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Consistent influence of tree diameter and species on damage in nine eastern North America tornado blowdowns

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Abstract

Are tree damage patterns in natural-forest windthrows predictable? Here, I synthesize published and unpublished findings from nine North American forest sites that were disturbed by tornadoes, to ask how well tree damage patterns might be predicted on the basis of tree diameter and species identity. All sites were sampled by the author and assistants, using generally similar methodology, thereby avoiding many of the barriers to direct cross-site comparison of wind damage. In almost all cases, there is a consistent pattern of steady increase in risk of treefall with tree diameter. In most sites, uprooting was substantially more common than trunk breakage, although their relative frequencies varied with tree diameter, and among species and sites in complex ways. Species differed substantially in risk of treefall, even when controlling for diameter. However, ranking among species in risk of treefall was consistent, suggesting that among species differences are general across sites and forest types. In only two out of nine sites was there a significant influence of wood strength properties, independent of species identity. Type of treefall was weakly related to tree diameter, although differences among species were not consistent among sites. Direction of treefall was significantly more eastward for large compared to small trees in six out of eight sites. Stand-level characteristics of height variation, and density, were not consistently related to level of damage at the plot scale. At the scale of individual trees, a moderate level of predictability exists for treefall risk, sprouting, and direction of fall on the basis of easily recorded tree diameter and species identity; type of damage remains poorly predicted on the basis of these traits.

Keywords: Disturbance; Windthrow; Tornado; Treefall; Uprooting; Vulnerability

1. Introduction

Knowing the probable consequences of a particular disturbance in a particular stand or landscape contributes to more informed decision-making (Savill, 1983; Nowacki and Kramer, 1998; Gardiner and Quine, 2000), as well as greater understanding of the influence of disturbances on forest dynamics (White and Jentsch, 2001). Yet, some disturbances such as windstorms exhibit a great deal of stochasticity in their timing, size, season, intensity and impacts. Added to the variation in stand and site characteristics, it is perhaps not surprising that two recent reviews of wind disturbance (Everham and Brokaw, 1996; Webb, 1999) concluded that generalizations and predictions are elusive. Nevertheless, both reviews clearly pointed out that one major barrier to generalizations was dissimilarities among the existing studies—variation in researcher objectives, sampling methods, categories and definitions employed, statistical analyses, and interpretations. Consequently, generalizations have unavoidably been tentative and subject to numerous caveats.

Empirical wind-disturbance literature reveals conflicting findings about the effects of tree size and species identity. On the basis of biomechanics, larger trees are expected to be more vulnerable to toppling in high winds (e.g. Peterson and Pickett, 1991; Asner and Goldstein, 1997), yet some researchers report unimodal or even bimodal relationships between tree size (diameter or height) and risk of treefall (Everham and Brokaw, 1996). Mechanistic models predict steady decrease in the critical windspeed required to overturn trees, as tree height increases for a constant basal diameter (e.g. Gardiner et al., 2000).

Several trends are expected for interspecific differences. Field surveys suggest that species with both strong wood and deep roots are the most windfirm (Webb, 1988). Tree-pulling experiments generally confirm expectations that more deeply rooted species are more stable than shallowly rooted species (e.g. Elie and Ruel, 2005), although this is not always the case (Achim et al., 2005), and the presence of confounding factors usually precludes consideration of single-trait differences between species (Micoll et al., 2005). Conifers are often

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proposed as less windfirm than broadleaf species and early-successional species may be less windfirm than later-successional species (Foster, 1988). Windthrow vulnerability differences between evergreen conifers and deciduous broadleaf species also depend on the season; leafless broadleaf species are much less vulnerable in winter than nearby conifers (Peltola et al., 1999). Both of these trends are related to differences in wood strength, since broadleaf species typically have stronger wood than conifers, and slow-growing late-successional species typically have stronger wood than fast-growing pioneer species (Webb, 1989). Moreover, few studies have employed the proper statistical tools to separate such potential species differences from differences in tree size (Everham and Brokaw, 1996; Webb, 1999).

Predictability of treefall risk would be greatly enhanced if tree size and species effects are consistent among sites. Putz and Sharitz (1991), however, found that damage in swamp forests was greatest among species that were shallowly rooted in the swamp, but would normally have deep, well-developed root systems in upland sites (e.g. *Acer rubrum*). In tree-pulling experiments, Elie and Ruel (2005) found that while black spruce stability was unaffected by soil conditions, jack pine was significantly less stable on shallow, stony soils. Thus the *relative* windfirmness of a species may be variable among sites; few studies have directly addressed this question (but see Foster and Boose, 1992).

In addition to effects on the risk of treefall, tree diameter and species (as well as numerous other factors) are likely to influence the type of treefall—trunk breakage or uprooting. These two alternatives have distinctly different consequences, because only uprooting creates areas of disturbed soil and the resulting microtopography (reviewed in Schaetzl et al., 1989). The environmental heterogeneity and physical variation created by uprooted trees diversifies germination conditions (Beatty, 1984; Kuuluvainen and Juntunen, 1998; Peterson and Pickett, 2000), and may provide refugia from herbivorous mammals (Long et al., 1998; Krueger and Peterson, 2006). All other things being equal, stronger wood should result in greater uprooting because a tree's trunk is stronger (Putz et al., 1983); however, other things are rarely equal, and there are as yet few generalizations about diameter or species effects on type of treefall.

When a wind-toppled tree falls, the direction of fall may be ecologically relevant. When trees fall in different directions, the resulting jumble may hinder movement of large mammals (Grisez, 1960), such as browsers, while offering greater protection from predators to smaller animals. This characteristic of wind-disturbed forests seems to have received very little attention, so no general patterns have been identified.

The demographic, rather than structural, consequences of wind disturbance center on mortality and sprouting, rather than on treefall (Everham and Brokaw, 1996). Such patterns are more directly relevant to population biology of component species, since survival of a pre-disturbance tree involves less turnover than death and establishment of new individuals. Numerous studies of hurricane damage in tropical forests propose that because of sprouting of damage trees, mortality from wind is often quite low (Walker, 1991; Bellingham et al., 1994; Yih et al., 1991), and some temperate studies reach similar conclusions (Cooper-Ellis et al., 1999; Webb, 1999). However, three factors are likely to influence this generality: severity of damage, type of species, and size of trees. More severely damaged trees are less likely to sprout (Everham and Brokaw, 1996), so in high-severity disturbances, sprouting should be less, and mortality greater, than after low-severity disturbances. Most conifers do not resprout (Foster, 1988; Webb, 1999), so sprouting will be low and mortality high in heavily conifer-dominated sites. And for species that sprout from dormant buds beneath the bark, such as *Fagus* (Jones and Raynal, 1986), the thicker bark of larger trees is likely to hinder sprout emergence; thus we expect reduced sprouting in larger trees.

Finally, foresters in particular have identified stand characteristics that contribute to tree damage from wind (Mitchell, 1998; Ruel, 1995). It is widely held that high-density stands allow less penetration of wind within the general canopy, and offer more mutual support to individual trees, thereby reducing risk of wind damage. Conversely, stands with very rough canopy surfaces, due to variation in tree heights, are expected to suffer greater wind damage than uniform canopies (Savill, 1983; Mason, 2002).

In this paper, I present findings from nine tornado-disturbed forest sites, all sampled by the author and assistants, using similar objectives, damage categories, and analyzed with similar statistical tools. I particularly focus on how the most easily measured tree characteristics – trunk diameter and species – influence patterns of tree damage (e.g. Canham et al., 2001; Peterson, 2004). I address the following questions: (1) What is the effect of tree diameter on probability of treefall—increasing, decreasing, unimodal, or bimodal? (2) Are interspecific differences in vulnerability explained in part by wood strength properties? (3) Are early-successional species more vulnerable than late-successional species, or conifers more vulnerable than hardwoods, after controlling for diameter? (4) Are species rankings consistent among sites? (5) Does type of treefall (uprooting versus trunk breakage) show consistent diameter or species trends? (6) Does direction of treefall show consistent diameter or species trends? (7) Is stand damage related to density or variation in tree sizes?

2. Study sites and methods

This paper is based on sampling in nine sites. Three of the nine sites have been the subject of previous publications by the author, thus this paper both presents new findings, and synthesizes trends across multiple sites and studies. There is some pairing among several sites: the Tionesta Scenic Area in western Pennsylvania was disturbed by two different tornadoes (in non-overlapping paths) in 1985 and 1994, and these sites are reported as Tionesta '85 and Tionesta '94, respectively. The Gould Farm and Texhill sites are only ~20 km apart, and were disturbed by the same tornado. The Hattons and Taylor sites are only ~10 km apart, and were disturbed on the same day in 1998 by two tornadoes. Details about the Tionesta 1985 and 1994 sites, and Mingo National Wildlife Refuge are in Peterson and Pickett (1991), Peterson and Rebertus (1997), and Peterson (2000). Pre-disturbance species composition and relative abundances for each site are given in Table 2.

At each site, either the entire disturbed area (Cathedral Pines, Hattons), transects (Tionesta ’85), or large plots (20 m × 20 m for Gould Farm and TexHill; 40 m × 40 m for Mingo, Gum Road, Tionesta ’94 and Taylor) were inventoried. Generally, the following was recorded for each tree >5 cm diameter at 1.4 m (DBH): species identity, DBH, type of damage, direction of fall, whether the tree was still alive or not, and whether the tree sprouted or not. Type of damage was categorized – in order of increasing severity – as intact (undamaged), branches broken, bent, leaning, crown broken (>50% of crown removed or damaged), trunk broken, or uprooted. Sprouting and mortality were not recorded at Gum Road, because the sampling was conducted just a few months after the disturbance (Table 1). At Tionesta ’85, the minimum tree diameter inventoried was 10 cm DBH. At Tionesta ’85 and Cathedral Pines, direction of fall was not recorded.

3. Statistical analyses

The primary statistical tool for examining diameter and species effects on treefall was logistic regression (Menard, 1995; Hosmer and Lemeshow, 2000). This is the best technique for relating binary response variables (e.g. tree standing or fallen; trunk breakage or uprooting) to categorical or continuous independent variables (e.g. tree diameter, species identity, wood strength; Trexler and Travis, 1993). One of the two alternative responses is defined as an “event”, and the log-transformed odds of the event is modeled as a function of the independent variable(s). In the analyses here, among tree fates, ‘fallen’ was considered the event and ‘standing’ the non-event; among types of treefall, ‘uprooted’ was considered the event and ‘trunk broken’ the non-event. Binary response variables cannot result in normally distributed errors, therefore a distribution which explicitly assumes binomially distributed errors is needed; the logit-transformation accomplishes this (Trexler and Travis, 1993; Menard, 1995). The logit-transformation is the natural log of the odds, or $\ln(\pi(x)/1-\pi(x))$, where $\pi(x)$ is the expected value of the response (i.e. probability of the “event”) for a given value of the predictor. Consequently, logistic regression has far fewer data restrictions than ordinary least-squares regression; because there is no assumption of normality or heteroscedasticity, there was no need for data transformations. However, logistic regression does assume that the logit-transformation of the response variable is linear in relationship to any continuous predictor variables. Following Menard (1995), the Box–Tidwell transformation was applied to tree fate (standing versus fallen) across several tree diameter categories in each site to verify the validity of this assumption; in all sites the logit was linear in the predictor. Similarly, the Box–Tidwell transformation was used to check for linearity of the logit of type of treefall (trunk broken versus uprooted) across tree diameter categories.

Table 1
Characteristics of the nine study sites and associated tornadoes

Site	Latitude (N)	Longitude (W)	Elevation (m)	Rooting depth, soil type and drainage	Disturbed	Sampled	Size (ha)	Wind speed
Gum Road	35°40′	85°10′	220	41 cm; silty clay loam over heavy clay; well drained[1]	April 2002	June 2002	8	181–253
Mingo NWR	36°58′	90°13′	350–400	76 cm; silt loam; poorly drained[2]	June 1993	Aug. 1994	35	117–180
Cathedral Pines	41°50′	73°20′	720–800	56 cm; silt loam and sandy loam over gravel; well drained[3]	July 1989	1991, ‘95	12	254–332
Tionesta ’85	41°39′	78°57′	500–600	66–91 cm; silt loam over clay loam; moderately well drained[4]	May 1985	1986–1989	370	333–418
Tionesta ’94	41°39′	78°57′	500–600	41–69 cm; loam over clay loam; moderately well drained[5]	July 1994	July 1996	2	181–253
Hattons	41°20′	75°07′	475	28–42 cm; loam over clay loam; moderately well drained[6]	May 1998	July 1999	85	181–253
Gould Farm	42°10′	73°15′	1250	91 cm; loam and sandy loam; well drained[7]	June 1995	July 1997	5	181–253
Texhill	41°20′	75°45′	1310	56 cm; silt loam over loam; well drained[8]	June 1995	July 1997	3	181–253
Taylor	41°17′	75°09′	440	22–36 cm; silt loam over loam; moderately poorly drained[9]	May 1998	2000–2001	4	181–253

Size refers to size of disturbed area contiguous with sample area. Wind speed is in km/h, estimated from the Fujita scale ranking of tornado intensity. Soil characteristics from published soil surveys. 1 = USDA Soil Conservation Service, 1978; 2 = USDA Soil Conservation Service, 1986; 3 = USDA Soil Conservation Service, 1970; 4 & 5 = USDA Soil Conservation Service, 1987; 6 = USDA Soil Conservation Service, 1990b; 7 = USDA Soil Conservation Service, 1990a; 8 = USDA Soil Conservation Service, 1988; 9 = USDA Soil Conservation Service, 1990b.

Linearity was clearly violated for the Gould Farm, Taylor, Tionesta ’85, Cathedral Pines and TexHill sites; therefore, tree diameter was used in the tree fate logistic regressions only in the Mingo, Gum Road, Hattons, and Tionesta ’94 sites.

Two main sets of multiple logistic regressions were conducted; in each set a separate logistic regression was done for each site. One set examined tree fate (standing versus fallen) as a function of several predictors, and used only data from species with $n > 14$ individuals per site. The other set of logistic regressions examined tree fall type (trunk broken versus uprooted) as a function of several predictors, again using only fallen trees, and data from species with $n > 14$ individuals per site. Predictors considered in these logistic regressions were species identity (as a nominal variable), tree diameter, wood specific gravity, wood modulus of rupture, and wood modulus of elasticity (continuous variables). Wood strength is a multi-dimensional concept, and therefore three strength indices were used here—these are typically the focus of mechanistic studies of biomechanical influences on tree breakage. Published values for these strength indices for green wood of the appropriate species are from USDA Forest Service (1987).

Multiple logistic regressions were performed in SPSS 11.5 (SPSS, Inc., Chicago, IL). Models were built using forward selection of variables, with a threshold of $p < .05$ to enter a variable in the equation, and $p > .10$ to remove a variable from the equation. The overall significance of logistic regression models was tested using the likelihood ratio χ^2 test (Trexler and Travis, 1993; Hosmer and Lemeshow, 2000); the Wald test was used to evaluate the significance of particular variables within the model. Back-transformations following logistic regression yield probabilities of the ‘event’, in relation to the independent variables, and such probabilities are presented in Section 4. Interpretation of multiple logistic regression is analogous to that for multiple linear regression. In the analyses of tree fate (standing or fallen), intact or partially damaged trees were considered ‘standing’, and uprooted or trunk-broken trees were considered ‘fallen’.

Explicit tests for change in species ranking among sites were conducted with subsets of each site’s data, because of substantial differences in species composition among sites. For example, the *Tsuga canadensis* and *Acer saccharum* data were used from those sites where these two species were abundant, and multiple logistic regression performed using only the data on those two species from each site, with independent variables of tree diameter, species, wood strength indices, and site. Similar approaches were used to examine potential change in rankings for other pairs of species. Direction of fall is angular, and therefore cannot be analyzed with tests designed for linear data. Comparison of mean direction of fall among groups was done with Reylaigh’s F-test, using the Oriana software package for circular statistics (Kovach Computing, Inc., Wales).

4. Results

4.1. Overall damage

The sites studied differed substantially in severity of wind damage, ranging from a low of 20.5% of the trees toppled at Gum Road, to 96.6% at Cathedral Pines (Table 2). In all nine cases, the loss of standing basal area was greater than that of density, ranging from roughly 34% at Gum Road and Tionesta ’94, to 99.7% at Cathedral Pines. Consistently greater loss of basal area demonstrates that larger trees are preferentially damaged in these windstorms. Seven of the nine sites experienced >50% reduction in standing basal area, suggesting that these seven sites experienced more severe disturbance than many sites studied in wind disturbance research (c.f. Fig. 2 in Everham and Brokaw, 1996).

Mortality was usually much lower than structural damage, ranging from 13.8% at Mingo to 94.3% at Tionesta (Table 2). It should be noted that inventories were conducted after different amounts of post-disturbance time in the different sites, so details of mortality are not directly comparable across sites. However, Table 2 shows that while severe wind disturbances in broadleaf forests often results in moderate mortality, conifer-dominated forests are indeed likely to experience very high levels of mortality. Thus, although many wind disturbances will have a lesser demographic effect than structural effect (sensu Everham and Brokaw, 1996), the demographic change can be very high when such storms strike coniferous forests.

4.2. Diameter effects

In all nine sites, incidence of windthrow increased with tree diameter (Figs. 1 and 2). Consequently, larger diameter classes lost greater proportions of basal area than smaller diameter classes (Table 3). In the tree fate set of logistic regressions, tree diameter was significant either as a main effect or in interactions in all nine sites (Table 4), and slope coefficients were positive, indicating an increase in risk of treefall with diameter. We found no evidence for bimodal distributions of tree diameter versus treefall risk. Moreover, for sites overall, and for most species within sites, there was no evidence of a unimodal diameter–risk relationship. In only a few species within sites, all with small sample sizes, was there a decrease in risk of treefall with diameter, and each of these species was found across a limited range of diameters.

In nearly all sites, and in most species, the prevalence of sprouting decreased, and that of mortality increased, with tree diameter (Table 3).

Type of treefall showed two types of trends in relationship to tree diameter. In several sites (e.g. Tionesta ’85, Taylor), considering only the fallen trees, uprooting was most common in intermediate diameter classes, and less prevalent in smaller and larger diameter classes (data not shown). In other sites (e.g. Gum Road, Mingo NWR), the proportion of fallen trees that uprooted increased steadily across diameter classes (data not shown). In Mingo, the multiple logistic regression of type of treefall revealed significant positive effects of tree diameter (Table 5) on probability of uprooting. At the Hattons and Gum Road sites, tree diameter had significant interactions with wood specific gravity and modulus of elasticity, respectively, in influencing type of treefall (Table 5).

Table 2
Pre- and post-disturbance abundance and basal area, sprouting, mortality, and uprooting in nine eastern North America tornado blowdowns, by site and species

Site and species	Abundance		Basal area		% of pre-disturbance trees		
	Pre	Post	Pre	Post	Sprouted	Died	Uprooted
Gum Road							
Acer saccharum	38	27	1.21	0.90	n.a.	n.a.	7.9
Carya glabra	84	77	1.84	1.60	n.a.	n.a.	2.4
Carya ovata	134	120	5.30	4.52	n.a.	n.a.	3.7
Fraxinus americana	110	77	6.27	3.68	n.a.	n.a.	10.0
Fraxinus quadrangulata	15	11	0.27	0.13	n.a.	n.a.	0.0
Juniperus virginiana	105	83	2.35	1.76	n.a.	n.a.	1.0
Ostrya virginiana	22	19	0.14	0.12	n.a.	n.a.	0.0
Quercus alba	63	53	6.35	5.55	n.a.	n.a.	1.6
Quercus prinus	52	46	1.48	1.23	n.a.	n.a.	3.8
Quercus rubra	148	87	23.8	11.6	n.a.	n.a.	26.4
Ulmus alata	100	91	1.82	1.49	n.a.	n.a.	3.0
Other spp.	56	46	2.61	2.23	n.a.	n.a.	3.6
All species	927	737	53.4	34.8	n.a.	n.a.	7.4
Mingo							
A. saccharum	51	47	0.54	0.44	41.2	9.8	0.0
Liquidambar styraciflua	50	40	1.36	0.99	82.0	0.0	0.0
Quercus "red"	44	16	6.84	1.23	34.1	52.3	18.2
Other spp.	139	97	8.50	3.27	53.2	20.9	7.9
All species	284	200	17.2	5.93	53.2	20.1	6.7
Cathedral Pines							
Tsuga canadensis	74	3	10.9	0.04	0.0	90.5	75.7
Other spp.	13	0	3.12	0	28.6	92.3	61.5
All species	87	3	14.0	0.04	6.9	90.8	73.6
Tionesta '85							
Acer rubrum	16	2	0.97	0.00	27.7	70.6	62.5
A. saccharum	62	10	4.72	0.37	4.5	97.0	48.4
Betula alleghaniensis	33	4	1.85	0.06	3.4	96.6	60.6
Betula lenta	17	0	0.82	0.00	0.0	100	76.5
Fagus grandifolia	304	40	29.5	1.42	10.9	93.2	58.2
T. canadensis	108	4	29.6	0.04	0.0	100	68.5
Other spp.	13	0	1.76	0.00	18.7	81.2	61.5
All species	553	60	69.2	1.89	8.1	94.3	60.0
Tionesta '94							
A. rubrum	39	27	1.42	0.89	48.7	25.6	20.5
A. saccharum	32	25	1.57	1.46	15.6	28.1	18.8
B. alleghaniensis	61	36	3.08	2.15	31.1	31.1	29.5
F. grandifolia	316	244	19.9	11.9	18.0	17.7	13.0
T. canadensis	182	139	28.5	19.1	0.0	15.9	15.4
Other spp.	13	6	0.71	0.64	15.4	38.5	23.1
All species	643	477	55.2	36.2	15.9	19.9	16.2
Hattons							
A. rubrum	406	155	19.8	4.79	47.5	13.3	36.0
Pinus strobus	48	37	1.19	0.70	0.0	6.3	14.6
Q. alba	65	41	4.02	1.94	23.1	23.1	23.1
Other spp.	24	16	0.47	0.20	33.3	12.5	4.2
All species	543	249	25.5	7.63	39.8	13.8	31.1
Gould Farm							
A. saccharum	61	14	2.01	0.25	36.1	24.6	52.5
B. alleghaniensis	35	16	1.01	0.37	25.7	17.1	42.9
F. americana	33	2	1.83	0.02	66.7	18.2	72.7
P. strobus	39	3	7.63	1.50	0.0	79.5	69.2
T. canadensis	146	27	4.92	0.50	0.0	30.1	50.7
Other spp.	46	16	2.31	0.22	60.9	13.0	54.3
All species	360	78	19.7	2.87	22.5	30.0	54.7
TexHill							
A. saccharum	38	5	1.19	0.11	21.1	7.9	63.2
Carya spp.	19	6	0.60	0.09	78.9	0.0	63.2
Q. prinus	104	1	6.40	0.00	58.7	33.7	89.4

Table 2 (*Continued*)

Site and species	Abundance		Basal area		% of pre-disturbance trees		
	Pre	Post	Pre	Post	Sprouted	Died	Uprooted
Q. rubra	17	2	1.33	0.00	41.2	47.1	76.5
T. canadensis	33	2	1.21	0.03	0.0	42.4	63.6
Other spp.	43	10	0.67	0.10	65.1	7.0	55.8
All species	255	26	11.4	0.34	46.7	24.7	73.3
Taylor							
A. rubrum	399	72	16.7	2.08	58.6	35.1	52.4
A. saccharum	196	29	9.48	0.97	53.1	37.2	69.4
Amelanchier arb.	18	9	0.17	0.05	72.2	0.0	16.7
B. alleghaniensis	57	14	2.81	0.73	14.0	64.9	43.9
Carpinus caroliniana	18	13	0.16	0.13	66.7	16.7	5.6
C. ovata	64	21	4.16	0.67	53.1	42.2	56.3
F. grandifolia	32	6	1.32	0.19	21.9	56.3	65.6
F. americana	148	12	9.38	0.54	50.0	46.6	62.8
O. virginiana	56	38	0.46	0.26	55.4	21.4	17.9
Q. alba	156	60	11.2	3.47	27.6	69.9	32.7
Q. rubra	45	6	3.44	0.31	20.0	80.0	75.6
Tilia americana	16	4	1.34	0.36	43.8	56.3	68.8
T. canadensis	32	6	3.89	0.69	0.0	78.1	50.0
Other spp.	43	13	2.35	0.49	18.6	53.5	48.8
All species	1280	303	66.9	10.9	45.6	45.4	52.1

Basal area in m^2. Sprouting and mortality not recorded at Gum Road site, and sprouting not recorded at Cathedral Pines.

4.3. Species effects

Tree diameter and species effects produced three broad types of treefall probability diagrams. In the simplest, from the Cathedral Pines site, treefall risk was unrelated to species or wood strength, and was a simple function of tree diameter (Fig. 2a). Species effects on treefall risk were more evident in the less-severely damaged sites. In the Gum Road site (Fig. 2b), tree diameter and species had a significant interaction, yielding probability curves with similar intercepts but differing slopes. The third and most complex type of treefall probability diagram is that shown for Tionesta '94 (Fig. 2c); here significant species

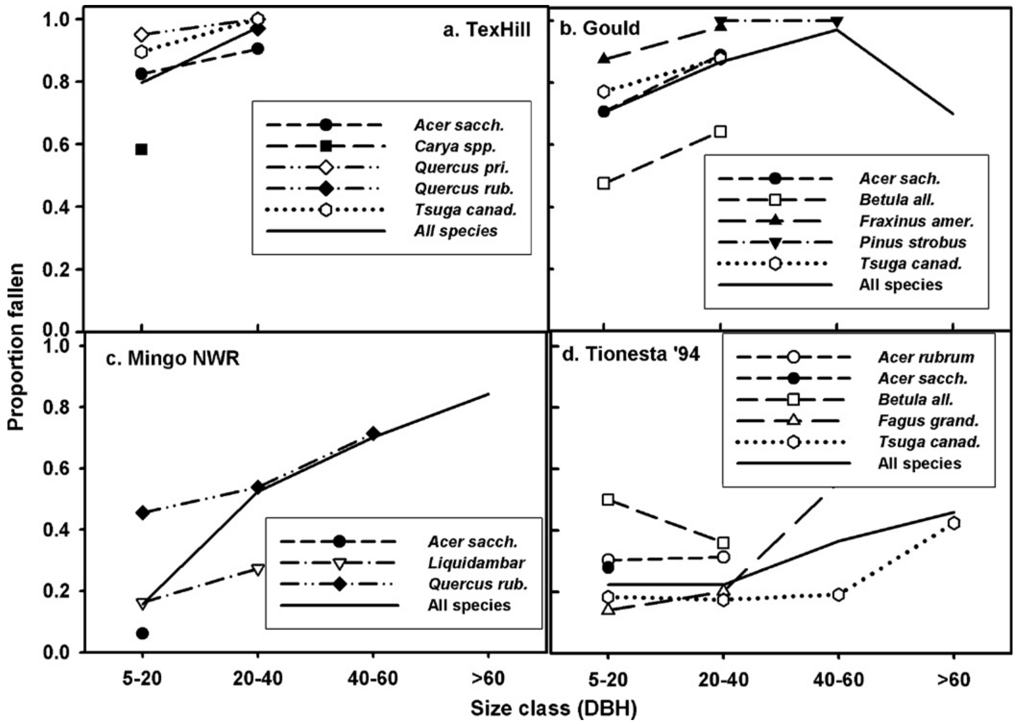

Fig. 1. Proportions of trees fallen across four of the nine study sites, for four diameter classes. Only species and diameter classes with $n > 10$ are included in the figure. 'Fallen' includes trunk breakage and uprooting; all partially damaged or undamaged trees are considered 'standing'. Abbreviations: 'Acer sacch.' = *Acer saccharum*; 'Betula all.' = *Betula alleghaniensis*; 'Fagus grand.' = *Fagus grandifolia*; 'Fraxinus amer.' = *Fraxinus americana*; 'Liquidambar' = *Liquidambar styraciflua*; 'Quercus pri.' = *Quercus prinus*; 'Quercus rub.' = *Quercus rubra*; 'Tsuga canad.' = *Tsuga canadensis*.

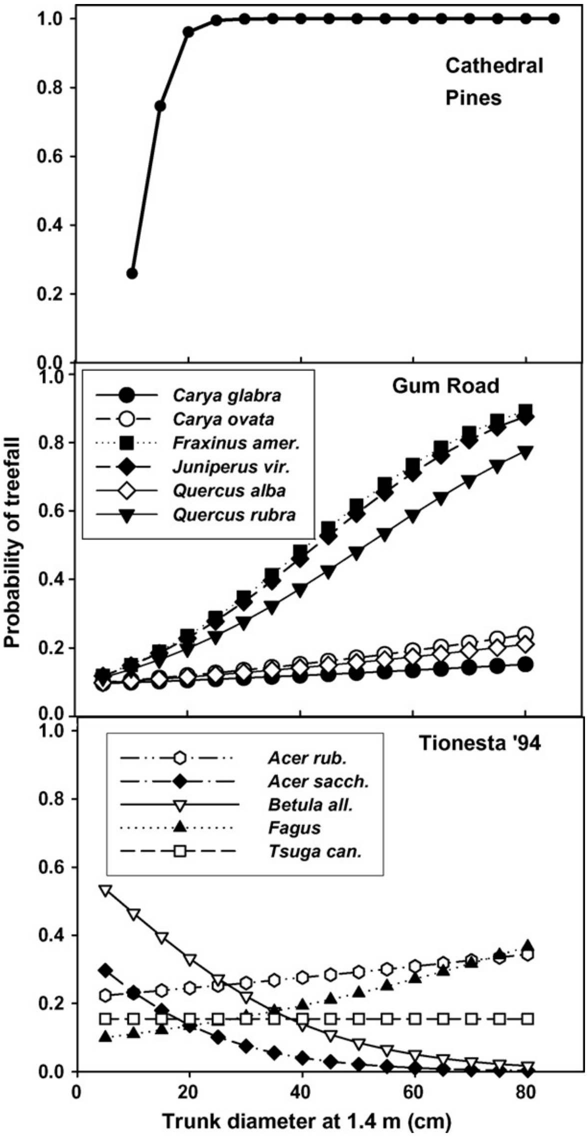

Fig. 2. Probability of treefall vs. tree diameter (in cm DBH), for common species in three of the nine study sites. Probability calculated from significant results in multiple logistic regression of tree fate against tree DBH and species identity. Only species with >14 individuals in a given site were included in logistic regressions. Panel 'a' shows results where only the 'DBH' main effect was significant; panel 'b' shows results where 'DBH' and 'species' had a significant interaction; panel 'c' shows results where there was a significant 'species' main effect, and significant 'DBH × species' interaction.

main effects combine with a significant species × diameter interaction term to yield non-parallel curves with different intercepts for the different species. For example, *Betula alleghaniensis* and *A. saccharum* are relatively more vulnerable than associated species in the smaller diameter classes, but becomes relatively less vulnerable relative in larger diameter classes.

Species varied in levels and types of damage within and among sites (Figs. 1 and 2), but in a consistent manner. For example, across most diameters and sites, *Quercus alba* and *Carya* species tend to be less vulnerable to treefall than most other species, while *Fraxinus americana* tends to be more vulnerable (Table 2). *A. saccharum* was often more windfirm than other species, except at the Gum Road site. Within a genus, *Quercus rubra* and closely related species were consistently more vulnerable than *Q. alba*, and *A. rubrum* was consistently more vulnerable than *A. saccharum* (Table 2). Species identity had significant main or interactive effects on risk of treefall, independent of tree diameter or wood strength, in six of the nine sites (Table 4).

Conifers were slightly more vulnerable than hardwoods, when diameter was controlled. *Juniperus virginiana* was abundant at only one site (Gum Road), and showed intermediate vulnerability there (Fig. 2); *Pinus strobus* was abundant at two sites, and while intermediate in vulnerability at Hatton's (Table 2), was more damaged at Gould Farm than other species in similar diameter classes (Fig. 1). The most common conifer in this study, *T. canadensis*, was common in six of the nine sites, and exhibited intermediate (Taylor, Tionesta '94) to high (Gould Farm, TexHill) vulnerability relative to other species (Figs. 1 and 2).

Early-successional species were not noticeably more vulnerable to treefall than late-successional species, when controlling for diameter. The intermediate to high vulnerability of *A. rubrum* (an early-to-mid successional species) and *Tsuga* (late successional) contributed to this pattern, as did the moderate to low vulnerability of *B. alleghaniensis* (an early-to-mid successional species).

While most of the hardwood species had some ability to sprout following wind damage (Table 2), sprouting was especially common in *A. rubrum*, *Carya* spp., and *F. americana*. Consequently, despite these species often suffering heavy wind damage, their mortality levels were often less than those of other species.

Type of treefall was significantly influenced by species identity (independent of wood strength properties) only at the Taylor site (Table 5). Among the fallen trees at Taylor, the proportions uprooted ranged from a low of 53% (*Q. alba*) and 56% (*Ostrya virginiana*) to a high of 84% (*Carya ovata*) and 87% (*Q. rubra*).

The consistency of species' relative windfirmness was tested with several reduced-dataset logistic regressions, using subsets of species and sites (Table 6). This ensured that the species actually were present at each site being included in the logistic regression. Of the seven reduced-dataset logistic regressions, six showed no significant species × site interaction, suggesting that the relative effects of species were consistent among sites (Table 6). Only the regression comparing *A. saccharum* and *B. alleghaniensis* across four sites (Taylor, Gould, Tionesta '85, and Tionesta '94) produced a significant interaction; these two species changed in relative risk of treefall among the four sites.

4.4. Wood properties

Wood strength appears to have consistent moderate influence on risk of treefall in these sites: one of the wood strength variables was significant in an interaction at six of the nine sites (Table 4). Notably, the wood strength properties were never significant as main effects in the logistic regressions of

Table 3
Pre- and post-disturbance abundance and basal area, sprouting, mortality, and uprooting in nine eastern North America tornado blowdowns, by diameter class

Site and diameter class	Abundance		Basal area		% of pre-disturbance trees		
	Pre	Post	Pre	Post	Sprouted	Died	Uprooted
Gum Road							
5–19.9	500	436	6.17	5.34	n.a.	n.a.	2.4
20–39.9	303	229	20.2	14.8	n.a.	n.a.	6.9
40–59.9	102	62	18.9	11.2	n.a.	n.a.	23.5
60+	22	10	8.15	3.53	n.a.	n.a.	54.5
Mingo							
5–19.9	192	165	1.58	1.24	58.9	6.8	0.5
20–39.9	46	22	3.21	1.55	58.7	32.6	10.9
40–59.9	33	10	6.56	1.87	24.2	60.6	27.3
60+	13	3	5.87	1.27	23.1	69.2	30.8
Cathedral Pines							
5–19.9	9	3	0.17	0.04	33.3	66.7	55.6
20–39.9	42	0	2.99	0.0	14.3	97.6	81.0
40–59.9	19	0	4.19	0.0	0.0	84.2	73.7
60+	17	0	6.68	0.0	0.0	94.1	64.7
Tionesta ’85							
5–19.9	198	50	2.51	0.37	18.2	64.6	40.4
20–39.9	163	3	11.4	0.19	6.1	95.7	71.8
40–59.9	116	7	21.1	1.33	2.6	93.1	70.7
60+	76	0	34.2	0.0	1.3	100.0	59.2
Tionesta ’94							
5–19.9	329	256	3.98	3.05	17.3	16.1	12.5
20–39.9	182	142	12.0	9.68	19.2	16.5	13.7
40–59.9	82	52	15.5	10.0	11.0	28.0	30.5
60+	50	27	23.7	13.4	4.0	44.0	26.0
Hattons							
5–19.9	229	153	3.46	2.06	36.7	5.2	15.7
20–39.9	296	96	20.0	5.44	41.9	18.6	42.2
40–59.9	18	1	2.58	0.18	38.9	44.4	50.0
60+	–	–	–	–	–	–	–
Gould Farm							
5–19.9	199	59	2.63	0.63	26.6	25.6	50.3
20–39.9	120	16	7.02	0.74	19.2	27.5	59.2
40–59.9	31	0	6.05	0.0	9.7	67.7	67.7
60+	10	3	4.00	1.50	20.0	30.0	50.0
TexHill							
5–19.9	108	22	1.53	0.15	50.9	19.4	54.6
20–39.9	138	4	8.24	0.18	45.7	26.1	88.4
40–59.9	9	0	1.64	0.0	11.1	66.7	66.7
60+	–	–	–	–	–	–	–
Taylor							
5–19.9	543	192	7.74	2.19	53.8	35.4	38.9
20–39.9	634	95	40.1	5.66	41.3	50.8	63.4
40–59.9	94	14	15.9	2.28	26.6	64.9	53.2
60+	9	2	3.15	0.83	22.2	77.8	44.4

Basal area in m^2. Diameter classes based on trunk diameter at 1.4 m (dbh). Sprouting and mortality not recorded at Gum Road site, and sprouting not recorded at Cathedral Pines.

risk of treefall, and their significant interaction was always with tree diameter rather than species. Specific gravity, modulus of rupture, and modulus of elasticity were each significant in interactions in two sites, and never in combination. *Carya* spp. have particularly strong wood (e.g. *Carya glabra* has the highest specific gravity and modulus of rupture among the species considered here), and were consistently less damaged than trees of other species in similar diameter classes (Fig. 2b). Another species with strong wood is *O. virginiana*; even considering its usual small size, this species is quite windfirm (Fig. 1). The intra-generic differences between *A. saccharum* and *A. rubrum* support a role for wood strength in contributing to treefall vulnerability, because the species with weaker wood (*A. rubrum*) is less windfirm. Among the oaks, *Q. alba* has

Table 4
Significant terms in multiple logistic regressions of tree fate (standing vs. fallen), for nine sites

Site	Main effects	Interactions	Model significance
Gum Road		DBH × species	$\chi^2 = 96.1$, 10 d.f., $p < .001$
Mingo NWR	Species	DBH × spgrav	$\chi^2 = 49.2$, 3 d.f., $p < .001$
Cathedral Pines	DBH (+)		$\chi^2 = 15.7$, 1 d.f., $p < .001$
Tionesta ’85		DBH × modelas	$\chi^2 = 67.7$, 1 d.f., $p < .001$
Tionesta ’94	Species	DBH × species, DBH × spgrav	$\chi^2 = 47.2$, 9 d.f., $p < .001$
Hattons	Species	DBH × modelas	$\chi^2 = 145.5$, 3 d.f., $p < .001$
Gould Farm	DBH (+), species	DBH × species	$\chi^2 = 61.7$, 9 d.f., $p < .001$
Texhill	DBH (+)	DBH × modrup	$\chi^2 = 40.5$, 2 d.f., $p < .001$
Taylor	Species	DBH × modrup	$\chi^2 = 184.3$, 12 d.f., $p < .001$

Predictors available for main effects or interactions were DBH, species, wood specific gravity, wood modulus of rupture, and wood modulus of elasticity. Only species with >14 individuals were included as separate species. When DBH was a significant main effect, the direction of its beta value is indicated as ‘+’ (positive) or ‘−’ (negative).

Table 5
Significant terms in multiple logistic regressions of type of treefall (trunk broken vs. uprooted), for five sites

Site	Main effects	Interactions	Model significance
Gum Road		DBH × modelast.	$\chi^2 = 49.2$, 1 d.f., $p < .001$
Mingo NWR	DBH (+)		$\chi^2 = 9.2$, 1 d.f., $p = .002$
Hattons		DBH × spgravity	$\chi^2 = 4.9$, 1 d.f., $p = .027$
Texhill	Spgravity, modelasticity		$\chi^2 = 11.8$, 2 d.f., $p = .003$
Taylor	Species		$\chi^2 = 68.8$, 18 d.f., $p < .001$

Regressions were overall not significant in the other four sites. Predictors available for main effects or interactions were DBH, species, wood specific gravity, wood modulus of rupture, and wood modulus of elasticity. Only species with >14 individuals were included as separate species. When DBH was a significant main effect, the direction of its beta value is indicated as ‘+’ (positive) or ‘−’ (negative).

wood with an identical modulus of rupture compared to *Q. rubra*, but *Q. rubra* has a higher modulus of elasticity; yet *Q. rubra* is often more heavily damaged where the two species co-occur. On the other hand, several examples demonstrate species effects beyond the effect of wood strength, with species of very similar wood strength experiencing substantially different levels of damage, such as the greater damage at Gum Road to *F. americana* compared to several species with weaker wood (e.g. *Ulmus alata* and *Juniperus*). At the Gould Farm and Taylor sites, *B. alleghaniensis* was noticeably less vulnerable than would be expected on the basis of modulus of rupture (it is of intermediate strength relative to other species in this trait), although *B. alleghaniensis* has a rather high modulus of elasticity, suggesting flexible wood.

Wood strength occasionally had an effect on the type of treefall (trunk breakage vs. uprooting); logistic regressions found significant wood strength main or interactive effects on type of treefall at TexHill, Gum Road, and Hattons (Table 5). At Gum Road, modulus of elasticity interacted significantly with diameter, and at Hattons specific gravity interacted significantly with diameter, to influence type of treefall. At TexHill, uprooting significantly increased (relative to trunk breakage) with wood specific gravity, and significantly decreased with modulus of rupture. At all the other sites, wood strength variables did not enter the regression models for type of treefall (Table 5). Nevertheless, there was substantial variation among species and sites in the type of treefall (Fig. 3). For example, *A. rubrum* was slightly more prone to uprooting than *Fagus grandifolia* at Tionesta ’85, while at the Taylor site, *Fagus* was much more likely to uproot than *A. rubrum*. *A. saccharum* and *T. canadensis* showed a similar reversal between sites (Fig. 3).

4.5. Direction of fall

In seven of the nine sites, direction of fall was recorded for fallen trees (not at Tionesta ’85 or at Cathedral Pines). In six of those seven sites, trees fell predominantly to the north or northeast; mean direction of fall was north-northwest at

Table 6
Significant main effects and interactions in multiple logistic regression models on reduced datasets

Sites and species	Main effects	Interactions
Tionesta ’85, Tionesta ’94; ACRU, ACSA, BEAL, FAGR, TSCA	Species, site	DBH × site, DBH × species
Tionesta ’85, Tionesta ’94; Gould, TexHill, Taylor; ACSA, TSCA	DBH, site	DBH × site
Gum, Taylor; CAOV, FRAM, QUAL, QURU	DBH, site, species	
Gum, Taylor; QUAL, QURU	DBH, site	DBH × site, DBH × species
Taylor, Gould, Tionesta ’85, Tionesta ’94; ACSA, BEAL	DBH	DBH × site, site × species
Gum, Gould, Taylor; ACSA, FRAM	DBH, site	
Gum, Taylor; OSVI, CAOV	DBH	DBH × site

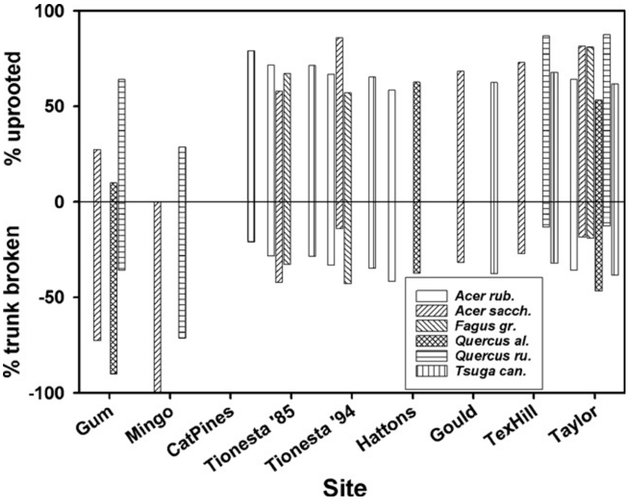

Fig. 3. Prevalence of uprooting and trunk breakage among fallen trees, by species, for nine study sites.

TexHill. In five of the seven sites, circular F-tests showed that larger trees fell further eastward than smaller trees ($p < .01$ in Gum, Gould, Tionesta '94, and Taylor, $p = .09$ at Mingo). For example mean azimuth for trees smaller than 18 cm DBH at Tionesta '94 was 12.6° west of north, while mean azimuth for trees larger than 18 cm was 39.6° (Fig. 4). Similarly, at Gould Farm, the mean azimuths were 4.8° and 26.4° for trees smaller than 11 cm, and larger than 27 cm, respectively (Fig. 4).

5. Discussion

Wind disturbances have a large element of stochasticity, yet the findings reported here demonstrate that there are generalities, and that they mostly are consistent among a variety of sites and forest types. The most robust (and unsurprising) trend is that the probability of treefall steadily increases with tree diameter; this trend is almost universal in the data reported here. Similar trends have been reported from coarser-scale stand- and landscape-level studies of wind damage (Scott and Mitchell, 2005), and mechanistic models often predict lower critical windspeeds for breaking or overturning larger trees (e.g. Gardiner et al., 2000). Ancelin et al. (2004) found that diameter was a poor predictor of level of tree damage in their simulations, although tree height was strongly related to vulnerability. In a field study, Peterson (2004) found sufficient consistency in a study of boreal wind disturbance to parameterize predictive treefall models from one part of a stand, and accurately predict the fates of trees in other parts of the stand, given the diameter and species. Consequently, it may be general that simple biomechanical effects of tree diameter explain much of the apparent stochasticity in major wind disturbances.

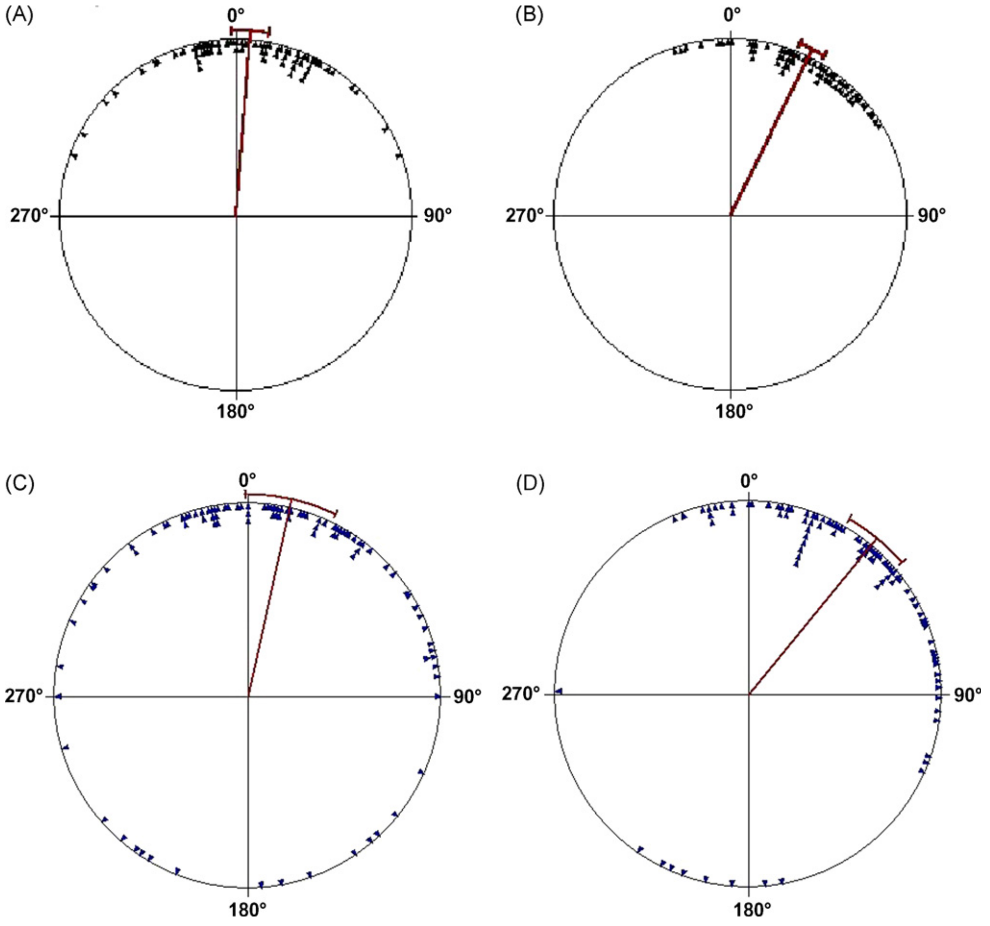

Fig. 4. Direction of fall for trees grouped by diameter in two different tornado-disturbed forest sites. (A) Gould-small; (B) Gould-large; (C) Tionesta '94-small; (D) Tionesta '94-large.

The sites reported here were all natural stands of mixed species, uneven sizes, and uneven spacing, and in several of the nine studies reported here, the disturbance might be considered quite severe. These characteristics of stands and disturbances may explain some of the difference between published unimodal and bimodal size–risk relationships (Everham and Brokaw, 1996), and findings reported here. Lanquaye-Opoku and Mitchell (2005) point out that most of the mechanistic modeling work on tree damage by wind has considered structurally uniform, single-species stands. Moreover, none of the mechanistic work has attempted to characterize detailed wind behavior in tornadoes. Thus is not surprising if the findings here conform only approximately to those from mechanistic studies; despite the differences, for natural, mixed-species stands of eastern North America, a monotonically increasing probability of treefall with tree diameter appears general (Ancelin et al., 2004). While tree diameter was more weakly related to type of treefall, for smaller size classes there was usually an increase in prevalence of uprooting relative to trunk breakage, suggesting an additional general trend (see also Nieuwenhuis and Fitzpatrick, 2002).

Differences among species have been documented in many wind disturbance studies (e.g. Webb, 1988; Foster, 1988; Foster and Boose, 1992). Most authors acknowledge that some of the interspecific differences might be due to size effects, but rarely have researchers been able to statistically separate effects of size and species. The findings reported here confirm several previous suggestions. First, as Canham and Loucks (1984) proposed, as severity of damage increases, interspecific differences diminish, until in the most severe events (e.g. Tionesta '85, TexHill), most trees above some diameter threshold are felled, with little difference among species. This is true even among different diameter classes within a particular study site; in severe wind disturbances, nearly all of the trees in larger diameter classes fall, obscuring any potential interspecific differences (Fig. 2a and d).

Second, consistent with the suggestions of Putz et al. (1983, see also Asner and Goldstein, 1997; Gardiner et al., 2000), wood strength does have some influence on treefall risk, and type of treefall. However, rarely was wood strength a significant effect on its own (Table 4). Significant main effects or interaction terms including species identity may incorporate the effects of some wood properties not captured by the wood strength indices used here, as well as numerous species architectural traits such as rooting depth, crown shape, crown depth on the trunk, and trunk taper (Mergen, 1954). Several mechanistic studies demonstrate that tree architectural traits can greatly influence vulnerability to, and type of, wind damage (Peltola et al., 1999; Gardiner et al., 2000; Achim et al., 2005). Indeed, a number of consistent interspecific patterns were clearly not explained by wood strength, and in some cases were contradictory to the pattern expected on the basis of wood strength. When species combine strong wood with deep rooting, though, as in *Carya* spp. and *A. saccharum*, a consistently windfirm tree is the general result (see also Webb, 1999). Thus the data presented here suggest a moderate role of wood strength in explaining tree damage in wind disturbances.

Third, the findings here provide some support for the widely assumed greater vulnerability of conifers and early-successional species, but it is weak. Most of the differences previously attributed to successional stage or the gymnosperm/angiosperm dichotomy are likely due to age and size of trees (e.g. Foster, 1988), or seasonal differences between conifers and broadleaf trees with and without leaves (Peltola et al., 1999). Heavy damage observed in plantations after windstorms may result more from stand characteristics such as recent thinning and concentration of foliage in the top of the crown, than with conifer identity per se (Ruel, 1995).

Some of the variation observed among species across sites may be the result of changes in the relative vulnerabilities of species to winds of differing intensity. Canham et al. (2001) showed that for a given diameter class of seven species common in northeastern North America, relative vulnerabilities changed with disturbance severity; e.g. two species might reverse their relative risk of treefall when subject to low- versus high-speed winds. The analyses reported here cannot separate the effects of site from those of wind speed in the various tornado blowdowns. However, it is worth noting that the shifts in interspecific rankings in Canham et al.'s (2001) study were rather modest; e.g. they consistently found *B. alleghaniensis* and *A. saccharum* to be among the most windfirm species. This paper's findings reinforce such consistency, and broaden the geographic and taxonomic scope of the trend; with a few exceptions, species rankings in treefall vulnerability are quite consistent among sites and forest types.

Site influences on treefall patterns are undoubtedly confounded with storm characteristics (Table 1). However, it is notable that uprooting was least prevalent at the Gum Road site, where rooting depth is greatest among the nine study sites. Mingo NWR also has potentially deep rooting, but the poorly drained soils there are frequently flooded (personal observation), potentially restricting root system stability. There was no clear relationship between soil composition and tree damage patterns, although those study sites (Tionesta '85, and Tionesta '94) with subsurface hardpans in the soils appeared to experience greater levels of uprooting. The strong influence of wind speed and exposure (Ancelin et al., 2004) can sometimes overwhelm other site traits: the deep, well-drained soils of Cathedral Pines did not moderate the severity of damage or increase the relative importance of trunk breakage when that highly exposed site was struck by a severe tornado.

When considering consequences of disturbance for regeneration opportunities, the potential for prediction is less than for whether or not trees are toppled. Type of treefall showed modest but consistent relationships to tree diameter in the smaller size classes, with an increase in uprooting relative to trunk breakage from the smallest to intermediate diameters. Species sometimes differed significantly in tendency to break or uproot (Table 5), but interspecific patterns were not consistent across sites (Fig. 3). The consequence is that predictability of the abundance of uprooting-related microsites (e.g. Falinski, 1978; Nakashizuka, 1989; Peterson et al., 1990) will likely be low.

When trees do uproot, there are consistent relationships between tree diameter and the size of the root pits and mounds (data not shown), and such relationships vary consistently among species. Thus a weak link in the chain of causality between pre-disturbance stand and tree characteristics, and future forest composition, is understanding the causes of particular types of treefall occur. When the relative abundances of trunk breakage and uprooting are known, estimates of the extent of disturbed soil (Fischer, 1992; Kuuluvainen and Juntunen, 1998; Fischer et al., 2002) provide a link to regeneration opportunities for pioneer species (Hutnik, 1952; Putz, 1983).

Regeneration will also be strongly influenced by the sprouting and survival of fallen trees (Cooper-Ellis et al., 1999). Decreasing sprouting and increasing mortality among fallen trees, as tree diameter increases, is a general trend (Table 3). These showed no clear relationships to tree species, though, other than the general lack of sprouting and quick canopy death in fallen conifers. In some circumstances, surviving fallen trees and new sprouts are major influences on colonization by shade-intolerant pioneer species (Yih et al., 1991; Cooper-Ellis et al., 1999), thus potentially affecting forest composition for decades or centuries after the disturbance. While the influence of tree diameter on sprouting is well established, much more study is needed to determine how and why sprouting varies among species.

No previous study has examined how direction of treefall varies with potentially influencing factors. Apparently, within the heavily impacted areas of tornado blowdowns, the prevalent direction of fall is to the north or northeast. Because tornadoes typically rotate anti-clockwise and move from west to east in the northern hemisphere, this suggests that the leading edge of the vortex may cause the majority of damage to trees. Here it is shown that often (Fig. 4) the larger trees fall further to the east than smaller trees, and while this appears to be a robust trend, it is not clear what interaction between tree biomechanics and wind movement might contribute to this pattern.

6. Conclusions

This synthesis shows that tree diameter and species have robust, consistent influences on risk of treefall in severe windstorms. Interspecific differences change slightly among sites, but the broad tends among species are consistent. These relationships appear to be quite steady across a broad taxonomic and geographic range, suggesting that treefall probability should be somewhat predictable given the occurrence of high winds in a particular stand. Wood strength properties have a consistent but not dominant influence on risk of treefall; species differences are due in part to wood properties and in part to architectural differences. Much further work is needed to determine the influences of diameter and species on type of treefall, and the influence of species on sprouting and survival of fallen trees, if we are to mechanistically link pre-disturbance tree and stand traits to regeneration potential after major windstorms. The finding of differences in direction of treefall for different diameter classes has not been previous reported, and may be a consequence of larger trees falling earlier in the period of extreme winds.

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