Interspecific variation in susceptibility to windthrow as a function of tree size and storm severity for northern temperate tree species[1]

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Abstract: Studies of wind disturbance regimes have been hampered by the lack of methods to quantify variation in both storm severity and the responses of tree species to winds of varying intensity. In this paper, we report the development of a new, empirical method of simultaneously estimating both local storm severity and the parameters of functions that define species-specific variation in susceptibility to windthrow as a function of storm severity and tree size. We test the method using data collected following a storm that struck the western Adirondack Mountains of New York in 1995. For intermediate-sized stems (e.g., 40 cm DBH), black cherry (*Prunus serotina* Ehrh.) and red spruce (*Picea rubens* Sarg.) showed the highest rates of windthrow across virtually all levels of storm severity, while yellow birch (*Betula alleghaniensis* Britt.) and sugar maple (*Acer saccharum* Marsh.) had the lowest rates of windthrow. For much of the range of storm severity, the probability of windthrow for the most susceptible species was at least twice as high as for the least susceptible species. Three of the species, yellow birch, red spruce, and beech (*Fagus grandifolia* Ehrh.), had significantly lower probability of windthrow at a given storm severity in old-growth stands than in second-growth stands. Our results suggest that the distinctive abundance of these three species in old-growth forests of the Adirondacks is due, at least in part, to their ability to survive the intermediate-scale disturbance events that appear to dominate the natural disturbance regime in this region.

Résumé : L'étude des régimes de perturbation par le vent a été limitée par le manque de méthodes permettant de quantifier la variation dans la sévérité des tempêtes et la réaction des espèces arborescentes à des vents de différentes intensités. Dans cet article, les auteurs font état du développement d'une nouvelle méthode empirique permettant d'estimer simultanément la sévérité locale d'une tempête et les paramètres définissant les variations spécifiques de susceptibilité au chablis en fonction de la sévérité de la tempête et de la dimension des arbres. La méthode a été testée à l'aide de données recueillies après une tempête qui a frappé la partie ouest des monts Adirondacks, dans l'État de New York en 1995. Pour les tiges de dimension intermédiaire (i.e. dhp de 40 cm), le cerisier tardif (*Prunus serotina* Ehrh.) et l'épinette rouge (*Picea rubens* Sarg.) présentaient les plus forts taux de chablis pour à peu près tous les niveaux de sévérité de tempête, tandis que le bouleau jaune (*Betula alleghaniensis* Britt.) et l'érable à sucre (*Acer saccharum* Marsh.) avaient les plus faibles taux de chablis. Pour une bonne partie de la gamme de sévérité de tempête, la probabilité de chablis des essences les plus susceptibles était au moins le double de celle des essences les moins susceptibles. Pour une sévérité donnée de tempête, trois des espèces : le bouleau jaune, l'épinette rouge et le hêtre (*Fagus grandifolia* Ehrh.), présentaient des probabilités plus faibles de chablis dans les peuplements vierges que dans les peuplements de seconde venue. Les résultats suggèrent que l'abondance distinctive de ces trois espèces dans les forêts vierges des Adirondacks est due, au moins en partie, à leur capacité de survivre aux perturbations de taille intermédiaire qui semblent dominer le régime naturel de perturbation dans cette région.

[Traduit par la Rédaction]

Introduction

Windthrow represents the predominant large-scale, natural disturbance in the northern temperate forests of northeastern and north-central North America. The sources of extreme winds include thunderstorm downbursts (Canham and Loucks 1984), hurricanes (e.g., Foster and Boose 1992), extratropical cyclones (severe low pressure systems) (Stoeckeler and Arbogast 1955), and, less frequently, tornadoes (Canham and Loucks 1984; Peterson and Pickett 1991). Studies of the responses of temperate forests to windthrow have generally focused on catastrophic disturbance associated with the most severe winds (e.g., Dunn et al. 1983; Glitzenstein and Harcombe 1988; Foster 1988; Peterson and Pickett 1991, Cooper-Ellis et al. 1999). Estimates of the return interval for catastrophic wind disturbance in northern hardwood forests range from over 500 years in the upper peninsula of Michigan (Zhang et al. 1999), to over 1000 years in Maine (Lorimer 1977) and northern Wisconsin (Canham and Loucks 1984), and to over 3000 years in parts of western New York state (Seischab and Orwig 1991).

It has become clear that these catastrophic disturbances

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represent simply the extreme in a continuous gradient in wind-disturbance intensity. While the return intervals for catastrophic disturbance of northern temperate forests may be measured in centuries to millenia, historical records from the past century suggest that storms with winds sufficient to topple a significant fraction of the canopy trees in a stand occur at frequencies measured in decades to scores of years (Lorimer and Frelich 1989; Foster and Boose 1992; Webb 1999). It has proven to be very difficult to quantify the frequency of disturbance along this gradient of storm severity. Tree-ring studies provide one of the most promising approaches (i.e., Lorimer et al. 1988; Lorimer and Frelich 1989; Frelich and Graumlich 1994), although there are a number of difficulties in the analysis and interpretation of disturbance regimes from tree-ring data (e.g., Clark 1991).

Reconstructing past frequencies of intermediate-scale wind disturbance may be of largely historical interest, given the likelihood of changes in the frequency and severity of storms under future climate change (Emanuel 1987). Frelich and Lorimer (1991) and He and Mladenoff (1999) present a promising alternative, the development of simulation models that allow us to explore the logical consequences of changes in disturbance frequency and severity for ecosystem structure and function in forested landscapes. There is a rich empirical literature on species-specific variation in colonization and regeneration following wind disturbance that can be used in the parameterization of such models. There is an equally large literature characterizing the nature of damage to canopy trees following individual storm events, recently reviewed for catastrophic wind disturbance by Everham (1995) and Everham and Brokaw (1996). Everham (1995) outlines a number of methodological limitations to the synthesis of that literature. We feel that the more critical limitation is conceptual. While those studies frequently document the extensive spatial variation in storm intensity within specific storm events, there have been few attempts to take advantage of that variation to develop functional relationships between storm severity and susceptibility of trees to windthrow. Boose et al. (1994) have made considerable progress in the development of predictive models of spatial variation in disturbance intensity from individual hurricanes. However, it is not clear that that approach would be sufficiently accurate to replace empirical estimates of storm severity.

In this paper we report the development of a new, empirical method of simultaneously estimating both local storm severity and the parameters of functions that quantify species-specific variation in susceptibility to windthrow as a function of storm severity and tree size. The method requires field data on the frequency of windthrow as a function of species and size in a series of plots that span a range of levels of disturbance. We test the method using data collected following a severe storm that struck the western Adirondack Mountains of New York state in 1995. That region contains one of the largest remaining contiguous tracts of old-growth forest in the northeastern United States, and our analyses allowed us to also examine differences in susceptibility to windthrow in old-growth versus second-growth forests. While studies of the responses of temperate forest to wind disturbance have traditionally focused on interspecific variation in regeneration following catastrophic disturbance, our analyses allow us to explore the degree to which interspecific variation in

canopy tree survival across a wide range of disturbance intensities may shape the structure and composition of forested landscapes.

Materials and methods

Study area and field methods

A rapidly moving line of thunderstorm cells crossed northern New York state on the morning of July 15, 1995. The storm had sustained winds of greater than 120 km/h and gusts estimated at greater than 160 km/h while over the western portion of the Adirondack Park (Jenkins 1995). The state Department of Environmental Conservation estimated that approximately 15 000 ha of forest suffered severe damage (≥60% of trees blown down) and that an additional 44 000 ha of forest suffered moderate damage (30–60% of trees blown down) (Jenkins 1995). The worst damage was concentrated in the Five Ponds Wilderness Area, southwest of Cranberry Lake.

We censused windthrow in forty-three 0.125-ha circular plots (19.95 m radius) between June 6 and July 15, 1996. Windthrow was assessed on all trees ≥10 cm DBH rooted within the plot. Saplings (stems >2 cm DBH and <10 cm DBH) were censused in a 5 m radius subplot at the center of the plot. Individuals were considered windthrown by the storm if they had been either uprooted so that the stem was less than 45° from the ground or if the trunk had been broken below the crown. Some of the uprooted trees continue to live and may, in effect, reproduce vegetatively by sending up vertical branches. In addition, some of the broken trunks may produce epicormic branches and gradually form a new canopy, although this is less common in northern temperate tree species (personal observations; Cooper-Ellis et al. 1999) than in tropical trees damaged by hurricanes (e.g., Everham 1995). In effect, our interest was in the effective removal of the tree from the canopy, rather than in physiological death.

The plots were distributed in an approximately 15 × 6 km area running perpendicular to the storm path, extending from the Dead Creek Flow at the south end of Cranberry Lake to Wolf Pond in the Five Ponds Wilderness Area (44°00′–44°05′N, 74°55′–75°00′W). The Five Ponds Wilderness contains one of the largest remaining tracts of old-growth forest in the northeastern United States (~20 000 contiguous ha), and our plots were roughly evenly divided between old-growth stands (20 plots) and second-growth stands (23 plots). The plots were distributed across a wide range of topography, ranging from the broad alluvial valley of the Oswegatchie River to the higher and more rugged landscapes of Panther, Partlow, and Cat Mountains.

The plots were selected to represent a broad range of overall levels of windthrow and were positioned so that the overall degree of windthrow was relatively uniform within the plot. Storm damage appeared to vary as a result of (*i*) proximity to the most intense center of the storm path, (*ii*) topography, particularly exposure to winds coming out of the northwest, and (*iii*) fine-scale patchiness in storm intensity at scales as small as 50–100 m. In some areas there was a distinct striation in storm intensity, i.e., swaths of intense windthrow running parallel to the storm track, alternating with swaths of much less windthrow. In contrast to severe winds from hurricanes, damaging winds from thunderstorm downbursts are often very brief, allowing turbulence to potentially play a greater role in determining the patterns of damaging wind at the ground level.

The 43 plots contained 2599 trees ≥10 cm DBH (windthrown and not windthrown combined). Seven species (*Acer rubrum* L. (red maple), *Acer saccharum* Marsh. (sugar maple), *Betula alleghaniensis* Britt. (yellow birch), *Fagus grandifolia* Ehrh. (beech), *Picea rubens* Sarg. (red spruce), *Prunus serotina* Ehrh. (black cherry), and *Tsuga canadensis* (L.) Carr. (eastern hemlock)) were

Table 1. Relative densities (RELDEN, %) and basal areas (RELBA, %) of canopy trees (stems ≥10 cm DBH) for old-growth and second-growth stands and for all plots combined.

Species	Old growth		Second growth		All plots	
	RELBA	RELDEN	RELBA	RELDEN	RELBA	RELDEN
Acer rubrum	0.9	1.2	21.3	22.6	11.8	11.6
Acer saccharum	12.7	9.0	23.0	24.1	20.4	16.1
Betula alleghaniensis	4.1	4.6	14.9	18.2	14.7	11.1
Fagus grandifolia	44.2	62.2	6.9	12.4	18.3	36.2
Picea rubens	26.4	18.7	10.0	10.9	16.4	14.4
Prunus serotina	2.1	0.5	23.4	11.6	12.4	5.9
Tsuga canadensis	8.2	2.5	0.4	0.2	3.0	1.3
Other species	1.3	1.4	5.5	5.5	2.9	3.4
Total/ha	30.3	503.6	28.8	466.8	29.5	483.9

present in both sufficient densities and numbers of plots for the analyses described below (Table 1). These seven species comprised 97% (2512) of the stems present in the plots (Table 1). Remaining species included *Abies balsamea* (L.) Mill. (41 stems), *Acer pensylvanicum* L. (23), and *Populus grandidentata* Michx. (16). The old-growth stands were dominated by shade-tolerant species, particularly beech and red spruce, with sugar maple and hemlock as subordinate species. The second-growth stands had a more even distribution of abundance, with sugar maple sharing dominance with red maple, black cherry, yellow birch, and red spruce (Table 1). There were no differences in the plot-level average basal area ($F = 0.694$, df = 1, 41, $p = 0.41$) or density ($F = 1.163$, df = 1, 41, $p = 0.287$) for the old-growth versus second-growth stands (Table 1). Mean stem diameter was actually significantly smaller in the old growth stands than in the second growth stands (mean DBH 24.0 vs. 25.4 cm, $F = 18.16$, df = 1, 2490, $p < 0.0001$, analysis of variance on log-transformed DBH), because the size distribution in the old-growth stands was dominated by very large numbers of small stems (10–20 cm DBH) and a small number of very large individuals, while the second-growth stands had a better representation by midsized stems (Fig. 1).

A maximum-likelihood model of interspecific variation in susceptibility to windthrow

Our general approach takes advantage of the fact that most severe wind storms contain considerable spatial variation in intensity. In its simplest form, our new method is an extension of traditional logistic regression, in which the probability of windthrow is a logistic function of (*i*) species, (*ii*) individual tree size, and (*iii*) local storm severity (as assessed using an index on some quantitative scale). In cases where an independent measure of local storm severity is available, standard logistic regression would suffice. In that case, the appropriate field methods would be to simply census the status of all trees in a series of plots that varied in storm severity, and then use a series of species-specific, logistic regressions to predict windthrow of individual trees as a function of plot-level storm severity and individual tree size, since there is ample empirical evidence that susceptibility to windthrow varies significantly as a function of tree size (Peterson and Pickett 1991; Leininger et al. 1997; Peterson and Rebertus 1997).

Unfortunately, accurate, plot-level measurements of wind speeds during severe storms are rarely available. Doppler radar systems can provide estimates of wind speeds aloft but are not useful in estimating spatial variation in surface wind speeds, particularly in complex topography. One alternative approach would be to simply use the plot-level degree of damage as an index of storm intensity, on a scale ranging from zero when the storm is below the intensity required to produce any measured degree of damage on any trees, to one when all canopy trees, regardless of species or size, would

Fig. 1. Tree diameter distributions (in 5-cm DBH size classes) for old-growth and second-growth stands in the Five Ponds Wilderness Area of New York. Data were aggregated across 20 old-growth stands and 23 second-growth stands.
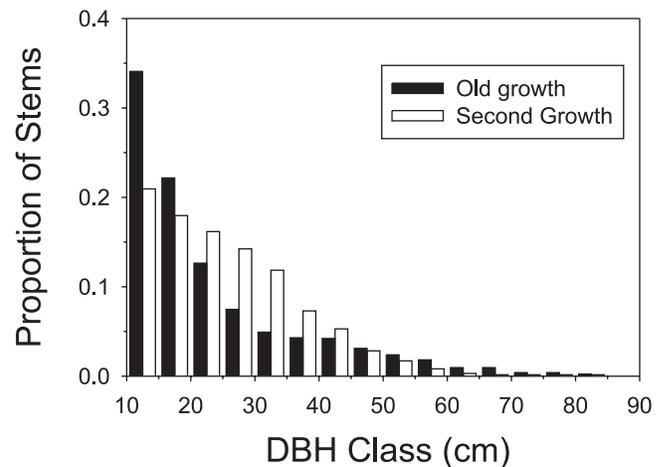
suffer catastrophic damage. When the plots contain a very well-mixed sample of species and tree sizes, this method is quite reasonable. In the field, however, individual plots may appear to have been subjected to particularly severe winds, simply because they are dominated by sizes and (or) species of trees that are particularly susceptible to windthrow even at relatively low storm intensities.

The new method we have developed eliminates this problem by simultaneously estimating both local storm severity and species susceptibility to windthrow. The field methods are the same as those described above, namely, censuses of the target species in a series of plots that vary widely in overall degree of damage. The plots need to contain a mix of species and sizes and be small enough to satisfy the assumption that local storm severity was roughly uniform within the plot. In practical terms, the plots need to be large enough to contain approximately 50 individuals to generate sufficient sample sizes. The method then uses maximum-likelihood estimation to fit a logistic model of the form:

$$[1] \quad \log\left(\frac{p_{isj}}{1 - p_{isj}}\right) = a_s + c_s S_i \mathrm{DBH}_{isj}^{b_s}$$

where p_{isj} is the probability of windthrow for the *j*th individual of species *s* in plot *i*; S_i is the estimated storm severity for plot *i* (on an arbitrary scale of 0–1); DBH_{isj} is diameter at breast height (cm

at 1.35 m height) of the *j*th individual of species *s* in plot *i*; and a_s, b_s, and c_s are estimated, species-specific parameters. The storm severity index (S_i) is allowed to vary from 0 to 1, with 1 representing the most severe level of windthrow observed in any of the plots in the data set.

The left-hand side of eq. 1 is a logit (i.e., the log of the odds ratio of event *p*). The right-hand side of the equation allows the models to fit a flexible, monotonic function to the data, with the general properties that damage varies as a product of both storm severity and tree size. Most commercially available software for logistic regression allows only linear combinations of the explanatory variables. However, the joint effects of storm severity and tree size on wind mortality are clearly multiplicative rather than additive.

Our approach follows directly from the principles of likelihood estimation (e.g., Hilborn and Mangel 1997). In that sense, our method determines both the plot-specific storm severities and the species-specific parameters that determine susceptibility to damage as a function of storm severity and size, that maximize the likelihood of observing the overall data set given the model described by eq. 1 (i.e., the pattern of damage observed across all individuals of all species and sizes in the entire set of plots). The method can be thought of as a form of bootstrapping, in which plot-specific parameters (the storm severity indices) and the species-specific parameters (susceptibility) are sequentially refined until the most likely parameter values are found.

Equation 1 provides the likelihood functions for our data set. p_{isj} is the likelihood of observing that a tree of a given species and size was windthrown by the storm, given a particular set of parameter values (a_s, b_s, c_s, and S_i), while $1 - p_{isj}$ is the likelihood of observing that the tree survived. Thus the log likelihood of observing the entire data set, given a set of parameter values is simply:

[2] log likelihood

$$= \sum_{isj} \begin{cases} \log(p_{isj}), & \text{if tree}_{isj} \text{ was windthrown} \\ \log(1 - p_{isj}), & \text{if tree}_{isj} \text{ was not windthrown} \end{cases}$$

We used simulated annealing (a global optimization procedure) to determine the most likely parameters (i.e., the parameters that maximize the log likelihood), given our observed data set (Goffe et al. 1994). The number of parameters in the model is $n + 3s$, where *n* is the number of sites (43 in our data set), and *s* is the number of species (7), yielding a total of 64 parameters to be determined simultaneously by the annealing procedure. The annealing algorithm is an iterative procedure that starts at a user-specified set of initial parameter estimates. The algorithm systematically varies parameters one at a time, within a specified potential range of possible parameter values, and computes the likelihood of the resulting model. If the likelihood has increased, the new parameter value is accepted and is used in the next iteration. The algorithm uses the Metropolis criterion to "escape" local optima in search of the global optimum solution by accepting "downhill moves" (i.e., new parameter values that generate a lower likelihood), with a probability of accepting the move that is proportional to both the size of the drop in likelihood and the "temperature" of the search process (hence the analogy with annealing of metal through a gradual cooling process). The algorithm converges on the optimal solution through a combination of both slowly lowering the temperature of the process and gradually narrowing the range of values from which the next iteration can be selected. Given the large number of parameters in our model, we used a very gradual annealing schedule to ensure that the algorithm found the globally optimal set of parameter values. We ran the algorithm for 3 million iterations, and considered it to have converged because the last million iterations did not produce a significant increase in likelihood. The procedure took approximately 4 h on a 366 MHz PC. We also subdivided our

data set into old-growth versus second-growth plots and ran the two subsets separately. Because of smaller sample sizes in the subsets, we were unable to fit functions for hemlock in second-growth stands and were only able to fit functions for four species in old-growth stands (sugar maple, yellow birch, beech, and red spruce).

In general, parsimony suggests the strategy of determining the likelihood of the model specified by eq. 1 and then systematically reducing the numbers of distinct parameters in the model to the simplest model that is not a significantly worse fit than any more complicated model, for instance, by lumping species that have very similar behavior or dropping terms like DBH if they don't appear to improve the likelihood of the model. In practice, one of the motivations for this study was to provide parameter values to be used to model the long-term effects of wind disturbance on forest dynamics (using SORTIE; Pacala et al. 1996). Thus, one of our goals was to determine the most likely parameter values for each species, given our data. In addition, we would argue that there are a priori reasons to believe that the true parameter values for each species are different, even if we don't have enough data to tell them apart statistically.

We calculated asymptotic 95% support limits (analogous to traditional confidence intervals) for each of the parameters by holding all other parameters at their maximum-likelihood value and then systematically increasing or decreasing the parameter of interest until the likelihood of the resulting model was significantly worse (at a 5% alpha level) than the maximum-likelihood model, using twice the difference in the log likelihoods of the two models as a χ^2 statistic with 1 degree of freedom (i.e., a likelihood ratio test; Hilborn and Mangel 1997).

There are a number of different approaches of assessing the goodness of fit of a logistic regression model (Demaris 1992). We used the following approach: (*i*) for each tree in the data set, we calculated the predicted probability of windthrow given the maximum-likelihood parameter values, and (*ii*) using the entire data set, we then grouped the predicted probabilities of windthrow into classes (0–10%, 10–20%, etc.) and then computed the percentage of trees in that class that had been windthrown by the storm. Thus, for individuals predicted to have 0–10% probability of windthrow, a model that fits well will have approximately 5% of the individuals actually windthrown. This method basically gives us a method of comparing "observed" with "expected," given the model. The benefit of this approach is that it is easy to see if the model fits equally well across the entire range of predicted probabilities or whether it falls apart within some particular range.
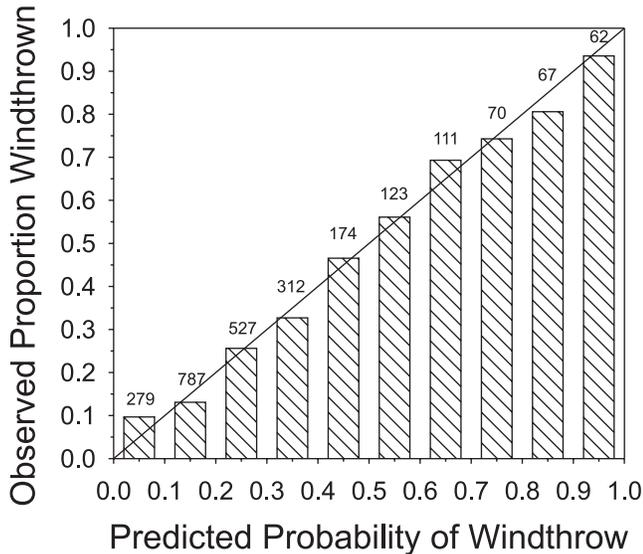
Results

Interspecific variation in susceptibility to windthrow

Our method of likelihood estimation produced an excellent fit of eq. 1 to the overall data set (Fig. 2). There was a wide range of variation in predicted probabilities of windthrow of the seven species along the gradient in storm severity (Fig. 3). For intermediate-sized stems (40 cm DBH), black cherry and red spruce showed the highest rates of windthrow across virtually all levels of storm severity, while yellow birch and sugar maple had the lowest rates of windthrow (Fig. 3). For much of the range of storm severity, the probability of windthrow for the most susceptible species was at least as twice as high as for the least susceptible species. A model that ignored the species-specific differences yielded a significantly worse fit to the data (likelihood ratio = 138.84, df = 1, *p* < 0.0001).

For small (10 cm DBH) stems, probability of windthrow in sites with the most severe winds was positively correlated with shade intolerance (Fig. 3); the three most shade-tolerant

Fig. 2. Goodness of fit of the maximum-likelihood analysis of probability of windthrow as a function of storm severity, species, and size for the data set combining both old-growth and second-growth stands. Bars represent the observed proportion of trees windthrown, as a function of predicted probability of windthrow. The numbers above each bar indicate the number of observations in that class. The diagonal line indicates a 1:1 correspondence between observed and expected.

Fig. 3. Predicted probabilities of windthrow, using eq. 1 and parameters reported in Table 2, as a function of storm severity, for three different tree sizes. ACRU, *Acer rubrum*; ACSA, *A. saccharum*; BEAL, *Betula alleghaniensis*; FAGR, *Fagus grandifolia*; PIRU, *Picea rubra*; PRSE, *Prunus serotina*; TSCA, *Tsuga canadensis*.


species (beech, hemlock, and sugar maple) all had similarly low rates of windthrow, while the three least tolerant species (red maple, black cherry, and yellow birch) had dramatically higher rates of windthrow (Fig. 3). This result is consistent with previous studies showing correlations between shade tolerance and wood density and strength (Loehle 1988). Rates of windthrow of intermediate and larger stems, however, did not show as strong a correlation with shade tolerance (Fig. 3). High rates of windthrow of large beech trees may be a function of weakening by beech bark disease, which is most severe on larger stems (Houston 1975; Gavin and Peart 1993). For very large stems (70 cm DBH), two of the three most resistant species were red maple and yellow birch. These two species have relatively low wood density relative to the other broad-leaved tree species. Our field observations suggest that both red maple and particularly yellow birch survive intense windstorms by sloughing large canopy branches, which presumably reduces wind load. Thus, while both species frequently suffer extensive canopy damage in intense storms, significant numbers of individuals survive with some portion of the canopy intact and are thus able to serve as a seed source for colonization of the site following disturbance.

Effects of tree size on susceptibility to windthrow

In general, all of the seven species showed an increase in probability of windthrow with increasing tree size (DBH) (Fig. 4). The increase was most dramatic in beech and least pronounced in yellow birch (Fig. 4). These differences are also apparent in the fitted model (Fig. 3). Very few stems <15 cm DBH of any species were windthrown, and censuses of sapling damage in the same plots revealed essentially no
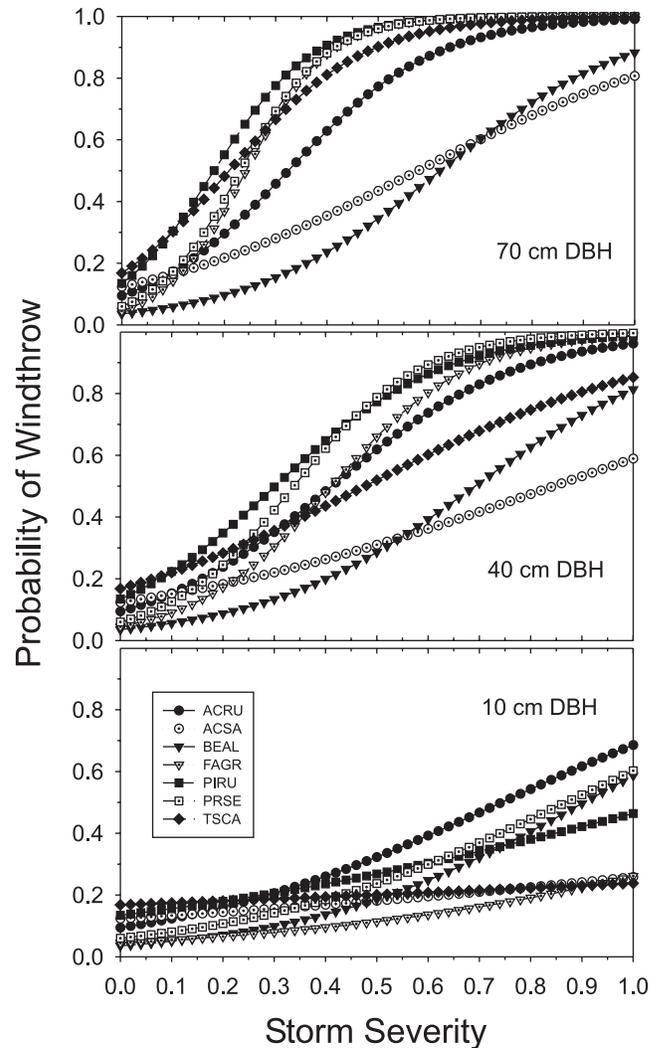
outright windthrow of individuals <10 cm DBH, with damage usually restricted to pinning of the crowns of saplings to the ground by falling debris (Papaik 1998). Interspecific variation in effects of tree size was reflected in the estimated exponents (b) on the DBH term in eq. 1, which ranged from a low of 0.19 for yellow birch (95% support limit 0.15–0.22) to a high of 1.47 (95% limit 1.31–1.58) in hemlock (Table 2). With the exception of hemlock, the increase in probability of windthrow with DBH was less than linear for all of the species (i.e., upper confidence intervals of b_s were <1 for all species except hemlock) (Table 2).

Spatial variation in storm severity

Our method of fitting eq. 1 effectively stretches out the observed plot-level variation in rates of windthrow across the allowed range of S (0–1 in our case). Our analysis suggests that plot-level measures of the percentage of canopy

Fig. 4. Observed percent of trees windthrown in old-growth and second-growth stands, combined, as a function of DBH class, for the six main species. See Fig. 3 for acronyms used in the legend.
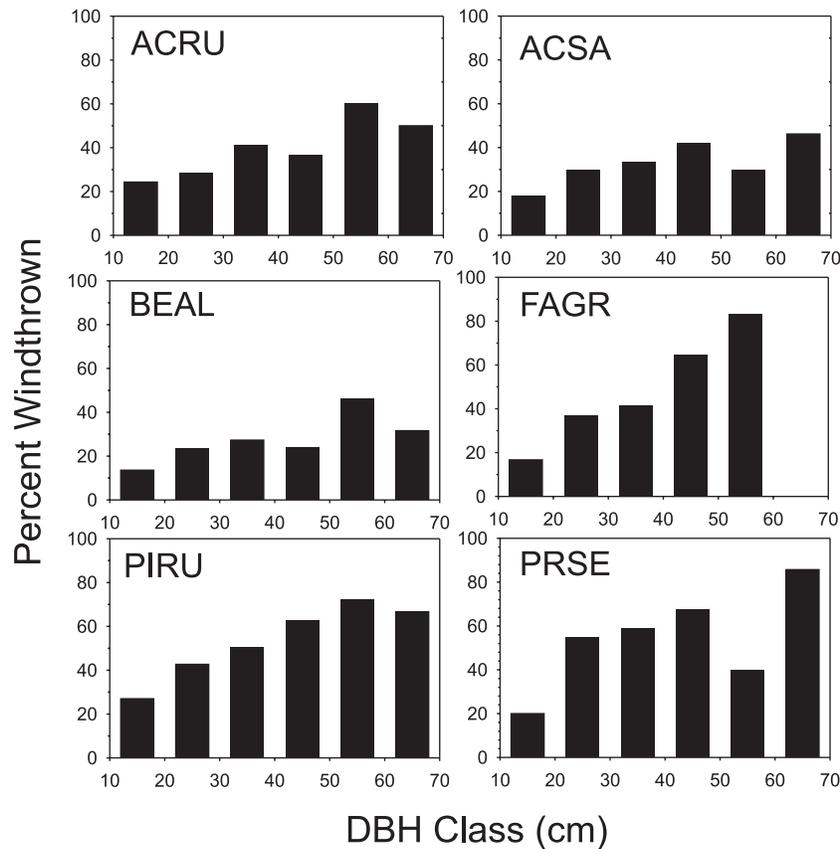

Table 2. Maximum-likelihood estimates of the species-specific coefficients in eq. 1, with 95% asymptotic support limits given in parentheses.
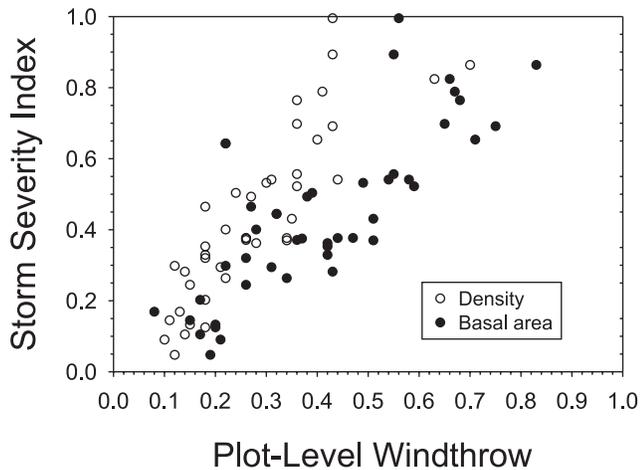
	a_s	b_s	c_s
Acer rubrum	−2.261	0.426	1.140
	(−1.990 to −2.532)	(0.377–0.475)	(0.969–1.333)
Acer saccharum	−1.960	0.679	0.190
	(−1.734 to −2.185)	(0.621–0.729)	(0.155–0.227)
Betula alleghaniensis	−3.302	0.193	2.341
	(−3.005 to −3.649)	(0.152–0.226)	(2.025–2.621)
Fagus grandifolia	−3.057	0.941	0.231
	(−2.905 to −3.256)	(0.908–0.965)	(0.210–0.247)
Picea rubens	−1.863	0.923	0.205
	(−1.639 to −2.105)	(0.877–0.960)	(0.177–0.231)
Prunus serotina	−2.752	0.680	0.663
	(−2.339 to −3.178)	(0.639–0.717)	(0.576–0.752)
Tsuga canadensis	−1.599	1.470	0.015
	(−0.824 to −2.327)	(1.316–1.580)	(0.008–0.022)

tree density or basal area windthrown are not necessarily very precise estimates of local storm severity in a region with variation in canopy composition and structure because of variation in susceptibility of different species and tree sizes to windthrow (Fig. 5). Our plots were selected to include sites with the full range of damage that occurred in the 1995 storm. While we consider the disturbance "catastrophic" in the plots with the most extreme levels of visual damage, there were only two plots in which >50% of all stems >10 cm DBH were windthrown. These were not the

stands with the highest estimated storm severity, however. Each of the two stands was dominated by a species with high predicted susceptibility to storm damage (red maple and black cherry, respectively). In contrast, the two plots in which predicted storm severity was much greater than overall plot windthrow were both dominated by sugar maple, a species with very low predicted susceptibility to windthrow (Fig. 3).

It should be noted that, when expressed as a fraction of plot basal area, levels of windthrow were much greater than

Fig. 5. Relationships between observed plot-level windthrow, expressed in terms of proportion of density (open circles) or basal area (solid circles) for the 43 stands, and the predicted storm severity index.

Fig. 6. Predicted probabilities of windthrow, using eq. 1 and parameters reported in Table 3, as a function of storm severity, for 40 cm DBH individuals of four species in old growth (OG; solid symbols) versus second growth (SG; open symbols) stands. ACSA, *Acer saccharum*; BEAL, *Betula alleghaniensis*; FAGR, *Fagus grandifolia*; PIRU, *Picea rubra*.

when calculated as a fraction of density (Fig. 5). Many of the stands that lost only 40–50% of stems greater than 10 cm DBH lost >60% of their basal area, and the surviving stems were generally small, subcanopy individuals. Thus, by most visual estimates these sites would have been considered to have suffered catastrophic damage in which essentially all canopy trees were lost.

Windthrow in old-growth versus second-growth forests

Overall, rates of windthrow were significantly higher in the 20 old-growth plots than in the 23 second-growth plots (χ^2 = 15.27, df = 1, p < 0.0001 for a log–linear model with successional stage and species as main effects). We did not attempt to randomly sample either old-growth or second-growth regions of our study site, so these differences could have been simply due to selection of old-growth stands in sites with higher storm severity. In fact, the mean estimated storm severity for the 20 old-growth plots (i.e., mean S_i) was slightly but not significantly higher in the old-growth stands (0.48 vs. 0.40 in old growth vs. second growth, respectively; pooled variance t statistic = 1.126, df = 41, p = 0.267).

We had sufficient sample sizes to estimate separate old-growth versus second-growth susceptibility functions for four of the seven species (yellow birch, red spruce, sugar maple, and beech) (Fig. 6). All of these species except sugar maple actually showed much lower susceptibility to windthrow at a given storm severity in old-growth stands, while susceptibility of sugar maple to windthrow did not vary with successional stage (Table 3). The most likely explanation for the slightly higher rates of overall windthrow in the old-growth stands is simply the much higher abundance of beech and red spruce, two species with relatively high susceptibility to windthrow (at least for moderate to large stems) (Fig. 3).

Discussion

Spatial variation in windstorm severity

The estimated storm severity indices (Fig. 5) illustrate the broad range of variation in disturbance intensity associated with the 1995 windstorm in the Adirondacks. We suggest
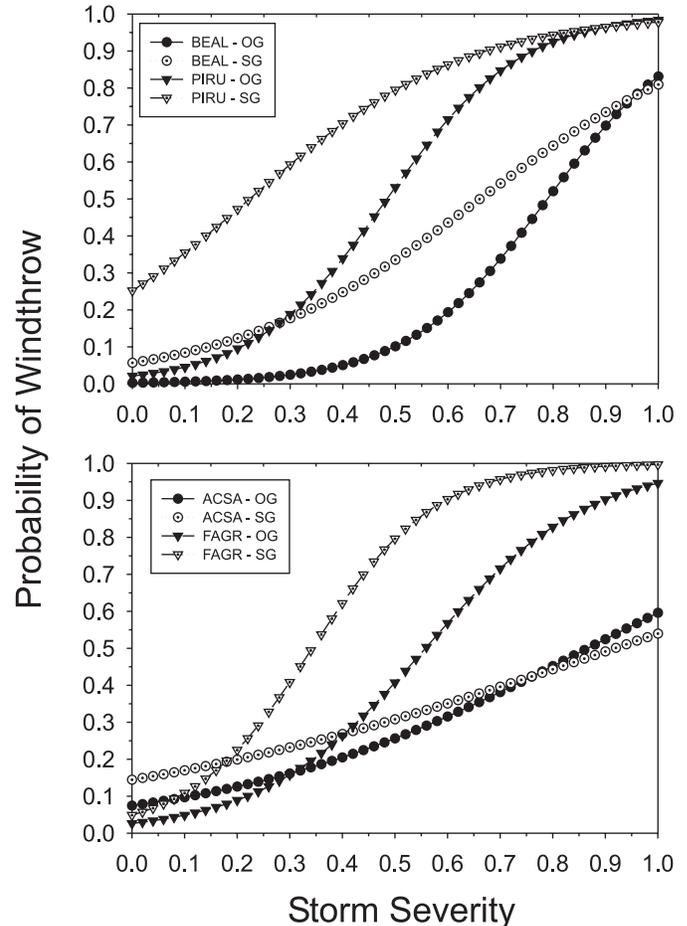
that this variation in disturbance severity is both a common and ecologically critical feature of wind disturbance in forests. The degree of spatial variation in wind intensity within individual windstorms is likely to vary as a function of storm type. Severe tornadoes (e.g., classes F3–F5 on the Fujita scale, winds >70 m/s) are likely to have the most uniform and complete windthrow of canopy trees, with relatively discrete boundaries between catastrophic disturbance and adjacent, minimal damage. However, the majority of tornadoes (classes F0–F1, almost 75% of reported tornadoes) are characterized by much more moderate winds (<50 m/s), and are likely to show a broad range of variation in proportion of trees windthrown within the tornado track. The tracks of individual thunderstorm downbursts are typically much shorter and wider than tornado tracks (Canham and Loucks 1984), but they share many similarities with tornadoes in the nature of spatial variation in wind intensity: the most extreme downbursts can have relatively discrete and catastrophic intensity (C.D.C., personal observations); however, the majority of downbursts are less intense and are characterized by considerable spatial variation in storm in-

Table 3. Maximum-likelihood estimates of the species-specific coefficients in eq. 1 for four species in old-growth versus second-growth stands with 95% asymptotic support limits given in parentheses.

Species	Second growth			Old growth		
	a_s	b_s	c_s	a_s	b_s	c_s
Acer rubrum	−1.936	0.569	0.776			
	(−1.646 to −2.217)	(0.506–0.626)	(0.629–0.940)			
Acer saccharum	−1.780	0.594	0.217	−2.521	0.618	0.297
	(−1.522 to 12.064)	(0.478–0.674)	(0.145–0.285)	(−2.092 to −2.924)	(0.563–0.671)	(0.241–0.358)
Betula alleghaniensis	−2.813	0.102	2.926	−5.959	0.126	4.746
	(−2.447 to −3.193)	(0.042–0.155)	(2.399–3.482)	(−5.363 to −6.674)	(0.090–0.154)	(4.129–5.007)
Fagus grandifolia	−2.973	0.955	0.256	−3.623	0.751	0.407
	(−2.527 to −3.464)	(0.874–1.022)	(0.200–0.310)	(−3.423 to −3.804)	(0.728–0.773)	(0.380–0.435)
Picea rubens	−1.088	1.210	0.056	−3.841	0.571	0.964
	(−0.745 to −1.475)	(1.010–1.337)	(0.028–0.087)	(−3.534 to −4.149)	(0.546–0.594)	(0.887–1.041)
Prunus serotina	−2.236	0.720	0.605			
	(−1.834 to −2672)	(0.673–0.763)	(0.511–0.708)			

tensity and degree of windthrow (Fujita 1985). Thunderstorm downbursts frequently occur in clusters associated with multiple thunderstorm cells, either organized into distinct squall lines or embedded in more complex, cyclonic storm events (Fujita 1985). A severe storm in northern Wisconsin in 1977 involved over two dozen distinct downbursts distributed along a long (~265 km), narrow (~27 km) storm path (Canham and Loucks 1984). In contrast, the 1995 "derecho" (straight line) storm in the Adirondacks had a much more complex pattern of damage that appeared to be associated with downbursts, straight-line frontal winds, and one long, sinuous path of severe windthrow that had the dimensions typical of a tornado, even though no funnel cloud was reported. In both storms, the total area of "catastrophic" windthrow was only a small fraction of the total area disturbed by the storm (personal observations; Canham and Loucks 1984; Jenkins 1995).

Both tornadoes and thunderstorms are usually embedded in much larger, severe cyclonic storms, whether the storms are of tropical origin (e.g., hurricanes and typhoons) or temperate origin (e.g., gales or extratropical cyclones). Foster and Boose (1992) documented a wide range of variability in wind damage associated with the 1938 hurricane in southern New England. They also highlighted the small size of distinct, contiguous patches containing relatively uniform damage. A subsequent model (Boose et al. 1994) indicates that variation in the intensity of disturbance at landscape to regional scales can be attributed to both the meteorological properties of individual hurricanes and the interaction between wind direction and topographic exposure.

Glitzenstein and Harcombe (1988) compared disturbance patterns from tornadoes, hurricanes and downbursts, and concluded that "catastrophic" windstorms are not nearly as catastrophic, in terms of proportional loss of living biomass, as fires. The patterns of damage from the 1995 storm in the Adirondacks reinforce this conclusion. Even in stands in which virtually all dominant canopy trees had been toppled, a significant fraction of smaller, subcanopy trees and most saplings survived (Fig. 5; Papaik 1998).

Variation among trees in susceptibility to windthrow

Our results provide the first quantitative estimates of interspecific variation in susceptibility of northern temperate tree species to windthrow as a function of variation in storm severity. For storms of intermediate severity, there was greater than twofold variation in susceptibility to windthrow among the seven tree species. Life-history theory suggests that late-successional tree species should invest more heavily in traits that contribute to a long life-span, including resistance to windthrow (Loehle 1988). Our results provide partial support for this prediction, at least among smaller size classes, where resistance to windthrow was positively correlated with shade tolerance (Fig. 3). We attribute the very low resistance to windthrow by large stems of beech, one of the most shade tolerant species in the region (Kobe et al. 1995), to the effects of beech bark disease. Among the six remaining species, however, there was little obvious relationship between shade tolerance and resistance to windthrow for canopy-sized stems (Fig. 3, 40 and 70 cm DBH). Brokaw and Walker (1991) came to the same conclusion in their review of interspecific variation in susceptibility of tropical tree species to damage from hurricanes.

Many studies have documented increases in susceptibility to windthrow with increasing stem diameter and tree height (e.g., Peterson and Pickett 1991; Foster and Boose 1992; Leininger et al. 1997; Peterson and Rebertus 1997; Marks et al. 1999). Our results indicate that the relationship between tree size and susceptibility to windthrow varied widely among species, ranging from an almost negligible effect in yellow birch to a greater than linear increase with DBH in hemlock (i.e., exponents (b coefficients) ranging from 0.19 to 1.47; Table 2).

Blackburn et al. (1988) concluded that static load (based on crown size) was not a good predictor of the force needed to blow over trees, because trees are often windthrown by winds with much less force than predicted from static load calculations. They argue that swaying is particularly important, and that this may explain why slender trees with high height/diameter ratios seem to be at much higher risk of windthrow. Some studies have concluded that dense, uniformly sized stands may be less susceptible to wind damage because the crown dissipates wind force more effectively, and interlocking root systems reduce individual tree vulnerability (e.g., Smith et al. 1987). Munishi and Chamshama (1994), however, argue that crowding increases risk of windthrow, because it leads to increased height/diameter ratios,

and that conversely, suppressed subcanopy trees are less susceptible. These arguments may help explain our striking results that three of four species showed much lower susceptibility to windthrow, across a broad range of storm severity, in old-growth stands than in second-growth stands, even when individual tree DBH is factored into account (Fig. 6, Table 3). Canopy trees in the old-growth stands are much more likely to have undergone periods of suppression (with the concomitant production of denser wood) during canopy recruitment (Canham 1985, 1990), and the longer time spent in the subcanopy may lead to lower height/diameter ratios for stems of a given DBH in old growth stands.

Implications for population and community response to wind disturbance regimes

Previous studies of species response to wind disturbance have generally focused on adaptations that either maintain a seedling and (or) sapling bank or allow rapid colonization following disturbance (Canham and Marks 1985). Our results suggest that the distinctive abundance of yellow birch in old-growth forests of the northeastern United States (Woods and Cogbill 1994) is due, at least in part, to its ability to survive the intermediate-scale disturbance events that appear to dominate the disturbance regime in this region. While the trees frequently lose some portion of their canopy during storms (personal observations), the surviving branches provide a ready seed source, and the dispersal of those seeds should be particularly effective given the thinning of the canopy (LePage et al. 2000).

The most severe storms reduce the role of interspecific variation in susceptibility to windthrow, and shift control of community response to traits that determine colonization ability and the presence of seedling and sapling banks. In effect, the very infrequent but extreme events "reset" the system, allowing the development of a forest with species that vary widely in susceptibility. Between those events, periodic storms of intermediate severity allow interspecific differences in susceptibility to play a strong role in succession, with forests becoming progressively wind-firm and less susceptible to wind disturbance in general, until the next truly catastrophic disturbance occurs. Simulations with a spatially explicit model (SORTIE) suggest that disturbance regimes characterized by relatively frequent storms of intermediate severity lead to a gradual increase in aboveground biomass, and a decreasing amplitude of disturbance associated with storms of a given severity, as the forest is increasingly dominated by species with low susceptibility to windthrow (Papaik 1998).

Acknowledgements

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