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Catastrophic wind damage to North American forests and the potential impact of climate change

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Abstract

Catastrophic winds from tornadoes and downbursts are a major cause of natural disturbance in forests of eastern North America, accounting for thousands of hectares of disturbed area annually. Wind disturbance shows substantial regional variation, decreasing from the mid-west to the east and from the south-east to New England. In terms of the relative importance among these types of storms, more forest damage results from tornadoes in the south-east and mid-west, while downbursts are the most important type of wind disturbance in the Great Lakes area. Downbursts vary widely in size, but large ones can damage thousands of hectares, while tornadoes are much smaller, seldom affecting more than several hundred hectares. Tornadoes cause the most severe wind disturbances. Site characteristics such as physiography, soil moisture, and soil depth; stand characteristics like density and canopy roughness; and tree characteristics such as size, species, rooting depth, and wood strength, are the factors most recognized as influencing damage patterns. The consequences of wind damage to forests, such as change in environmental conditions, density, size structure, species composition, and successional status, occur on both immediate (hours-to-days) and long-term (months-to-decades) time scales. Most wind disturbances result in the post-disturbance vegetation being comprised of surviving canopy trees, and varying amounts of sprouts, released understory stems, and new seedlings. Stand size structure is usually reduced, and successional status of a forest is often advanced. Diversity can be either increased or decreased, depending on the measure of abundance used to calculate diversity. Because tornadoes and downbursts are in part products of thermodynamic climatic circumstances, they may be affected by anticipated changes in climatic conditions as the 21st century progresses. However, the current understanding of tornado and downburst formation from supercell storms is very incomplete, and climate-change model predictions sufficiently coarse, that predictions of changes in frequency, size, intensity, or timing of these extreme events must be regarded as highly uncertain. Moreover, retrospective approaches that employ tree demography and dendrochronology require prohibitively large sample sizes to resolve details of the relationship between climate fluctuations and characteristics of these storms. To improve predictions of changes in the climatology of these storms, we need improved understanding of the genesis of tornadoes and downbursts within thunderstorms, and greater

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resolution in global climate models. To improve coping strategies, forest scientists can contribute by giving more attention to how various silvicultural actions influence stand and tree vulnerability. Finally, increased focus on the dynamics of forest recovery and regrowth may suggest management actions that can facilitate desired objectives after one of these unpredictable wind disturbances.

Keywords: Tornado; Downburst; Thunderstorm; Supercell; Treefall; Blowdown; Wind disturbance; Forest

1. Introduction

Forests of eastern North America are subject to numerous types of disturbances, many of which are at least partially influenced by climatic characteristics and thus, subject to the magnitude, direction, and timing of climate changes. Wind disturbances, while poorly studied, can affect areas up to thousands of hectares per event and in locations where fire is rare, may be the most important disturbance type in terms of influences on forest composition and dynamics (Everham and Brokaw, 1996; Turner et al., 1997). This review examines the existing literature on the occurrence of continental (non-hurricane) windstorms, the forest damage and recovery following catastrophic wind in eastern North America, and potential implications of changes in climate to this disturbance/forest interaction. Catastrophic continental wind events for the purpose of this review are those with wind speeds exceeding 150 km/h, and in eastern North America consist of downbursts and tornadoes, although I will utilize findings and recommendations from other types of wind disturbances, when appropriate. As defined by Pickett and White (1985), disturbance in this context can be considered as any discrete wind event that disrupts population or community structure, and increases substrate and/or resource availability.

1.1. Economic and human importance

Tornadoes cause more human mortality in the US than any other weather phenomenon except lightning (Snow, 1984). The 30-year mean annual number of US fatalities (1961–1990) was 82 (Leftwich et al., 1992), but the deadliest recent years in terms of tornado fatalities have been 1974, 1984, and 1998, when 350, 122, and 129 people, respectively, were killed by these storms (McCarthy and Schaefer, 1999). The weather system that caused severe tornadoes in Oklahoma and Kansas, then later in Tennessee, in May 1999, led to 54 deaths in just 4 days. Despite their small size relative to other meteorological events, tornadoes can also cause immense economic disruption: a single North Carolina tornado caused an estimated US$100 million damage in November of 1988 (Ferguson et al., 1989), as did the Catoosa, Oklahoma tornado of April 1993 (Crowther, 1994). Groups of tornadoes in an outbreak can be even more destructive: the November 1992 tornado outbreak caused a total of at least US$291 million in damage (NOAA, 1993), and property damage estimated at US$300 million resulted from a storm system that caused tornadoes in Mississippi, Alabama, Georgia and Tennessee on 8 April 1998 (McCarthy and Schaefer, 1999). Estimated annual damages from tornadoes can be high even in years without exceptional tornado outbreaks: damages in 1994 totaled US$481 million in the US (Crowther, 1995). The National Climatic Data Center (NCDC 1999) reports that the USA has suffered 44 weather-related disasters during 1980–1999 that have surpassed US$1 billion (estimated) in total costs and damages. Of these, three were tornado-related: the Oklahoma/Kansas tornadoes of May 1999 (US$1 billion), the Arkansas/Tennessee tornadoes of January 1999 (US$1.3 billion), and the combined flooding and tornadoes of March 1997 in the Mississippi and Ohio valleys (US$1 billion). In an assessment of all types of damage associated with tornadic and non-tornadic thunderstorms, Changnon and Changnon (1992) reported the most costly tornado outbreak as that of April

1974, which resulted in US$1.4 billion in *insured* losses. During the period of 1950–1989, the catastrophic thunderstorm/tornado damages totaled US$25.4 billion (Changnon and Changnon, 1992).

Downbursts are more poorly-understood than tornadoes, and because of the difficulty of recognizing them, poorly documented. Analogous statistics on long-term average deaths and costs are not available, primarily because downbursts were not widely recognized as distinct meteorological phenomena until the early 1980s. Nevertheless, it is known that downbursts, and especially the small ones called microbursts, can pose a major safety hazard to aircraft during takeoff and landing (Caracena et al., 1989). During the period 1964–1984, at least 27 commercial aircraft accidents were associated with microbursts, causing 491 deaths and 206 injuries (McCarthy and Serafin, 1984). A series of downbursts that struck Adirondack Park in upstate New York in 1995 damaged forests across 392 000 ha, which had an estimated total salvage value of US$197.3 million, most of which was unsalvaged (Robinson and Zappieri, 1999).

Despite these findings, some consequences of tornadoes and downbursts may be positive, at least for the forests themselves. The loss of canopy and consequent increases in soil temperature (Peterson et al., 1990) are likely to increase microbial activity and thereby enhance nutrient turnover in the soil. In locations where soil podzolization is likely, the turnover of surface soil horizons by uprooting trees in windstorms counteracts this process (Lutz, 1940; Mueller and Cline, 1959). As noted below, the microsites created by windthrow can sometimes provide regeneration niches that allow certain species to be retained in what would otherwise be a lower-diversity forest (Sharitz et al., 1993; Long et al., 1998). For species that are short-lived, but persist in a soil seed bank, the periodic disturbances created by windstorms facilitate the persistence of the seed bank species by providing another opportunity for growth and replenishment of the seed pool in the soil (Peterson and Carson, 1996). Thus, while most human and economic effects are strongly negative, there are ways in which ecological consequences of windstorms can be beneficial.

2. Storm events: meteorology and patterns

2.1. Definitions and formation

A tornado is a high-speed vertical vortex of wind that develops, usually, from thunderstorms, but occasionally from hurricanes (Snow, 1984). The vast majority of detailed tornado research has taken place in the area of highest concentration in the US (Fig. 1): Oklahoma, Texas, Kansas, and Nebraska. Consequently, while these storms are not representative of all tornadoes (Davis et al., 1997), our understanding of tornado formation is predominantly based on those storms that strike in the Great Plains. In this region, tornadoes often form from intense thunderstorms called supercells, which are defined (Doswell and Burgess, 1993) as those thunderstorms with 'a deep and persistent' cyclonic rotation called a mesocyclone. While some small and weak tornadoes form in non-supercell conditions, the supercell storms produce 'by far the most intense convective vortices and certainly are the type of storm most likely to produce' tornadoes (Doswell and Burgess, 1993); indeed, strong tornadoes 'are almost uniquely associated with supercell storms' (Doswell, 1997). The classical interpretation is that such storms are initiated when a low-level warm, moist air mass breaks through a stable intermediate air layer into an overlying mass of cool, dry air. This eruption starts an updraft that feeds the convection of a thunderstorm. In a tornadic storm, the concentrated updraft is needed to form a rotating structure with horizontal dimensions of several kilometers, called a mesocyclone, which is a necessary precursor to most tornadoes, although the final step that leads to tornado formation from a mesocyclone remains poorly understood. The formation of non-supercell tornadoes, which appear most often along the Front Range in Colorado, and in Florida, is much more poorly understood.

The penetration of the lower, warmer air mass into the higher, cooler air mass can be caused by fronts, certain arrangements of the jet stream, or perhaps even topography. Thus, the conditions conducive to tornado formation include the cool, dry air mass over a warm, moist one, and an

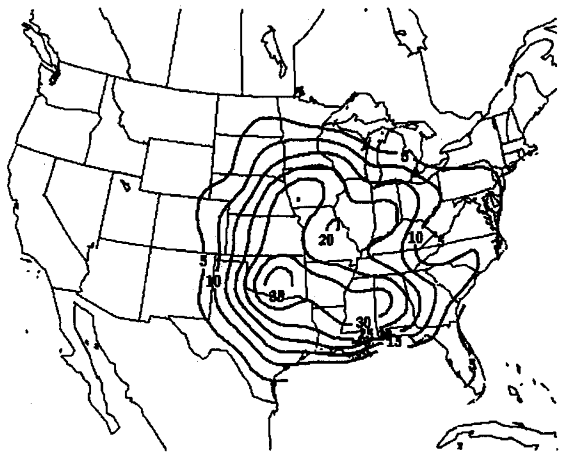

Fig. 1. Mean number of days per century with at least one F2 or greater tornado touching down within an 80 × 80-km grid cell, based on data from 1921–1995. Counters show intervals of five, where lowest contour is 5 days/century (from Concannon et al., 2000).

initiator, like a front or jet stream, to start the convection of the nascent thunderstorm (Snow, 1984; Davies-Jones, 1995). The stable intermediate layer is often a 'capping inversion', which can temporarily suppress the potential instability of a lower, warmer air mass. This may in part explain why tornadoes are very common in the later afternoon: as a day progresses and the ground is heated, the lower parcel of air warms and may increase in humidity (due to evaporation), until something triggers its eruption up through the inversion and into the upper air layers. The atmospheric conditions that favor formation of intense thunderstorms occur most frequently during the spring and summer in the central and south-eastern US, as a result of the position of the polar front, where the cool and (relatively) dry continental polar air mass meets the warm and moist maritime tropical air mass (Snow, 1984). Tornadoes can also form in hurricanes, although their genesis and behavior are substantially different than those that form in more typical fashion (Wilkinson et al., 1978); approximately 25% of hurricanes produces tornadoes (Anthes, 1982).

Downbursts are recently-described meteorological phenomena that occur in convective thunderstorms, when atmospheric conditions produce an air mass that has negative buoyancy as a consequence of evaporative cooling of many small particles of precipitation. Typically this is an air mass that has risen in the updraft of a convective storm, and is then pushed aside from the updraft by high-level winds. Because of the negative buoyancy and (in a 'wet' downburst) the additional acceleration added by falling raindrops, this air mass accelerates downward, forming an extremely powerful downdraft (Doswell, 1994). The cold air mass spreads out when it hits the surface, as the water from a faucet spreads out in a sink. Although a range of atmospheric conditions can result in downburst formation, the extremes are categorized as 'dry', typical in semi-arid regions in the west of North America, and 'wet' and intermediate, which are typical of the eastern portions of the continent (Caracena et al., 1989). Dry downbursts are not accompanied by ground-level precipitation, while wet and intermediate downbursts are; but in both cases, the initiation of the downdraft results from evaporative cooling of an air parcel. While the conditions leading to formation of dry downbursts are comparatively well-understood those preceding wet microbursts are less known (Doswell, 1994). Nevertheless, Brooks and Doswell (1993) identified several atmospheric conditions that seem to facilitate development of these types of storms: very moist surface-level air, substantial storm-relative helicity, and weak storm-relative mid-level (mid-tropospheric) winds. Such conditions can arise in a single convective storm cell, resulting in a relatively small downburst, or can occur in a series of cells along a squall line (a mesoscale convective system), resulting in potentially very large areas of damage, sometimes called derechos (Doswell, 1994).

The patterns of wind damage resulting from downbursts can be complex, because it is believed that a vortex ring (or even multiple vortex rings) can form around strong downbursts; such a vortex would approximate a horizontal tube whose ends were joined to form a ring with winds moving down on the inner edge, outward on the bottom, and then curling up on the outer edge. Moreover, downburst winds have been observed to strengthen after impact with the ground (Wilson et al., 1984). Fujita and Smith (1993) show that it is not uncommon for small downbursts and tornadoes to occur in the same storm, most often with the microbursts occurring along the right of the path of the tornadoes. For example, eight microbursts were documented along the right (east) of the path of a 30-km, F4 tornado that moved south-to-north across the Connecticut/Massachusetts border in October 1979 (Fujita and Smith, 1993).

2.2. Frequency and locations

While tornadoes have been documented on every continent except Antarctica, they are most common in North America, Australia, northern India and Bangladesh (Snow, 1984; Davies-Jones, 1995). However, the US is by far the nation suffering the most tornadoes. The total number of tornadoes occurring, on average, within the US is a subject of much discussion, because of the limitations and subjectivity of older records in the long-term databases used to construct tornado climatologies (see Doswell and Burgess, 1988; Grazulis, 1993; Grazulis et al., 1993; Schaefer et al., 1993). One estimate is that, on average, nearly 1000 tornadoes per year occur in the conterminous USA (Pendick, 1995). The official record number was recorded in 1992, when 1293 tornadoes were documented (Crowther, 1994), but unofficial counts total 1426 tornadoes in the US in 1998 (NCDC, 1999). The area of highest concentration is called 'tornado alley' and stretches from north-eastern Texas, through Oklahoma and Kansas, and into Nebraska (Fig. 1). Areas of secondary concentration are centered over northern Alabama, central Florida, and southern Indiana (Kelly et al., 1978; Snow, 1984; Fig. 1). During the 11-year period of 1984–1994, inclusive, the states with the highest annual tornado frequency per 10 000 km^2 were: Delaware (4.09); Florida (3.66); Iowa (3.10); Kansas (2.74); Nebraska (2.71); Louisiana (2.69); Mississippi (2.56); New Jersey (2.55); Oklahoma (2.32); Indiana (2.13); and Texas (2.01) (calculated from preliminary data in Weatherwise). While the anomalous high rankings for Delaware and New Jersey result from two unusual years, the remaining states' order and frequencies are probably representative. Canadian Prairie provinces are at the north end of 'tornado alley', and thus, experience a substantial

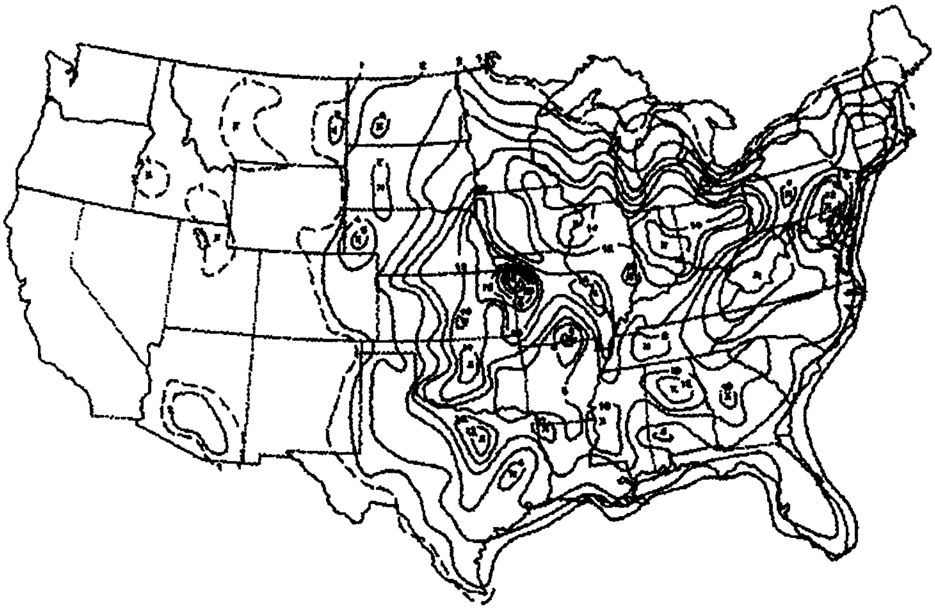

Fig. 2. Contours of average annual frequency of reported severe convective wind events, per 25 900 km^2 (10 000 mi^2), for the period 1953–1980. Maxima are denoted by 'X' and minima by 'N' (from Doswell, 1994).

number of tornadoes (Etkin, 1995); the greatest number of these storms occur in July.

Downburst geographical distribution is, at a very rough approximation, similar to that of tornadoes (Fig. 2). Like tornadoes, downbursts show an area of greatest concentration in the southern Great Plains, although the location of the continental maximum is shifted somewhat to the north-east compared to the tornado maximum; downbursts peak in occurrence in north-western Missouri. Two regional peaks that occur in the tornado distribution, over Indiana and northern Alabama, also occur in downburst distribution, but an area of difference is the relative scarcity of downbursts in Florida (Fig. 2).

The frequency of downbursts varies depending on the size of the event considered, with frequency inversely proportional to the size of the event. The Joint Airport Weather Study (JAWS) project, conducted near Denver in 1982, documented roughly one microburst per day in the monitored area of 1600 km^2, or 0.0007/day per km^2 (McCarthy and Serafin, 1984). These were the 'dry microburst'-type, typical of the High Plains environment, but less common further east. At the other extreme, Brooks and Doswell (1993) estimated that approximately one of the very large (i.e. hundreds of km^2), high-precipitation supercell derecho downbursts occurs annually in North America. While data for one particular year must be regarded with caution, Fujita (1981) reported that 789 non-tornadic high-wind incidents (mostly downbursts and gust fronts; sizes not presented) were documented in the US in 1979.

2.3. Size and duration

Tornadoes are short-lived phenomena, often lasting only a few tens of minutes, but occasionally for several hours. However, within that short time span, they strike sporadically and violently. Typical tornado paths are several dozen to several hundred meters wide, and 15–25 km long (Ruffner and Bair, 1977), although occasionally paths may be much longer: two of the tornadoes in the 94-tornado outbreak of November 1992 had path lengths of 205 and 256 km (NOAA, 1993). Despite these reported path lengths, tornadoes do not necessarily cause surface damage along the entire path, so the actual surface area damaged may be much less (e.g. Glitzenstein and Harcombe, 1988). Howe (1974) proposed that ground damage occurs over roughly one-third of the reported tornado path length, while Pryor and Kurzhal (1997) made an even more conservative estimate of 10%. Nevertheless, they suggested 0.60 km^2 as the mean ground surface area actually disturbed by an average tornado. Multiplying this figure by 1000 as an average tornado frequency yields 600 km^2 of ground area affected by tornadoes annually in the US.

Recently, tornado experts have concluded that despite entrenched 'common knowledge', tornadoes *do not* 'skip' in the sense of a vortex repeatedly picking up and touching down on the ground (Fujita and Smith, 1993; Doswell and Burgess, 1993); instead, it is believed that the wind circulation strengthens and weakens very dynamically, on a time scale of mere seconds.

Downbursts are potentially much larger phenomena than tornadoes. Fujita (1978, 1985) divided downbursts into classes based on size: microbursts are those downbursts with maximum horizontal extent of < 4 km; and downbursts affecting areas > 4 km are called macrobursts. These size distinctions are arbitrary and a given storm can change from one size category to another. When downbursts occur in groups within a mesoscale convective storm system (a *derecho* event) the damage can affect areas up to hundreds of squared kilometers, often in an elongate, oval or fan shape (Stearns, 1949; Lyford and MacLean, 1966), although areas of several hundred to a few thousand hectares may be more common (cf. 1953 event in western Upper Michigan, Frelich and Lorimer, 1991). Brooks and Doswell (1993) mention four distinct downburst events that produced damage areas 10–30 km wide, and many tens of kilometers long. In each case, wind speeds were estimated to exceed 50 m/s. One of these, the derecho described by Cummine et al. (1992) had a damage path 75 km long and roughly 20 km wide, in north-western Ontario, Canada. Each of these would be classified as a 'wet downburst', as the winds were believed to be embedded in high-precipitation supercells (Brooks and Doswell, 1993).

Several recent large downburst/derecho events have caused spectacular forest destruction: a thunderstorm with derechos impacted 392000 ha of forest on 15 July 1995, in Adirondack Park of upstate New York; 15300 ha of this were classified in the 'high' damage category, with 60–100% of timber blown down (Robinson and Zappieri, 1999). On 25 October 1997, unspecified non-tornadic winds severely damaged 20000 acres of forest in the Mount Zirkel Wilderness of Routt National Forest, Colorado (Storm Data, 1997). The same month and year, a windstorm event likely to have been a derecho damaged slightly more than 4000 ha of forest in the central upper peninsula of Michigan (Storm Data, 1997). Most recently of all, an exceptionally large storm damaged nearly 200000 ha of forest in a region 16 × 48 km in the Boundary Waters Canoe Area wilderness of northern Minnesota on 4 July 1999 (Myers, 1999).

The temporal duration of downbursts is similar to that of tornadoes. Fujita (1985) stated that large downburst (macroburst) winds last from 5 to 30 min. Microbursts are typically short-lived, on the order of 10 min or less (Caracena et al., 1989), although occasionally they can last five or six times as long. The JAWS project near Denver documented 75 microbursts in 1982, and based on those, there is a typical lifetime of 5–15 min (McCarthy and Serafin, 1984).

2.4. Intensity

Tornado and downburst intensity are rated on a categorical scale from F0 (64–116 km/h) to F5 (420–512 km/h), based entirely on the damage caused by the event. Thus, estimates of wind speeds are far from certain, and the F-scale rating for an event is based on the severest damage produced, even if that is a small percentage of the affected area. The most intense storms (F4 and F5) are uncommon, but because they are larger and have longer paths than F0–F3 events, these events contribute a disproportionate amount to the total area damaged (Snow, 1984). Nationally, 90% of US tornadoes are rated F0 or F1, 9.4% are rated F2 or F3, and just 0.6% are rated F4 or F5. Median path lengths increase with intensity, from 0.5 km for F0 and 1.5 km for F1 tornadoes, to 22 km for F4 and 37 km for F5 tornadoes, during the period 1950–1978 (Schaefer et al., 1986). Median path widths follow a similar relationship to intensity category. Recent thinking by meteorologists points towards the role of embedded suction vortices within a given tornado as the cause of the most severe damage for that event (Fujita and Smith, 1993; Doswell and Burgess, 1993); a tornado may develop one or more suction vortices within the main funnel, and these subvortices rotate about the primary translational axis of the tornado itself, often causing spiral patterns of the most severe damage (Fujita and Smith, 1993). Deriving from observations of suction vortex patterns, Fujita (1978) originated the currently accepted concept that each tornado produces a damage area that includes a portion of all F scale levels from the estimated maximum intensity down. Thus, within a particular severe tornado (e.g. F4), only a fraction of the area affected will suffer F4 damage, the remainder will experience lesser (e.g. F3, F2, F1 and F0) wind speeds (Grazulis et al., 1993).

Downburst wind speeds can reach levels that cause F3-level damage (estimated 70–92 m/s or 250–328 km/h). The distribution of 798 downbursts and gust fronts among F-scale ratings in 1979, was 33% as F0, 58% as F1, 9% as F2, and 0.6% as F3 (Fujita, 1981). Fujita (1985) stated that large downburst (macroburst) winds can be as high as 60 m/s (214 km/h), while smaller downburst winds can reach 75 m/s (269 km/h). Typical horizontal wind speeds at ground level for the microbursts studied in the JAWS project were 10–50 m/s (McCarthy and Serafin, 1984).

2.4.1. Seasonal, topographic, and geographic variation in storm size, intensity and frequency

Tornadoes are most common early in the year (February and March) along the Gulf Coast states (Fig. 3), and their peak frequency shifts to later months further north (peak tornado frequency in Minnesota is in July). The months with the greatest number of tornadoes nationally (US) are May and June, for which the record number of torna-

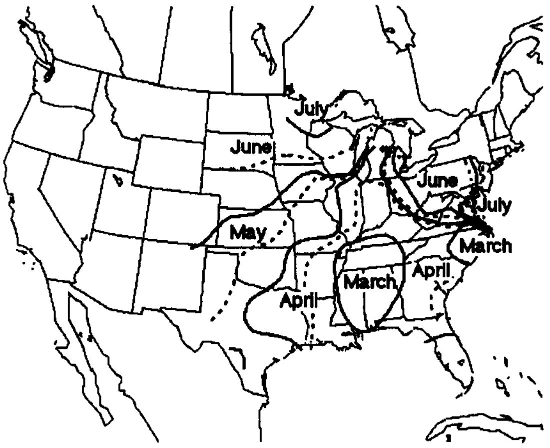

Fig. 3. Progression of maximum threat of significant tornado during the year. Date based on mean of 75-year sample. Solid lines indicate first day of month, dashed lines 16th day of month (from Concannon et al., 2000).

does are 391 and 399, respectively (McCarthy and Ostby, 1996). There is often a secondary peak of tornado activity in the south-east during November and December (Garinger and Knupp, 1993).

Regional climatologies reveal finer patterns of tornado occurrence, and possible influencing factors. In Indiana, for example, strong or violent tornadoes are relatively more common, making up 3.4% of those rated (Pryor and Kurzhal, 1997); conversely, Florida has an especially high incidence of weak (F0 or F1) tornadoes (Garinger and Knupp, 1993). In the north-east (Maryland and West Virginia and states to the north-east), 75% of tornadoes occur in May through August, showing the shift towards later occurrence than for the nation as a whole (Leathers, 1993). An average of 30/year struck this region during 1950–1986, and the frequency distribution was again different from that of the entire US: 64.7% were F0 or F1, 32.8% were F2 or F3, and 2.5% were F4 or F5; relative to the national distribution, this again shows that strong and violent tornadoes make up a greater proportion of those in the north-east. Within this region, three areas of concentration were identified: western Pennsylvania; south-eastern Pennsylvania; and central Massachusetts (Leathers, 1993). March and April tornadoes are concentrated near the Atlantic in Delaware and New Jersey; May and June tornadoes are most frequent in western Pennsylvania and central Massachusetts; and fall tornadoes occur most often in south-eastern Pennsylvania (Leathers, 1993).

More local-scale variation may exist for tornado frequencies as well; in Arkansas, tornadoes are less common in mountainous areas (Gallimore and Lettau, 1970). On a county-by-county basis, the analysis by Pryor and Kurzhal (1997) suggested that areas of Indiana with greater surface roughness had lower tornado frequencies.

2.4.2. Forest disturbance regimes

Because of the role of vegetation characteristics, physiography, and other site factors, not all areas within a storm's path are equally vulnerable to wind damage, and some may be sheltered or otherwise resistant. Thus, the spatial distribution of high winds during storm events is not exactly reflected by the spatial distribution of damaged areas within forests (e.g. Glitzenstein and Harcombe, 1988). Thus, more accurate assessments of realized disturbance regimes come from direct study of forest blowdowns themselves. Stand reconstructions from fire scars, fallen trees, and tree ring analyses (e.g. Henry and Swan, 1974; Oliver and Stephens, 1977; Lorimer, 1980; Foster, 1988a; Frelich and Lorimer, 1991) have revealed that disturbances are not uncommon at the time scale of centuries, and that most of the forest landscapes of the US are in some stage of recovery from disturbance at any given time.

At the landscape and regional scale, several studies have utilized presettlement survey records to determine the abundance and extent of disturbances across space for a small window of time (Stearns, 1949; Lorimer, 1977; Canham and Loucks, 1984; Whitney, 1986, 1990; Seischab and Orwig, 1991). These historical studies require a number of assumptions, and the data truly represent only the disturbance regime of the years immediately prior to the survey. The most widely-reported disturbance regime parameter is the return time (also called rotation period or recurrence interval), which is the time required for a given type of disturbance to affect an area equal to 100% of the area under consideration

(Canham and Loucks, 1984; Whitney, 1986). Based on these land survey studies, the return times for catastrophic wind disturbances (affecting a majority of canopy individuals and areas greater than a few hectares) vary substantially among locales, from a possible low of 1000 years in north-western Pennsylvania (Whitney, 1990), to nearly 2000 years in western upper Michigan (Frelich and Lorimer, 1991). Intermediate return times for blowdown of 1210 and 1220 years were estimated by Canham and Loucks (1984), Whitney (1986), respectively, for hemlock–northern hardwoods in Wisconsin, and hemlock–pine-hardwoods in northern lower Michigan. Cogbill (1996) estimated 1400 years between events that cause large blowdowns in northern and western Maine, while Lorimer (1977) calculated an analogous figure of 1150 years for north-eastern Maine. The frequency for smaller or less intense disturbances, which cause partial canopy removal, is much higher (Frelich and Lorimer, 1991).

The various types of wind events have differential importance among regions. Hurricanes do not affect western Great Lakes forests (Wisconsin and Michigan), but the majority of presettlement windthrow damage in northern Wisconsin was caused by large-scale events (Stearns, 1949; Canham and Loucks, 1984), showing that downbursts were important influences on forest dynamics in this region. Tornado tracks, while accounting for a smaller fraction of the area disturbed, were also common in the northern Wisconsin forests. In Itasca State Park, northern Minnesota, thunderstorm winds are important components of the disturbance regime (Webb, 1989). In several extensive tracts of hemlock-northern hardwood forest in western Upper Michigan, only one disturbance of high severity (> 60% canopy removal) was documented within the past 130 years; this storm was probably a downburst (Frelich and Lorimer, 1991). Wind disturbances on the Allegheny Plateau of western New York were apparently primarily from thunderstorms (Seischab and Orwig, 1991), and in northeastern Maine much of the historical wind damage may have derived from undefined events or perhaps a single storm around 1795. Further south along the Atlantic and Gulf coasts, hurricanes become the predominant type of wind disturbance in terms of total area affected (DeCoster, 1996), although tornadoes are also common on the Piedmont and Coastal Plain (DeCoster, 1996; Bluhm, 1997). A few areas, such as cove forests of the Great Smoky Mountains, rarely if ever experience catastrophic wind.

More locally, retrospective studies further reveal how frequency of wind disturbance varies among forest types and landscapes. Seischab and Orwig (1991) state that all windthrows reported by surveyors were confined to the Allegheny Plateau in their study area, with no windthrows reported from the adjacent glacial till plain. In north-eastern Maine, blowdowns were restricted to bottomland and swamp forests (Lorimer, 1977), and in northern Lower Michigan, hemlock–white pine–northern hardwoods and swamp conifer forests were much more affected by windthrow than other forest types (Whitney, 1986). However, in northern Wisconsin, all forest types were affected (Canham and Loucks, 1984); and in western Upper Michigan, disturbance rates were similar across study areas, coastal vs. lakeshore stands, aspects, and topographic positions (Frelich and Lorimer 1991).

2.4.3. Factors influencing damage patterns

Because of the variety of factors that influence the damage caused by wind events, and the scarcity of studies, ecologists have identified only a few general patterns (Everham and Brokaw, 1996). Here, I begin by summarizing how damage by wind events varies with differences in the three major types of factors — storm characteristics, site characteristics, and vegetation characteristics.

2.4.3.1. Storm characteristics: size, precipitation, intensity. As described above, the forest damage that results from a tornado or downburst is far from uniform. Some areas within the same damaged patch will experience much greater or lesser winds than other areas, resulting in an intergrading heterogeneity of damage. Even if area is categorized simply as disturbed vs. intact after a wind disturbance, the spatial pattern and size distributions of disturbed patches that result from tornadoes and downbursts has yet to be quantitatively examined, as has been done for hurricane disturbance patches (Foster and Boose, 1992). However, forest damage studies following tornadoes report damaged areas from 1 to 2 ha (Bluhm, 1997; Peterson, in press) up to several hundred hectares for individual tornadoes (Peterson and Pickett, 1991; Bluhm, 1997), presumably reflecting to some degree the size of the causal storm event.

Storms vary widely in the amount of precipitation that accompanies the wind, which may potentially influence the realized forest damage. Indeed, it has been historically assumed that large amounts of precipitation would saturate soils, reducing soil shear strength and thus, rooting stability, thereby increasing vulnerability to wind damage (see review in Schaetzl et al., 1989). However, this assumption has recently been questioned (Foster and Boose, 1995), and the existing evidence is equivocal. In an attempt to experimentally simulate a hurricane, the Harvard Forest staff pulled down trees across 0.8 ha on upland glacial till soil, and found that proportions of trees uprooted were no different than those observed following the 1938 hurricane, which was accompanied by 15–35 cm of rain (Cooper-Ellis et al., 1999). Similarly, established thinking assumed that saturated soils of swamps and other wetlands would provide poor anchorage and thus result in greater amounts of treefalls than in drier, upland soils (Behre, 1921; Schaetzl et al., 1989). However, Foster and Boose (1992) reported limited damage from the 1938 hurricane to spruce wetlands in central Massachusetts and Stoeckeler and Arbogast (1955) found lesser damage in a swamp than adjacent forest areas after a 1949 windstorm. Thus, while wet sites *may* lead to shallow rooting and consequently a greater likelihood of treefall in high winds, this is not universally the case.

Damage apparently increases with increasing wind speed (intensity of storm; Fig. 4), but because of the logistical barriers to measuring local wind speed during a storm, no study has directly examined the relationship between wind speed and damage in natural forests (DeCoster, 1996). Across published ecological studies, there are significant increases in both percent mortality and percent of trees toppled, with increases in estimated wind speed (Fig. 4). Severity of disturbance reaches > 75% canopy destruction in areas affected by Class 4 and 5 hurricanes, tornadoes rated F3 and above, and powerful downbursts (Dunn et al., 1983; Peterson and Pickett, 1991; Foster and Boose, 1992). However, the relationship between storm intensity and severity of disturbance is not constant across different forests and species, due to multiple factors influencing tree responses (DeCoster, 1996, see Sections 2.4.3.2 and 2.4.3.3see). Thus, the same event (with presumably similar wind speeds) may have distinctly different effects on different areas of forest (Glitzenstein and Harcombe, 1988; Peterson and Rebertus, 1997), and conversely, similar types of storms that differ in severity can have very distinct consequences in the same forest (Peterson, in press). In general, though the trend of increasing damage at higher wind speeds is robust at this level, current data are insufficient to characterize the relationship in detail, or to confirm the presence or location of asymptotes or thresholds.

2.4.3.2. Site characteristics: physiography, soil type and depth. Physiography is perhaps the most obvious characteristic of a site that influences levels of forest damage in wind events. Greatest damage in a downburst generally occurs in ex-

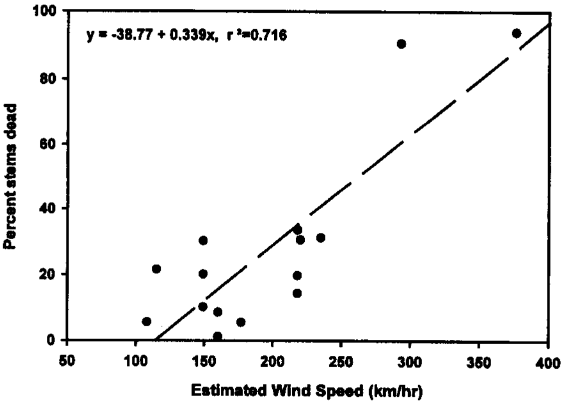

Fig. 4. Relationship of forest damage to estimated wind speed, ranked by the Fujita F-scale (from numerous published studies).

posed areas, while tornado movement and behavior are poorly understood relative to physiographic conditions, thus making it problematic to define any area as exposed or protected. While some studies have suggested that tornadoes may occur less frequently in areas of substantial topographic relief (Gallimore and Lettau, 1970; Pryor and Kurzhal, 1997), individual tornadoes have been known to track up hills and mountains, and then down into steep valleys (Stanford, 1987). This suggests that while the influence of particular topographic positions on forest damage may be predictable in large storm events (e.g. Foster and Boose, 1992), the erratic behavior of tornadoes may preclude similar predictions of how tornado damage will vary with topography. However, physiography can also have an underappreciated, opposing influence: trees growing in areas subject to chronic winds may develop stress-response architectures, which result in greater resistance to damage when high winds occur (Everham and Brokaw, 1996). Because of the role of physiography in creating exposed and protected areas, it can have a major influence on the nature of the distribution of sizes, shapes, and locations of disturbed and undisturbed areas.

Differing substrate conditions (other than moisture level) can result in substantially different tree stability in wind events (Schaetzl et al., 1989). Lutz (1940) suggested that very stony soils may contribute to increased tree vulnerability to wind, because of decreased abundance and strength of bracket roots. In cases where trees are able to infiltrate roots into solid bedrock, however, trees may be resistant to uprooting, leading to greater proportions of stem breakage vs. uprooting (Foster, 1988b). When Hurricane Andrew struck hammocks on rockland substrate in south Florida, trees whose roots penetrated into the underlying porous limestone were only rarely uprooted (Loope et al., 1994). Whether this may influence the total number of trees windthrown is not clear. Very deep rooting may accomplish the same level of substrate stability: Cypress trees in forested sloughs of the south-eastern Coastal Plain exhibit 'sinker' roots that may explain why few of these are uprooted by wind (Putz and Sharitz, 1991; Duever and McCollom, 1993). Certainly, soil depth or depth to hardpans/fragipans may limit the depth to which a potentially deep-rooted species may grow its roots thus, in some cases preventing the deep rooting a species might achieve on other soils (Mueller and Cline, 1959). Such shallow root distribution may decrease resistance to wind (Trousdell et al., 1965; Savill, 1983; Harris, 1989).

2.4.3.3. Vegetation characteristics: tree size, species composition, and disturbance history. Several characteristics of forest vegetation influence the level of damage realized in a given wind event. Most obvious and well-documented is the increase in damage with tree size. This is perhaps the most consistent generalization in studies of wind disturbance: taller trees are more likely to be damaged or felled by high winds (Glitzenstein and Harcombe, 1988; Peterson and Pickett, 1991; Matlack et al., 1993; DeCoster, 1996; Bluhm, 1997; Peterson and Rebertus, 1997; Peterson, unpublished, but see Webb, 1989 for an exception). The threshold tree size above which damage is concentrated decreases with increasing wind speed. Thus, moderate intensity events primarily damage canopy trees (Webb, 1988; Matlack et al., 1993), while in the most extreme events, essentially all individuals above some small size threshold are damaged (Foster, 1988a; Peterson and Pickett, 1991; Peterson, in press), obscuring relationships between vulnerability and size or species that are apparent in less intense storms. To some degree, the effect of relative size is important in addition to absolute size: trees emerging above the canopy height of neighbors, or along a stand edge immediately downwind from shorter vegetation, are more vulnerable than their absolute size might suggest (Harris, 1989).

Because of the high correlation between age and size, wind damage also dramatically increases with stand age (Foster, 1988b). This trend of increasing damage with increasing age probably reflects not only the effect of absolute tree height, but also such influences as sublethal stress, pathogen attack, and relative size (see Mergen, 1954; Webb, 1988; Matlack et al., 1993).

Not surprisingly, species-specific differences in rooting depth, above-ground architecture, and wood strength cause substantial variation among species in probability of damage, beyond the effects of size (Touliatos and Roth, 1971; Foster, 1988b). In a 1985 Minnesota thunderstorm wind event, canopy white and red pines (*Pinus strobus* and *Pinus resinosa*) were disproportionately windthrown, relative to surrounding hardwoods (Webb, 1988; Foster, 1988b). The greater pine damage was true even when size effects were statistically controlled. Similarly, when tornadoes struck old field pine–oak forests on the Piedmont in Georgia and North Carolina, pines were more likely to suffer treefall than hardwoods of the same size (DeCoster, 1996; Bluhm, 1997). However, both of these latter studies were done in blowdowns caused by late November tornadoes, therefore, deciduous trees would have been mostly leafless, perhaps accentuating the greater vulnerability of pines relative to hardwoods.

Interspecific differences in vulnerability to wind damage can also result from microsite regeneration preferences (Harris, 1989). Putz and Sharitz (1991) found that cypress and tupelo in a South Carolina swamp forest were rarely toppled, while most individuals of other species fell, due to their occurrence on unstable substrates such as rotting logs. In some habitats, slight depressions or low areas may be more moist and thus, favor establishment of certain species, which are then less likely to suffer damage from later wind events as a consequence of being slightly sheltered (e.g. *Betula papyrifera* at Itasca, Webb, 1989). However, such locations may also be more likely to be damaged if underlying shallow water tables prevent root penetration and thereby decrease tree stability (Savill, 1983; Harris, 1989).

The history of other disturbances can also influence trees and, therefore, stand vulnerability via biotic factors. The potential influence of wood-rotting fungi on tree stability has long been recognized. Webb (1989) and Matlack et al. (1993) found that trees with extensive heartrot or rootrot were structurally weaker, and more likely to suffer stem breakage, than trees without heartrot. Among oaks in New Jersey (Matlack et al., 1993) and pines in Minnesota (Webb, 1989), increased vulnerability to wind as a result of heartrot, was a consequence of trees having been scarred in fires occurring decades earlier, thereby allowing entrance to pathogenic fungi. The result was a delayed synergism between fire injury and later treefall during a localized windstorm. Analogously, weak points in a tree's crown or trunk resulting from previous wind stress or damage and can leave such trees especially vulnerable to breakage in subsequent wind events (Mergen, 1954).

3. Immediate consequences

The consequences of wind damage can be considered as immediate, such as those occurring within a few days of the event, and long-term, which span periods from a few months to decades or even centuries. Several of the parameters and processes of change exhibit patterns of change at both time scales.

3.1. Mortality

Wind events can produce spectacular scenes of forest destruction, although an emerging generalization is that actual impact on forest community dynamics is often much less than first impressions might suggest (Merrens and Peart, 1992; Foster et al., 1997; Cooper-Ellis et al., 1999).

Mortality is not synonymous with treefall: it occurs to differing extents among species and sizes of trees, and occurs over an extended time period of up to several years (e.g. Walker, 1995). Generally, across sites and across studies, levels of damage and levels of mortality are positively correlated, but the relationship is noisy. Mortality patterns are especially influenced by sprouting of trees after catastrophic wind. Where mortality figures are explicitly presented (or can be calculated), it ranges from <1 to $>94\%$ of canopy (>20 cm dbh) trees, but is usually less — sometimes much less — than levels of total treefall (trunk breakage plus uprooting). Mortality is often much greater among larger trees, due to the combination of greater levels of damage, and lower probability of sprouting (see below), in larger size classes. For similar reasons, mortality often varies greatly among species (e.g. from 0 to

80%, Glitzenstein and Harcombe, 1988), but the inter-specific differences are more difficult to generalize than those for size differences. Most conifers are unable to sprout after being snapped, so complete trunk breakage is generally fatal to conifers (Glitzenstein and Harcombe, 1988; Peterson and Pickett, 1991; DeCoster, 1996); in contrast, trees of many hardwood species sometimes survive this extreme damage by sprouting, although the resulting tree is much smaller (e.g. Cooper-Ellis et al., 1999). The various types of wind damage cause differing amounts of mortality, generally increasing from defoliation through branch breakage and trunk bending, to uprooting and trunk breakage (DeCoster, 1996; Cooper-Ellis et al., 1999).

3.2. Size structure

Because of the greater vulnerability of larger trees, the most immediate effect of catastrophic wind events on forest size structure is to shift surviving tree size distribution into smaller size classes, for example, from 38.0 to 18.0 cm after a strong Pennsylvania tornado (Peterson and Pickett, 1991). While these reductions in mean size are common, they are not universal among wind-damaged forests, and the potential changes in the shape of size distribution among surviving stems (more or less variable, skewness) remain unexplored relative to catastrophic wind disturbances.

3.3. Species composition and diversity

When wind damage is not equal among species (which it rarely is), the immediate post-disturbance stand may be left with substantially different relative species abundances (Fig. 5). Most catastrophic windstorms cause some level of change in species composition, *beyond the effects on size structure and density*. These changes may decrease with time, over the course of years to decades, as sprouts of damaged individuals reclaim canopy positions. However, in circumstances where numerous new seedlings are established, or where surviving understory stems substantially differ in composition from the pre-disturbance canopy, the immediate changes in relative composition may be lasting, or followed by further changes as the post-disturbance cohort of seedlings recruits to canopy stature (e.g. Peterson and Pickett, 1995).

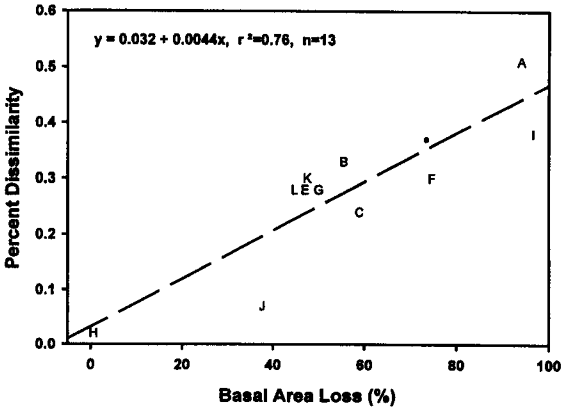

Fig. 5. Relationship of forest short-term compositional change (pre- to post-disturbance) to severity of wind damage. Counting only living, standing trees. Letters indicate the following studies: A, Dunn et al. (1983); B, Peterson and Rebertus (1997), upland; C, Peterson and Rebertus (1997), lowland; D, Peterson and Rebertus (1997), swamp; E, Kapustka and Koch (1979); F, Glitzenstein and Harcombe (1988), Hickory Creek; G, Glitzenstein and Harcombe (1988), Turkey Creek; H, Matlack et al. (1993); I, Peterson and Pickett (1995); J, Peterson, in press; K, Bluhm (1997); L, DeCoster (1996).

Independent of successional status (see below), change in relative species abundances from pre- to post-disturbance can be readily quantified if sampling is not too delayed. When compositional change is measured as percent dissimilarity, and severity is measured as percentage of (pre-disturbance) basal area downed, a strong relationship emerges. It appears that change in community composition increases with the amount of damage (Fig. 5).

One type of change that is of particular interest is the possibility that damage may shift composition toward more early-successional species, or toward more late-successional species. Some observers suggest that because of their fast growth (resulting in a tendency to occupy dominant canopy positions in young forests) and weak wood, early-successional species are inherently more vulnerable (Everham and Brokaw, 1996), resulting in a general expectation of shifts in species composition towards late-successional species. Several studies do report on wind events that have selectively damaged or killed earlier-successional pines, leaving a more late-seral composition of hardwoods (Glitzenstein and Harcombe, 1988; Foster, 1988b; DeCoster, 1996; Bluhm, 1997). However, this trend is not universal. In three adjacent sites struck by a tornado in southeastern Missouri, Peterson and Rebertus (1997) report only modest change in the contribution of different shade-tolerance classes, despite 64% of basal area downed. Similarly, when an F3 tornado struck an old secondary white pine–hemlock forest in Connecticut, both early-successional white pine and late-successional hemlock suffered similar severe damage; notably, white pine and hemlock are both shallow-rooted species, and they had similar size distributions at this site (Peterson, unpublished data). Together, these findings suggest that shallow-rooted species in general are vulnerable, and that the greater levels of damage to early-seral species is a consequence of their being larger and often shallow-rooted; any species sharing these traits should show similar vulnerability, regardless of successional status.

The above findings indicate that immediate effects of catastrophic wind disturbance on species composition appear highly contingent upon the pre-disturbance species and size characteristics of the forest. To the extent that the surviving canopy trees and/or understory saplings are late-seral species — which is often the case — the wind event will advance succession (e.g. Kapustka and Koch, 1979; Foster, 1988b; DeCoster, 1996; Bluhm, 1997). More generally, such events are likely to selectively decrease the contribution by pre-disturbance canopy dominants, resulting in dominance by species whose pre-disturbance size distributions included smaller trees (Glitzenstein and Harcombe, 1988). However, even this generalization must be used cautiously: in two Minnesota forests subject to diffuse windthrows, the differing strength and stability of understory species determined how wind damage altered tree composition by determining the windfirmness of the understory plants themselves (Webb, 1988, 1989).

By selectively removing the most dominant individuals from a forest, wind disturbances may immediately alter canopy diversity by changing either species richness or evenness among the survivors. The available data suggest that decreases in diversity may be more common than increases, if calculations are based on density as the measure of abundance. Peterson and Rebertus (1997) found that, for data pooled across three adjacent forests, canopy tree diversity decreased significantly following tornado damage that removed 64% of the basal area; species richness declined in seven of nine plots, while evenness declined in five of nine plots.

A very intriguing pattern is suggested when changes in diversity are compared for calculations using density as the measure of abundance, and those using basal area (Fig. 6). While not every study presented data for basal area, the most striking pattern is that while diversity (measured as H') usually declines if density is used as the measure of tree abundance, diversity usually increases if basal area is used. For nine of the 11 studies that present both density and basal area data, the change in diversity is in opposite directions for density vs. basal area. Note that these calculations are based solely on relative abundances, so this does not reflect reductions in absolute abundances. The probable reason for this unusual pattern is that wind disturbance tends to increase evenness of basal area among species by preferentially removing large individuals; this same selectivity by wind disturbance will tend to decrease evenness of density among species, by damaging dominant individuals that are often in low absolute density. This finding makes it very clear that the abundance measure used in diversity descriptions can have critical influences on the results. Thus, whether wind disturbance increases or decreases diversity entirely depends on what measure of abundance is used.

3.4. Environmental conditions

Surprisingly, very few studies that have attempted to characterize environmental conditions within catastrophic blowdowns. Canopy cover was measured by DeCoster (1996), and found to be

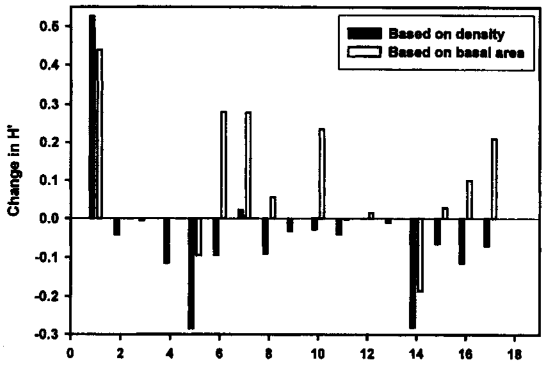

Fig. 6. Diversity change in wind disturbances, calculated *H'* based on density and based on basal area.

significantly lower in the area damaged by a tornado, than in the surrounding intact forest. Bluhm (1997) reported that the heterogeneous nature of damage resulted in a gradient of leaf area index in the tornado blowdown he studied, from a low of 0.55 to 5.74 m^2/m^2.

Peterson (1992 and unpublished data) measured instantaneous point light levels 2 years after a tornado blowdown, and found significantly greater light levels in the damaged area than in the adjacent forest edge. These appear to be the only published figures for overall blowdown vs. intact areas for eastern North America. A few additional findings are discussed below under microsite differences.

4. Longer-term consequences: post-disturbance dynamics

When a disturbance makes resources and space available, a number of distinct sources may contribute to reestablishment of the forest. In order of presumed importance among disturbances of increasing severity (Oliver and Larson, 1990), such sources are: growth of surviving canopy trees; sprouting of surviving canopy and understory trees, saplings, and seedlings; root sprouting; release of suppressed seedlings (seedling bank); germination of seed from a seed bank; and germination of newly-dispersed seeds. Several factors that may influence the relative importance of these sources, in decreasing importance, are: level of canopy damage; size and species of damaged canopy trees; pre-disturbance abundance and spatial distribution of advance regeneration (suppressed seedlings); abundance of seeds in the seed bank; size of area disturbed; and the suite microsites present immediately after the disturbance. How these factors interact to affect which sources of vegetation predominate, will determine how the disturbance influences long-term trends in composition, diversity, size and age structure, and ecosystem function.

Most wind disturbances do not destroy the entire canopy and thus, leave varying proportions of the pre-disturbance stand in situ. The contribution of pre-disturbance trees to post-disturbance vegetation is of course directly determined by how many survive intact or lightly damaged. When most of the canopy remains in place, there will be little contribution from the other sources, and little change in community characteristics (e.g. diversity, composition, successional stage; Webb, 1989, sloughs of Duever and McCollom, 1993; Sharitz et al., 1993). Only when there is substantial canopy damage is the way opened for important contribution from the other sources.

Sprouting of surviving canopy trees varies widely in importance, with differences in size and species composition of the damaged pre-disturbance trees (DeCoster, 1996; Cooper-Ellis et al., 1999). Given sufficient canopy opening, sprouting will be important when there are many small-to-intermediate-size damaged trees, of species that sprout (e.g. *Acer rubrum*, *Liquidambar styraciflua*). Where non-sprouting or very large trees predominate among pre-disturbance individuals, sprouting may be of lesser importance (Peterson and Pickett, 1991). The type of damage sustained by the pre-disturbance trees also has some effect on sprout abundance; bent and leaning trees are more likely to produce sprouts than more severely damaged trees. To the extent that sprouting is the predominant form of canopy reestablishment, species composition and diversity will remain unchanged, but the physical structure and size distributions of tree populations will be altered (generally toward smaller stems). Because the physiological processes conducted by photosynthetic tissues in sprouts is usually constrained to a lower leaf area than was present before the disturbance, ecosystem function will be reduced, although if recovery of leaf area is rapid, rates of ecosystem processes may quickly rebound to near-pre-disturbance levels (Foster et al., 1997).

Advance regeneration, the collection of surviving understory (seedling or sapling) stems, is often sparsely affected directly in a wind event, although it sometimes suffers substantial indirect damage. Indeed, Webb (1989) suggests that where advance regeneration is comprised of species having weak wood, the indirect damage from falling canopy individuals will greatly diminish the importance of these suppressed stems to contribute to the future canopy. Pre-disturbance levels of herbivory can be a critical determinant of the abundance of palatable species within the advance regeneration (e.g. Long et al., 1998). Finally, stand age at the time of disturbance is important because young stands are likely to be depauperate in advance regeneration. Thus, advance regeneration can be expected to be a major component of post-disturbance vegetation dynamics where it is not destroyed indirectly in the wind event, where the stand is old enough to have passed the stem exclusion stage, and where it has not been eliminated by herbivores. In the great majority of North American wind disturbances, advance regeneration is among the major sources of future canopy trees (e.g. DeCoster, 1996; Bluhm, 1997), although in a few cases, that role is minimized by the rapid growth and abundance of new seedlings (Dunn et al., 1983; Peterson and Pickett, 1995).

Seedlings germinating about the time of the disturbance can be very abundant, if several conditions are met — there must be sufficient canopy opening by the disturbance, there must be areas unoccupied by advance regeneration or sprouts, and there must be sources of seeds. It is important to note that an abundant and evenly distributed layer of advance regeneration can effectively prevent widespread seedling establishment (Webb, 1989). If advance regeneration is abundant but has a clumped distribution, new seedlings may colonize the interstitial areas (e.g. Peterson and Pickett, in press).

The contribution of seeds germinating from a soil seed bank varies widely, but can be very important (e.g. Peterson and Carson, 1996). Several influences will determine the abundance of seeds in a seed bank, but one that appears to be critical is the age of the stand when it is disturbed. Spurr (1956) noted the lack of pioneer, seed-bank species in initial regeneration of the old-growth Pisgah Forest in southern New Hampshire after the 1938 hurricane (see also Peterson and Pickett, 1995). Building on this observation, Peterson and Carson (1996) present evidence from a variety of sources to show that if stands are large and more than roughly 120 years old when disturbed, the contribution of pioneer, seed-bank species (especially *Prunus pensylvanica*, and *Rubus* spp., but also, perhaps, *Sambucus* spp.) is expected to be little or none, because of time depletion of seeds from the seed bank.

Newly-arriving seeds can contribute to an important role for new seedlings, but these too can be critically limited by availability. If a disturbance is severe enough to eliminate sources of seeds within the disturbed area (admittedly an unusual circumstance for wind disturbances), then the abundance of seeds arriving from less-disturbed locations will be determined, in part, by distance to these locations. Under extremely severe wind events, distance to seed sources may reduce the abundance of seedlings of some species in the center of the disturbed area (see Hughes and Fahey, 1988). More commonly, there should be no limitation of fresh seeds, particularly of the wind-dispersed, small-seeded species such as *Populus* spp. and *Betula* spp.

The importance of new seedlings to future vegetation in a disturbed area is potentially determined by the abundance of seeds available to germinate, as just discussed, but also by the abundance of conditions that prompt germination of those seeds. The most obvious example is the role of increased light and temperature from canopy opening, which provides cues for germination of a number of species. Another pertinent example is the importance of bare soil for germination of several small-seeded species (e.g. *Populus* spp. and *Betula* spp.). A major determinant of the amount of bare soil is the proportion of the soil

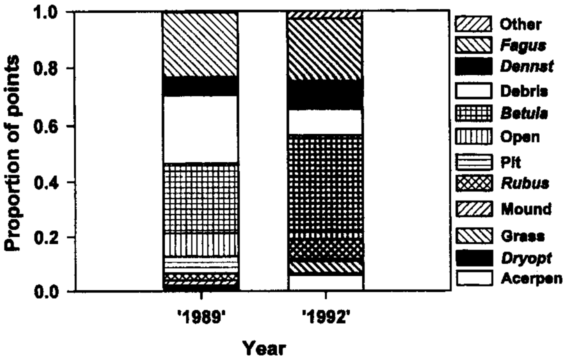

Fig. 7. Relative abundances of microsites at two times post-disturbance, in a catastrophic windthrow in Pennsylvania, USA.

surface disrupted by the uprooting of trees. When uprooting exposes bare soil in root pits and mounds, these microsites are often abundantly colonized by certain species (Hutnick, 1952; Peterson et al., 1990; Carlton and Bazzaz, 1998), although in cases lacking sufficient canopy and/or understory opening, these microsites may have little influence on germination (Webb, 1989). Thus, the relative abundance of different types of microsites (Fig. 7) can form an overlay on top of the abundances of seeds, to determine the abundance of new seedlings in catastrophic windthrows. Microsites may also influence the relative contribution of the various sources of colonists, by eliminating smaller stems of advance regeneration (see also Cooper-Ellis et al., 1999).

5. Coping strategies and interaction with human effects on forests

Coping with wind disturbances takes several forms, which might be grouped as actions during the interim between events, or those immediately after an event. However, since the timing and location of tornadoes and downbursts cannot be predicted, coping strategies must consist of minimizing the detrimental effects if a storm event does occur, and post-disturbance responses to damage. Interim actions may reduce the damage should a storm occur at the location in question. Such measures are mainly silvicultural actions that are possible in managed forests.

Savill (1983) reviewed silvicultural measures that may be taken, from a predominantly British perspective, although many apply equally well in the US. While acknowledging that in the most severe storms the majority of trees will be downed regardless of tree and stand conditions, Savill suggested that in somewhat less intense storms proactive management can be beneficial. He separated actions into four types: ground preparation, actions affecting tree rooting traits, species selection, and stand-level measures.

Because a widespread limitation to tree stability is shallow rooting due to wet or hardpan soils (Ruel, 1995), Savill (1983) advocated plowing and draining techniques that would reduce soil saturation and allow wider and deeper rooting of trees.

When tree seedlings are planted from planting stock, the resulting root architecture is often highly distorted, resulting in greatly reduced tree stability years later. When planting is necessary, the suggested solution is to use container-grown seedlings in larger holes, which would encourage more natural root development (Savill, 1983).

Species selection in managed forests can favor more windfirm species over particularly vulnerable ones. Globally, as well as in the US, pines, spruces and firs are typically less windfirm than other conifers, and most deciduous species are more windfirm than most conifers (Savill, 1983; Harris, 1989). Indeed, it is even possible to identify certain varieties, clones, or provenances within a species that show greater or lesser windfirmness (Savill, 1983; Webb, 1999). Thus, when future stand composition can be controlled, it is possible to shift composition to mixtures or species that are more windfirm, although this selection must be made carefully — root restrictions can affect various species differently, with the result that relative windfirmness among species is not fixed (Ruel, 1995).

Stand-level measures consist primarily of two components: rotation length (the age of the stand when harvested) and the spacing among trees. When possible, utilizing short rotations minimizes the length of time in which trees are large enough to be vulnerable to windthrow (Savill, 1983). Spacing is a much more undecided issue, with proponents of narrow and wide spacings both claiming improved windfirmness. All other factors being equal, thinning that substantially reduces density is likely to increase damage in the event of a storm, because it decreases communal support among the trees (Touliatos and Roth, 1971; Harris, 1989). Alternatively, thinning may allow greater wind penetration than an intact canopy. A complicating factor involves the trees that are removed in a thinning operation; if the most vulnerable trees (emergents, weak, or stem-damaged trees) are removed, the remaining stand may be more windfirm than before thinning (Stoeckeler and Arbogast, 1955). Close examination of the data shows that under a close-spacing situation (high density), windfirmness is not a trait of the individual trees as much as of the stand: trees are less likely to experience windthrow because of the mutual support offered by adjacent trees (Savill, 1983; Everham and Brokaw, 1996). Moreover, in dense stands, the relatively more uniform canopy minimizes wind turbulence penetrating into the stand and thereby reduces windthrow. Another possible contributor to windfirmness in dense stands is that root interlocking may occur in some species (Ruel, 1995). Thus, Harris (1989) states that 'even-aged stands may be quite windfirm so long as they remain intact and dense'. In contrast, when grown at wider spacings, individual trees become more windfirm as a result of developing well-tapered stems (low height/diameter ratio) that can bend in high winds (Savill, 1983; Everham and Brokaw, 1996). However, thinning of existing high-density stands exposes tall, thin trees to winds so that they are highly vulnerable for a period after the thinning (Savill, 1983; Harris, 1989; Everham and Brokaw, 1996). Harris (1989) points out that thinning can be beneficial and result in windfirm trees, if that thinning begins at a very early stage in stand development. Savill's ultimate recommendation to minimize the potential for wind damage was to favor high density stands on sites where soils imposed rooting constraints on individual tree stability, and to favor wide spacing from the outset elsewhere.

An additional component of stand-level management considers stand edges. Savill (1983) pointed out that a major effect of vertically-distinct edges on the rest of the stand is the eddies and turbulence caused behind the edge, which may extend to 60 m. Actions that minimize the contrast in height at the edge between one stand and the next will minimize potential for wind damage (Somerville, 1980). Harris (1989) advocated choosing the angle of edges relative to wind, and utilizing sequential strip cuts that offer a stair-step edge rather than a more abrupt vertical change.

After wind disturbance, managed forests are generally salvaged to minimize economic losses (Savill, 1983; Harris, 1989). Both Savill and Harris advocate prompt salvaging after a disturbance, to extract logs prior to decomposition. Furthermore, since down timber may cause curved or twisted stems in the young regeneration (Savill, 1983; Harris, 1989), salvaging might encourage more straight, clean boles in the next cohort of trees in a managed forest. Salvaging might have another, future, benefit because a number of species have tendencies to establish on elevated microsites such as mounds of uprooted trees, logs, or stumps, which may lead to unstable stilt-rooting (Harris, 1989). Removal of the logs would reduce the abundance of elevated microsites and thus, presumably reduce the proportion of trees that eventually become stilt-rooted and unstable.

Given the ways in which various silvicultural actions influence windfirmness of both trees and stands, it is likely that inherent vulnerability of North American forests has been altered across many millions of hectares by human activities. Most obviously, very limited areas of temperate hardwood forest remain in a late-mature or old-growth stage, which because of advanced tree age and large sizes, would be particularly vulnerable to wind damage. Thus, because many forest lands of the mid-west now consist of younger and smaller trees than in the centuries prior to European colonization, a large-scale human effect has been to reduce vulnerability to windthrow. This trend may be enhanced by increasing utilization of short rotations, e.g. in the Great Lakes area aspen forests, since modern pulp-producing procedures can utilize smaller dimension wood. In contrast, forests that have regenerated after the depopulation of parts of rural New England in the mid-19th century are probably vulnerable because of their larger size and the preponderance of white pine, a vulnerable species (Foster et al., 1997).

High market values for certain species may also gradually influence forest vulnerability to wind across large areas. To encourage oak regeneration, forest managers are increasingly utilizing controlled burns, which if they do in fact result in larger proportions of oaks, are likely to increase windfirmness of future stands.

Current cutting practices could either increase or decrease susceptibility of forests to windthrow, depending on circumstances. While selective removal of single trees leaves most of the canopy intact, the resulting openings could allow entry of air turbulence and decrease mutual support among surrounding trees, increasing the probability of small-scale windthrow (Ruel, 1995). Other cutting approaches remove small groups of trees, and are likely to have the same consequences, though perhaps resulting in a greater likelihood of destabilizing influence. Recent clearcuts are smaller than those of decades past, which could decrease the stretch of unforested ground over which wind could move unhindered and therefore reduce wind speeds (Ruel, 1995). However, today's smaller clearcuts generally leave riparian strips and buffers that have a very high vulnerability to subsequent windthrow (Ruel, 1995). Thus, there can be few conclusive statements on how human influences alter forest vulnerability to windthrow, even within the scope of a single action such as a clearcut. Much research remains to be done to improve our understanding of how human activity influence the risk of wind damage.

6. Impact of climate change

While there have been few published studies that consider how projected climate change might influence the tornado and downburst disturbance regime, numerous publications mention that climate change models predict increased frequency and intensity of catastrophic wind storms (e.g. Pearce, 1995; O'Hare, 1999). One line of thought is that with warmer air masses over middle latitudes such as North America, the temperature contrast with polar air masses will be greater, providing more energy and thus, more violent storms over the US. Another, more general, expectation is that with increased mean temperature, if variance around that mean remains constant, extreme weather events become statistically more probable (O'Hare, 1999); however, the assumption of constant variance about an increased mean appears to be questionable (O'Hare, 1999). In addition, the important factors for thunderstorm formation are not simply warm air, but the juxtapositioning of air masses such that deep convection can be initiated and low-level vorticity can be developed. Several projections suggest an increase in frequency, severity and/or size of hurricanes during the coming century (e.g. Anthes, 1982), and Agee (1991) found a positive correlation between mid-latitude cyclone frequency and temperature, suggesting future increases in cyclone events. However, these types of storms have different bases of formation than the thunderstorm systems that spawn downbursts and tornadoes, so such predictions about hurricanes and other storm types may have little relevance to the mesoscale dynamics of tornado and downburst formation.

Nevertheless, the above sorts of projections, and a number of very costly and much-discussed recent hurricanes, has led to detailed scrutiny of both the historical climate record and current models from an unexpected source: the insurance industry (Friedman, 1988; Leggett, 1993; Pearce, 1995). Because of unprecedented losses during the past 12 years, insurers and reinsurers are examining the climate change issue in an effort to project risk in the coming decades of the 21st century. For example, Munich Re, the world's largest reinsurance company, hired a meteorologist, Gerhard Berz, to head its technical research division. In a recent publication (Berz, 1993), he says 'the increased intensity of all convective processes in the atmosphere will force up the frequency and severity of tropical cyclones, tornadoes, hailstorms, floods and storm surges'. Such a statement gets much closer to an essential ingredient for thunderstorm formation: the vertical dynamic movement of convection. If warmer mid-latitude climates contribute to greater levels of convective storms, then increased frequencies and perhaps intensities of tornadoes and downbursts would not be surprising.

When it comes to specifics of tornado frequencies, few projections are available. Etkin (1995) predicted increased frequency of tornadoes in western Canada during the coming century (see also White and Etkin, 1997), based on a historical increase in tornado frequency in 'shoulder' months of May, June, August and September, when temperatures were warmer and more 'July-like'. This appears to be the only specific projection, beyond the extremely general ideas such as that of Berz quoted above. However, prominent tornado experts seriously question the validity of attempts to predict how climate change will influence tornado occurrence, because the details of how mesoscale meteorological conditions influence tornado formation are still poorly understood (Doswell, personal communication). Ongoing research by numerous groups currently is using recently-available technologies (e.g. portable Doppler radar and lidar) to examine intense thunderstorms to improve models of tornado formation under these conditions, and confirm or refute new conceptual models of tornadogenesis (Davies-Jones, 1995), and increased attention is focusing on non-supercell tornadoes and tornadic storms outside of 'tornado alley'. It is clear that storms from outside of the Great Plains can form under a wide variety of synoptic conditions, which may be somewhat distinct from typical tornado weather on the Great Plains (Davis et al., 1997). Until knowledge of supercell thunderstorm formation, both in 'tornado alley' and elsewhere, is much improved, we can have only limited confidence in long-term projections about tornado and downburst climatology under a changed 21st-century climate, although some very general suggestions warn that an increase in number and severity would be consistent with predicted continental and regional-scale changes in climate.

7. Conclusions and research needs

Catastrophic winds are a common type of disturbance in the forests of eastern North America. Hurricanes are predominant along the Atlantic and Gulf coasts, and downbursts in the Great Lakes region. Tornadoes are the most intense wind disturbance but are very small relative to the other types of wind events. While these generalizations seem valid, we lack detailed quantitative studies of size, frequency, and intensity of downbursts and tornadoes, and for all types there is a need for studies defining the characteristics of patch size and distribution on the landscape.

Wind events of increasing speed cause greater levels of damage to forests, and some studies suggest that amounts of precipitation that accompanies a wind storm strongly influences the amount and type of damage incurred to forests. Other recent studies question this pattern. There are still no direct measures of the amount of damage caused by winds of a given speed, or any accurate direct measures of wind speeds in tornadoes or downbursts. Site factors such as physiography and soil characteristics can greatly influence the damage that occurs in a hurricane, by determining the exposure of a stand to winds, and the ability of trees to firmly root, however, the interaction of downbursts and tornadoes with physiography remains virtually unknown.

The most important tree characteristics influencing damage from winds are size and species. Larger trees are more damaged, as are species with shallow roots. Strong wood appears to confer some advantage to a number of species, particularly understory species. Early successional species often suffer the greatest levels of damage in a mixed-species stand, but this may be mostly due to their common occupation of larger size classes. Manipulative experiments have been attempted, and their repetition at a variety of sites will answer several questions about how damage type varies with size, species, and soil characteristics.

Stand characteristics that determine levels of damage in some cases include density and recent history: lower-density stands are at greater risk of wind damage, and pathogens that cause weak spots in trunks result in elevated levels of tree snapping in high winds.

Mortality is highly correlated with treefall (via snapping or uprooting), but can be delayed. Certain species that do not readily sprout, particularly gymnosperms, are at greater risk of death than sprouting species. Sprout production generally decreases with tree size. Still poorly understood are the growth and long-term viability of sprouts, and whether available moisture influences sprout production or survival.

Wind disturbances produce both immediate and longer-term changes in a forest. Among the common immediate changes are reduction in size of surviving trees, and a shift in species composition towards a more late-seral suite of species. Diversity is generally changed, but the direction of the change is dependent upon what measure of abundance is used for diversity calculations. Examination of a wider variety of forest types and wind events must be accomplished before firm conclusions can be drawn about how species composition and diversity are altered by tornadoes, downbursts and hurricanes. Wind disturbances also appear to alter environmental conditions by increasing light and soil temperature, but the data are very limited.

Regeneration after a wind disturbance can come from a variety of sources. Some surviving trees nearly always are present, and advance regeneration often plays an important role. The importance of sprouting varies widely as a function size and composition of the pre-disturbance stand. Seedling establishment can be abundant, and is often of pioneer or mid-seral species. Long-term monitoring is needed to define what sources of colonists ultimately succeed in the post-disturbance community. The variety of microsites that are created in blowdowns may influence composition and abundance of seedling colonization, but again the data are too few for generalizations. Research on the environment of microsites must be combined with studies on their influence on germination and growth of potential colonists. Six influences are presented that should determine the relative importance of different sources of future vegetation.

The current understanding of catastrophic windthrow allows some generalizations, however, many of the mechanisms causing the observed patterns remain speculative. The nature of relationships and quantitative parameters are very poorly known. Further studies at the stand and landscape scale are needed to characterize coarse-level patterns of damaged area size and distribution, and the influence of stand variables, while studies of large samples of individual trees are needed to characterize how tree characteristics influence damage from, and response to, catastrophic winds. A potentially useful sampling protocol that addresses many of these research needs is as follows. First, a substantial number of wind disturbance events must be studied with consistent methods to provide adequate variation in size, severity, and other parameters for generalizations. This could be accomplished by establishing a series of large parallel belt transects, perhaps 1000 × 10 km, and performing several coarse-scale examinations of each storm event within these belts. Five belts oriented from south-east to north-west beginning along the Appalachians would encompass much of the range of forest types in eastern North America if the southern-most were to begin in Georgia, and the northern-most to begin in western New York and extend through Ontario. Remotely-sensed images of each event that crossed these transects could be used to determine size, severity of damage, and their spatial variation, particularly in relation to topography, forest type, and soil type. Comparison among the five belts could show latitudinal differences. In a smaller number of selected blowdowns within each belt, quick-response work in situ could establish the pre-disturbance forest structure and composition, details of types of damage in relation to tree and stand characteristics, and begin long-term demographic monitoring of marked stems that would eventually reveal the outcome and consequences of initial post-disturbance survival, establishment, and sprouting. Dendrochronological work as part of the quick-response sampling could be used to determine the disturbance history and stand age of wind-damaged areas. If such general prescriptions were instituted, many of the ecological unknowns relative to wind disturbance and forest dynamics could be thoroughly addressed.

In the meteorological realm, to improve projections of changes in tornado and downburst intensity, size, and frequency, we need first an improved understanding of the micro- and mesoscale meteorological processes that lead to formation of these phenomena within thunderstorms. Beyond that, research must eventually generate improved projections of conditions that will lead to thunderstorm formation. Consequently, the additional need is for improved spatial resolution of climate change models, which may be able to more closely approach mesoscale patterns than the current regional emphasis. And in order to better predict the likely consequences of tornadoes that do occur, we will need to expand the current very limited ecological and silvicultural database, to encompass studies of how various management choices influence stand vulnerability, and studies of natural forest regeneration after these disturbances. Such an improved understanding of natural regeneration will then allow informed management decisions to be made to facilitate the type of future forest desired in areas subject to these unpredictable and violent storms.

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