of recovery. Schaetzl et al. (1989a) use the term "floralturbation" for the mixing of soil associated with uprooting, which creates microsites for germination of pioneer species (Foster, 1988a). Consequently, pioneer trees were more common in gaps caused by uprooting than in those caused by snapped stems in a Panamanian forest (Putz, 1983).

Frequency of sprouting may also vary with disturbance type. Putz et al. (1983) found higher sprouting in snapped stems (51%) than in uprooted stems (6%). Walker (1991) found the immediate and delayed mortality of snapped stems to be lower (15%) than that of uprooted stems (23%). Since the number of stems uprooting affects sprouting, survival of damaged stems, and establishment of pioneer species, it has been suggested as a measure of the severity of disturbance (Peterson & Pickett, 1991).

Table XI summarizes the conditions associated with uprooting of stems reported in 39 papers (19 tropical, 20 temperate sites). The reported percentages are the proportion of total stems damaged that were uprooted rather than snapped. Cruickshank et al. (1962) suggested that stem breakage increases with intensity of wind disturbance, but this trend is not evident in either the tropical or temperate sites where low proportions of uprooting (and therefore high stem breakage) occurs with both chronic winds (23%: Putz et al., 1983; 0%: Harcombe & Marks, 1983) and intense (>300 km/hr) winds (10%: Gunter & Eleuterius, 1971; 25.8%: Whigham et al., 1991). Allen (1992) reported more uprooting in moist forests and swamps and in connection with storms accompanied by high rainfall. This trend seems evident for tropical sites, where uprooting does not exceed 26% for either xeric or mesic sites. No clear trend relative to site or storm moisture occurs in temperate sites.

### d. Multiple Disturbance Interactions

Wind disturbance may render a forest more susceptible to other disturbances (Glitzenstein & Harcombe, 1988; Ogden et al., 1991) that alter recovery. Wind disturbance may interact with fire, drought, insect invasion, anthropogenic activities, and subsequent wind disturbance. We have already seen that wind disturbance may increase or decrease susceptibility of a stand to subsequent wind events (see D.1.b and D.2.d).

Because catastrophic wind disturbance creates large fuel loads, fire is the most commonly predicted subsequent disturbance (Clapp, 1938; Gardner et al., 1991; Glitzenstein & Harcombe, 1988; Hook et al., 1991; Lindo, 1968; Putz & Sharitz, 1991). Glitzenstein and Harcombe (1988) and Hook et al. (1991) calculated the increased fuel load resulting from catastrophic wind events; the former found that a tornado increased fuel load 400% in a Texas forest, and the latter found eight times the normal fuel load after Hurricane Hugo struck forests in South Carolina. However, just a few cases of fire after catastrophic wind have been reported. Craighead and Gilbert (1962) reported that extensive fires followed the 1935 hurricane in Florida. Whigham et al. (1991) estimated that post-hurricane fires in the Yucatan had more impact on mortality of trees than did Hurricane Gilbert (and see Furley & Newey, 1979).

Fire after wind disturbance has a greater likelihood of significantly changing community composition than does wind alone. Windthrow and fire together increase the severity of disturbance, establishment of early-successional species, likely development of large, even-aged stands, and time for recovery (Canham, 1978; Canham & Loucks, 1984; Glitzenstein & Harcombe, 1988; Veblen et al., 1989; Webb, 1958; Wyatt-Smith, 1954).

Fires do not always follow wind disturbance. After gale damage in Britain there were no fires even though summers were unusually dry (Holtam, 1971); fire risk, however, was reduced by timber salvage. Furley and Newey (1979) noted fires in Belize following a hurricane disturbance in 1961, but an earlier study (Wolffsohn, 1967) reported that the fires were caused by an extremely dry year. In comparing hurricane-disturbed areas to those protected from the wind, Wolffsohn (1967) found fire no more common or likely to spread in the former. However, timber downed by the hurricane did make access and

### Table XI

Percent uprooting in response to wind

| Percent uproot | Wind intensity | Forest type | Moisture | Citation |
|---|---|---|---|---|
| | | | | **Temperate Forest** |
| 0 | Chronic | Mixed | Mesic | Harcombe & Marks, 1983 |
| 25 | Chronic | Conifer | Mesic | Gordon, 1973 |
| 18 | Chronic | Conifer | Mesic | Veblen, 1986 |
| 30 | Chronic | Conifer | Mesic | Veblen, 1986 |
| 22 | Chronic | Broadleaf | Mesic | Runkle, 1982 |
| 87 | Chronic | Mixed | Mesic | Falinski, 1978 |
| 81.2 | 60–75 | Conifer | Mesic | Versfeld, 1980 |
| 72.4 | | Broadleaf | Mesic | Reiners & Reiners, 1965 |
| 84 | | Broadleaf | Hydric | Reiners & Reiners, 1965 |
| 58 | 80–120 | Conifer | Hydric | Stoeckeler & Arbogast, 1955 |
| 7 | 80–120 | Broadleaf | Mesic | Stoeckeler & Arbogast, 1955[b] |
| 38 | 80–120 | Conifer | Mesic | Stoeckeler & Arbogast, 1955[b] |
| 63 | 80–120 | Conifer | Mesic | Stoeckeler & Arbogast, 1955[b] |
| 20 | 96–120 | Conifer | Mesic | Webb, 1988 |
| 63 | 96–120 | Conifer | Mesic | Webb, 1988 |
| 99 | 144 | Conifer | Mesic | Trousell et al., 1965 |
| 37 | 155 | Mixed | Hydric | Putz & Sharitz, 1991 |
| 45 | 155 | Mixed | Mesic | Putz & Sharitz, 1991 |
| 90 | 160 | Mixed | Mesic | Cruickshank et al., 1962 |
| 30 | 160 | Mixed | Mesic | Cruickshank et al., 1962 |
| 93 | 200[a] | Conifer | Mesic | Foster, 1988a |
| 11 | 200[a] | Conifer | Mesic | Foster, 1988a |
| 89 | 200[a] | Mixed | Mesic | Foster, 1988a |
| 88 | 200[a] | Mixed | Mesic | Foster, 1988a |
| 95 | 200[a] | Mixed | Mesic | Foster, 1988a |
| 82 | 221 | Conifer | Mesic | Boe, 1965 |
| 86 | 221 | Broadleaf | Mesic | Boe, 1965 |
| 24 | 180–250 | Mixed | Mesic | Glitzenstein & Harcombe, 1988 |
| 48 | 180–250 | Broadleaf | Hydric | Glitzenstein & Harcombe, 1988 |
| 48 | 194–235 | Conifer | Mesic | Hook et al., 1991 |
| 33 | 194–235 | Conifer | Mesic | Hook et al., 1991 |
| 25–33 | 242 | Conifer | Mesic | Loope et al., 1994 |
| 37.4 | 320 | Conifer | Mesic | Van Hooser & Hedlund, 1969[c] |
| 56.9 | 320 | Broadleaf | Mesic | Van Hooser & Hedlund, 1969[c] |
| 10 | 349 | Mixed | Mesic | Gunter & Eleuterius, 1971 |
| 66.5 | 430 | Conifer | Mesic | Peterson & Pickett, 1991 |
| | | | | **Tropical Forest** |
| 23 | Chronic | Broadleaf | Mesic | Putz et al., 1983 |
| 80 | Chronic | Broadleaf | Hydric | Uhl et al., 1988 |
| 90 | Chronic | Broadleaf | Hydric | Hartshorn, 1980 |
| 40 | Chronic | Broadleaf | Hydric | Putz & Appanah, 1987 |

**Table XI** *(continued)*

Percent uprooting in response to wind

| Percent uproot | Wind intensity | Forest type | Moisture | Citation |
|---|---|---|---|---|
| | | Tropical Forest (continued) | | |
| 51 | Chronic | Broadleaf | Hydric | Lawton & Putz, 1988 |
| 14.6 | 150 | Broadleaf | Mesic | Wood, 1970 |
| 51 | 166 | Broadleaf | Hydric | Walker et al., 1992 |
| 43 | 166 | Broadleaf | Hydric | Walker et al., 1992 |
| 55.6 | 166 | Palm | Hydric | Frangi & Lugo, 1991 |
| 45 | 166 | Broadleaf | Hydric | Walker, 1991 |
| 47.9 | 166–194 | Broadleaf | Hydric | Zimmerman et al., 1994 |
| 17.8 | 220 | Mixed | Hydric | Thompson, 1983 |
| 78.5 | 212 | Broadleaf | Hydric | Dallmeier et al., 1991 |
| 87.8 | 230 | Broadleaf | Hydric | Basnet et al., 1992 |
| 58.3 | 241 | Broadleaf | Hydric | Lugo et al., 1983 |
| 20 | 241 | Broadleaf | Xeric | Lugo et al., 1983 |
| 29 | 250 | Broadleaf | Hydric | Yih et al., 1991 |
| 62 | 250 | Conifer | Hydric | Boucher et al., 1990 |
| 42 | 250 | Broadleaf | Hydric | Boucher et al., 1990 |
| 60.6 | 205–255 | Broadleaf | Hydric | Bellingham, 1991 |
| 40.6 | 255 | Broadleaf | Hydric | Bellingham, 1991 |
| 26 | 255 | Broadleaf | Hydric | Bellingham et al., 1992 |
| 28 | 255 | Broadleaf | Hydric | Bellingham et al., 1992 |
| 41 | 255 | Broadleaf | Hydric | Bellingham et al., 1992 |
| 66 | 255 | Broadleaf | Hydric | Bellingham et al., 1992 |
| 53 | 255 | Broadleaf | Hydric | Bellingham et al., 1992 |
| 48 | 255 | Broadleaf | Hydric | Bellingham et al., 1992 |
| 25.8 | 300 | Broadleaf | Mesic | Whigham et al., 1991 |

[a] Heavy rains accompanied storm; [b] single species; [c] average of multiple plots.

fire control more difficult. Periods of low rainfall following catastrophic wind may increase the possibility of fire and may limit the establishment and survival of recruiting or regrowing vegetation. A drought after Hurricane Camille struck Mississippi increased subsequent mortality (Touliatos & Roth, 1971), and moisture stress delayed refoliation when drought followed a cyclone in Australia (Applegate & Bragg, 1992).

The woody debris brought down by wind disturbance also creates conditions for explosive growth of insect populations such as wood-boring beetles, engraving beetles, weevils, and termites. Numerous researchers have noted the possibility of increasing insect populations following catastrophic wind disturbance (Decker et al., 1962; Gardner et al., 1991; Nelson & Stanley, 1959; Steven, 1953a), and actual increases have often been reported (Bates, 1930; Gunter & Eleuterius, 1971; Luitjes, 1977; Touliatos & Roth, 1971; Wilkinson et al., 1978). Fewer studies have documented commensurate damage by insects to vegetation (Fuhrer & Kerck, 1978; Hook et al., 1991). Wilkinson et al. (1978) stated there was no evidence of insects spreading to adjacent vegetation after catastrophic wind in the southeast United States. Thompson (1983) reported that insect populations did not

increase as expected after a hurricane in Jamaica and offered three explanations: 1) an unusually wet season, 2) too rapid decomposition, or 3) plentiful food on the forest floor that diverted invasion of living trees.

Downed timber is sometimes salvaged after catastrophic wind disturbance. This human disturbance may reduce the risk of fire, as was the case following gale damage in Scotland (Holtam, 1971). Soil disturbance by salvage logging may, like fire, increase available sites for pioneer establishment. Pickering (1986) found twice the number of seedlings in tornado-disturbed sites that were salvage logged than in disturbed sites that were not logged. Spurr (1956) described the interaction between these two disturbances in three scenarios after a hurricane: 1) if advance regeneration exists in the understory and no salvage logging is done, the recovery will be an "accelerated succession" (release); 2) if advanced regeneration exists and salvage logging occurs, advanced regeneration will be mixed with pioneer species (recruitment); and 3) if no advance regeneration exists, pioneers will establish regardless of human activity.

### F. TEMPERATE AND TROPICAL DIFFERENCES

The frequency of disturbance from catastrophic wind relates to position on the globe, and this difference in frequency may result in differences in the effects of and recovery from wind disturbance. Temperate and tropical systems may vary in 1) disturbance frequency or "return time," 2) type and severity of damage, 3) recovery time, and 4) path to recovery.

Calculations of return time (Table XII) are hard to compare. They may indicate the average time between disturbances at a given point or for a region, or they may be "turnover time," calculated by dividing the total area of interest by the amount of area affected per unit time by disturbances. Taking another approach, Barker and Miller (1990) looked at the number of hurricanes that struck Jamaica each year for the last century and calculated the probabilities for a given number to occur in a year (0.45 probability of more than one hurricane per year). It is also difficult to compare return times for storms of contrasting intensity. With these provisos in mind, it appears that return times for the tropics are generally shorter than those for temperate regions, and tropical storms tend to be more intense events, i.e., cyclones and hurricanes. Where return times in the temperate zone are short, these often involve less intense windstorms.

Species characteristics differ among these regions of the globe. Comparing all tropical species to all temperate species in Table IV, the temperate sites have a greater proportion of susceptible species (53.7%, $n = 95$) than the tropical sites (40.2%, $n = 164$). The reverse is, of course, true for the resistant species. Temperate sites tend to have a greater proportion of uprooting (51.8%, $n = 36$, compared to 47.3%, $n = 28$; Table XI) and a corresponding lower average percent of sprouting (35.9%, $n = 4$, compared to 51.5%, $n = 8$; Table X). The increased sprouting at tropical sites may also relate to average differences in water availability. Putz et al. (1983) related the increased incidence of snapping in the tropics to a greater incidence of less dense wood.

There appear to be latitudinal differences in the factors that influence severity of damage, but these may reflect the focus of investigators. In Table VI, temperate forest researchers identified soil depth, the presence of an impermeable soil layer, and restricted root growth as important factors much more often than did researchers at tropical sites. Soil water has been identified as an important factor more often in the tropics. Differences also exist in the perceived role of topography. Only tropical researchers have noted

**Table XII**

Frequency of catastrophic wind disturbance

| Return time (years) | Based on | Location | Citation |
|---|---|---|---|
| Temperate Forest | | | |
| 2 | Windstorm | OR, USA | Weidman, 1920b |
| 5.8 | Hurricane | SC, USA | Gresham et al., 1991 |
| 10–12 | Windstorm | Australia | Cremer et al., 1977 |
| 20–25 | 80 km/hr | WI, USA | Stoeckler & Arbogast, 1955 |
| 34 | Gale | Ireland | Gallagher, 1974 |
| 50 | 25 m/s | Britain | Allen, 1992 |
| 75 | Gale | Scotland | Fraser, 1971 |
| 70–100 | Hurricane | MA, USA | Foster, 1988b |
| 10 | Windstorm | New Zealand | Shaw, 1983 |
| 100–150 | Windstorm | Britain | Moore, 1988 |
| 100–280 | Soil turnover | New Zealand | Wardle, 1970 |
| 220–400 | Turnover | New Zealand | Ogden et al., 1991 |
| 220–2439 | Soil turnover | MI, USA | Whitney, 1986 |
| 1150 | >25 ha gaps | ME, USA | Lorimer, 1977 |
| 1210 | Windstorm | WI, USA | Canham & Loucks, 1984 |
| 1000–3000 | Windstorm | NY, USA | Seiscab & Orwig, 1991 |
| 1316–2632 | Soil turnover | MI, USA | Whitney, 1986 |
| 1587–3174 | Soil turnover | MI, USA | Whitney, 1986 |
| 1730 | Soil turnover | IL, USA | Schaetzl et al., 1989a |
| 12500–25000 | Soil turnover | MI, USA | Whitney, 1986 |
| Tropical Forest | | | |
| 1 | Cyclone | Mauritius | Vaughan & Wiehe, 1937 |
| 11 | Cyclone | Mauritius | Bauer, 1964 |
| 1.2 | Hurricane | Jamaica | Bellingham, 1991 |
| 1.25 | Cyclone | Solomons | Whitmore, 1974 |
| 7.2 | Cyclone | Queensland | Bauer, 1964 |
| 3–40 | Cyclone | Queensland | Webb, 1958 |
| 10 | Hurricane | Puerto Rico | Bauer, 1964 |
| 13 | Hurricane | Belize | Lindo, 1968 |
| 6–20 | Cyclone | Fiji | Gane, 1970 |
| 18 | Windstorm | Sri Lanka | Dittus, 1985 |
| 20 | Hurricane | St. Vincent | Beard, 1945 |
| 24 | Cyclone | Sri Lanka | Dittus, 1985 |
| 225–300 | Turnover | Sri Lanka | Dittus, 1985 |

decreased damage on exposed ridges, and only temperate researchers have reported on the role of lee slopes in either increasing or decreasing damage.

Measures of rate of recovery are too rare in the literature to identify clear differences among regions on the globe (see Table VIII). Peterson and Pickett (1991) found only 44% plant cover on tip-up mounds following a tornado in Pennsylvania and compared this to

recovery in Panama, where Putz (1983) found 100% cover after one year and proposed only a three- to five-month window of opportunity for establishment after gap creation. Peterson and Pickett (1991) propose several explanations for this contrast: mound size, rate of pit filling, seed availability, and growing season. Comparing differences in recovery rates is further hampered by a lack of a standard for comparing severity of damage.

An examination of Table IX shows differences in the reported paths to recovery for temperate and tropical forests. As reported above, regrowth (sprouting) has been reported twice as often in tropical sites (85.2%) as in temperate ones (40%). Both tropical sites and tropical forest species have been observed to have higher proportions of sprouting. Suppression also occurs slightly more often in the tropics (29.6%, compared to 20%). Temperate forest researchers have reported release much more often that tropical forest researchers (65%, $n = 20$, compared to 22.2%, $n = 27$).

## IV. Summary

This review has identified some clear trends in forest damage and recovery from catastrophic wind, and it has illuminated questions for focusing future research. We presented seven critical questions at the start of this paper and will now review the significant findings relative to each and suggest hypotheses derived from these findings.

Intensity of wind disturbance should be quantified based on wind speed, both sustained and gusts. These values vary over the landscape, so distance from the wind measurement site must be included. In addition, the duration of the winds may influence the severity of impacts. Finally, hurricanes and cyclones often involve significant rainfall, which may influence the type and severity of damage. Building on the work of Scatena and Larsen (1991), we suggest that all studies of catastrophic wind impacts should include these five measurements: 1) maximum sustained wind, 2) maximum gusts, 3) storm duration, 4) rainfall total and percent of average annual rainfall, and 5) distance between the study site and the site of measurement of the above parameters.

How should catastrophic wind impacts be quantified? Different measures of hurricane damage result in different conclusions about severity of disturbance. To facilitate comparisons among sites we suggest a dual measure of severity: 1) structural loss—percent basal area lost; and 2) compositional loss—percent mortality. Regardless of individual research questions, catastrophic-wind researchers should report totals for their sites that include structural loss and compositional loss.

Two specific damage-quantification issues require additional research. First, what are the conditions that control stem snapping vs. stem uprooting? All researchers should distinguish between these two types of "windthrow" and, where possible, report variations in their proportion relative to environmental conditions. Second, the issue of delayed mortality following catastrophic wind disturbance needs further examination. Evidence supports the hypothesis that mortality rate returns to background levels within five years following disturbance. This should be tested by following plots of damaged and undamaged forests through the first decade of recovery.

Does catastrophic wind result in homogeneous damage across the landscape? Catastrophic wind damage does not uniformly affect the landscape. Increasing intensity of wind results in a gap size distribution increasingly skewed to larger gaps, but the full range of gap sizes from small to large is still created. With increasing damage, the landscape changes from a forest with gaps to one with isolated stands of intact forest.

Future research should include analysis of gap size distribution and measures of landscape fragmentation to allow comparisons across a wind-intensity gradient and among regions of the globe.

How do biotic factors influence severity of damage? Stem size, species, stand conditions, and pathogens may all influence the severity of damage during a windstorm. We hypothesize that the relationship between stem size and damage is unimodal and that studies indicating other patterns are limited in sample size or by the categories of stem size used in the analysis. The differential effects of wind on different species are so thoroughly documented in the literature that further studies focusing exclusively on this issue are not recommended; energy might be better spent focusing on more general trends such as how damage relates to successional class. Pioneer species appear to be more susceptible to damage and more likely to die. The relationship between stand conditions and damage has been examined for managed stands, but not as thoroughly for natural forests. Another focus for future study should be the role of pathogens in influencing damage, particularly in the tropics.

How do abiotic factors influence the severity of damage? Topography, disturbance history, and soil conditions all influence severity of damage. The role of topography in channeling wind is complex. Valleys are not always protected sites, even when their aspects do not align with the storm winds. Of particular interest is the influence of lee slopes, which may provide protection and may be sites of turbulent airflow and therefore increased damage. Analysis of landscape patterns of damage should help us develop models to assess exposure accurately.

Disturbances that partly open the canopy promote further disturbance from wind. More homogeneous disturbance can create even canopies that are resistant to wind. Multiple wind-disturbance events often reduce further damage, as each removes susceptible individuals and leaves more windfirm ones. Soil conditions that restrict root systems promote disturbance. Although root growth has been extensively studied in plantation forests, again, this would be a valuable focus for future research, particularly in the tropics.

The relative roles of different biotic and abiotic factors in controlling catastrophic wind damage are difficult to identify when each varies over the landscape, usually not independently. Plots should be established, either before disturbance in areas of high storm frequency or following a catastrophic wind event, specifically to isolate these variables and determine their relative importance.

What are the dynamics of recovery from catastrophic wind impacts? Much more work is required in this area over longer time frames. Four distinct paths to recovery are identifiable: regrowth, recruitment, release, and repression. But the influence of disturbance severity and environmental gradients on these paths is little understood. It is critical to determine the factors that lead to these different recovery paths. We propose that the dual-damage parameter of structural and compositional damage holds promise for predicting the principal path to recovery. More data is needed to map regions of recovery paths within this gradient space.

Several other issues of recovery deserve further analysis. First, what is the role of soil moisture in influencing the rate and path to recovery? Here it would help to manipulate water in areas of different damage severity. Second, what cues stimulate flowering and fruiting after wind disturbance? Simulating disturbance of varying severity through defoliation, debranching, and stem snapping could help to identify the critical signal for this response and determine how this response varies in different species. This could be an example of an adaptation specifically for catastrophic wind disturbance, since defolia-

tion does not occur with background tree mortality. Additionally, the question of whether this response relates in any way to successional class of the tree has not been examined. Third, is there a reorganization period following catastrophic wind disturbance, and how does its length vary over regions of the globe? The difficulty here is in identifying a parameter to use in quantifying recovery. A measure of net system energy transfer—e.g., photosynthesis to respiration ratio—might be appropriate. Fourth, the issue of interacting disturbances is a complex one. But since most forests are subjected to a variety of types of disturbances, understanding the interactions between them and the resulting dynamics of recovery is critical.

What are the differences between tropical forests and temperate forests in terms of disturbance and recovery? There appears to be a latitudinal gradient of increasing frequency and intensity of catastrophic wind toward the tropics and corresponding differences in the rate and path to recovery. Numerous authors have developed maps of storm events for different regions of the globe. Combining these efforts into one map that scores regions of the globe based on their catastrophic wind disturbance regime would be a valuable addition to the literature.

Catastrophic wind disturbance may be an important factor in determining patterns of vegetation community structure. Much of the research examining these events has been merely descriptive and has focused only on the severity of disturbance and the initial response. To develop robust theories incorporating catastrophic wind disturbance, we must focus future research toward determining the relative roles of different biotic and abiotic factors in controlling the patterns of severity of damage, and we must relate environmental gradients and severity of damage to long-term dynamics of recovery.

## V. Acknowledgments

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