

# Wind-throw mortality in the southern boreal forest: effects of species, diameter and stand age

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## Summary

1. Patterns of tree mortality as influenced by species, diameter and stand age were assessed across a gradient in wind disturbance intensity in a southern boreal forest in Minnesota, USA. Few previous studies have addressed how wind impacts boreal forests where fire was historically the dominant type of disturbance.

2. We surveyed 29 334 trees of nine species within a 236 000 ha blowdown in the Boundary Waters Canoe Area Wilderness (BWCAW), in forests that have never been logged and were not salvaged after the windstorm. Within the disturbed area, a range of disturbance severity from zero to complete canopy mortality was present, overlaying an existing mosaic of fire origin stands. For this study, we derived an index of wind disturbance intensity by standardizing the observed disturbance severity using common species with similar diameter at breast height (d.b.h.) distributions. We then used multiple logistic regression to assess patterns of tree mortality across gradients in tree size and wind intensity index, and for three stand ages.

3. Probability of mortality was higher with increasing ln d.b.h. for all nine species, with two species (*Abies balsamea* and *Picea mariana*) showing much more dramatic shifts in mortality with d.b.h. than the others. As hypothesized, the species most susceptible to windthrow at all d.b.h. classes were early successional and shade intolerant (*Pinus banksiana*, *Pinus resinosa*, *Populus tremuloides*) and those least susceptible were generally shade tolerant (e.g. *Thuja occidentalis*, *Acer rubrum*), although the intolerant species *Betula papyrifera* also had low mortality.

4. Mortality rates were higher in mature (c. 90 years old) stands than for old and very old (c. 126–200 years old) stands, probably because old stands had already gone through transition to a multi-aged stage of development.

5. *Synthesis.* Quantification of canopy mortality patterns generally supports disturbance-mediated accelerated succession following wind disturbance in the southern boreal forest. This wind-induced weeding of the forest favoured *Thuja occidentalis*, *Betula papyrifera* and *Acer rubrum* trees of all sizes, along with small *Abies balsamea* and *Picea mariana* trees. Overall, the net impact of wind disturbance must concurrently consider species mortality probability, abundance and diameter distributions.

*Key-words:* boreal forest, Boundary Waters Canoe Area Wilderness (BWCAW), forest dynamics, mortality, stand age, susceptibility, wind disturbance, wind-throw

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## Introduction

From minor gusts that damage and tear individual leaves to tornados, derechos and hurricanes capable of levelling forest stands, wind disturbance changes

forest structure, alters species composition, and shifts resources spatially and temporally (Canham & Loucks 1984; Foster 1988; Peterson & Pickett 1995; Rebertus *et al.* 1997; Ishizuka *et al.* 1998). The effects of wind disturbance on forested landscapes are heterogeneous for several reasons. Disturbance intensity varies spatially because of the physics of the disturbance itself and its interaction with physiography (Boose *et al.* 1994; Sinton *et al.* 2000). Variability in mechanical characteristics

among tree species, and size and age within species, leads to differential susceptibility to disturbance (King 1986; Mattheck *et al.* 1995; Wood 1995; Asner & Goldstein 1997; Webb 1999). The resulting heterogeneity of disturbance impacts across the landscape is among the most important determinants of spatial and temporal patterns within forested ecosystems (Turner *et al.* 1997; Kashian *et al.* 2004, 2005).

Wind disturbance has been largely overlooked in boreal forests until very recently (Lässig & Močálov 2000; Ulanova 2000; Gromtsev 2002; Pham *et al.* 2004; Achim *et al.* 2005), unlike temperate and montane forest systems where wind has been extensively studied (Dunn *et al.* 1983; Foster 1988; Peterson & Pickett 1990; Peterson & Pickett 1991; Peterson & Rebertus 1997; Webb 1999; Peterson & Pickett 2000; Canham *et al.* 2001). In most boreal forests, particularly those in central North America (the site of this study), the predominant natural disturbance regime consists of crown and ground fires occurring at intervals shorter than the lifespan of dominant canopy trees (Johnson 1992). However, the rarity of extensive wind disturbances does not diminish their potential ecological importance in reorganizing forest dynamics. In boreal systems where forest tree species are adapted to fire, wind disturbance may alter forest development and successional trajectories because adaptations for fire are unlikely to be the same as for wind. In addition, the ecological importance of severe windstorms may increase in the future due to global climate change.

We studied tree mortality within a large-scale blowdown caused by a severe thunderstorm that swept through the southern boreal forests of north-eastern Minnesota, including the Boundary Waters Canoe Area Wilderness (BWCAW), on 4 July 1999. This storm produced downburst winds at speeds  $> 53 \text{ m s}^{-1}$  ( $190 \text{ km h}^{-1}$ ; USDA Forest Service 2001), causing a 64 km long by 6–20 km wide path of damaged forest that included many stands of varying tree species, ages and level of damage.

The wind-disturbed BWCAW landscape provided an opportunity to examine hypotheses on how wind disturbance changes forest dynamics within upland boreal forests. Disturbance-mediated accelerated succession (called accelerated succession from here on) hypothesizes that disturbance supplants successional time by early release of “less pioneer”, more shade tolerant, later successional species (Abrams & Scott 1989; Sinton *et al.* 2000). In essence, wind may accelerate succession by selectively weeding out early successional species, shade-intolerant species and larger trees.

In the BWCAW forest communities, accelerated succession would be characterized by shifts in composition from early successional, primarily fire-adapted species, such as jack pine (*Pinus banksiana*), red pine (*Pinus resinosa*) and aspen (*Populus tremuloides*), to species such as white cedar (*Thuja occidentalis*), balsam fir (*Abies balsamifera*) and black spruce (*Picea mariana*), which are able to regenerate continuously in old multi-aged

stands, including in moderate to deep shade, in the absence of stand-killing disturbance. This successional trajectory has been observed in near-boreal stands that escape fire (Grigal & Ohmann 1975; Bergeron & Dubuc 1989; Frelich & Reich 1995). Paper birch (*Betula papyrifera*) occupies both early and late successional positions in boreal forests, as it is both fire-adapted and relatively intolerant, but also colonizes and/or persists in mixed stands over long time periods between major disturbances (Burns & Honkala 1990; Frelich & Reich 1995). Given this, *B. papyrifera* could have negative, neutral or positive response in an accelerated succession.

Shade tolerance has been linked to wind firmness because it is thought to represent a trade-off between mechanical safety and competitive ability (Loehle 2000). Generally, shade-intolerant species are thought to allocate more resources to rapid growth, especially height growth, instead of overall structural strength (Givnish 1995), leading them to be less wind firm. A longer lived, slower growing shade-tolerant tree may have denser wood, compact shape or other mechanical advantages in wood strength or structural attributes (USDA Forest Service 1999) that confer wind firmness. This suggests that mortality from wind will decrease with shade tolerance among canopy trees. Thus, we expect the following species order from least to most wind firm: *Pinus banksiana*  $>$  *Populus tremuloides*  $>$  *Pinus resinosa*  $>$  *Fraxinus nigra*  $>$  *Betula papyrifera*  $>$  *Acer rubrum*  $>$  *Picea mariana*  $>$  *Abies balsamea*  $>$  *Thuja occidentalis* (Fowells 1965; Lusk & Reich 2000).

Tree diameter is expected to be positively correlated with wind-caused mortality because larger trees are more exposed to wind forces (Foster 1988; Canham *et al.* 2001). In the simplest case, increases in mortality with diameter would occur in the same manner for all species across the entire range of intensity. However, Canham *et al.* (2001) found that changes in susceptibility with respect to diameter and storm severity varied widely among species and that expected mortality probability rankings among species may shift across both size and storm severity gradients. Although susceptibility increased with d.b.h. and storm severity across all species, the relative susceptibility of *Fagus grandifolia* and *Tsuga canadensis* switched from rank 1 and 2 at smaller d.b.h. or low severity to ranks 5 and 6 at larger d.b.h. or high severity (Canham *et al.* 2001; Papaik & Canham 2006).

As the consequences of wind disturbance (i.e. severity) will be less well related to wind intensity the greater the heterogeneity in composition and tree size (Canham *et al.* 2001; Papaik & Canham 2006), it would be useful to derive a measure of intensity against which to assess differences in mortality, in place of severity. Given that measures of disturbance severity represent disturbance intensity if uniform indicators are used at all sites, we create an intensity index by standardizing the observed severity gradient (see below). The simplest expectation is that the probability of mortality will increase with intensity for all species in the same manner.

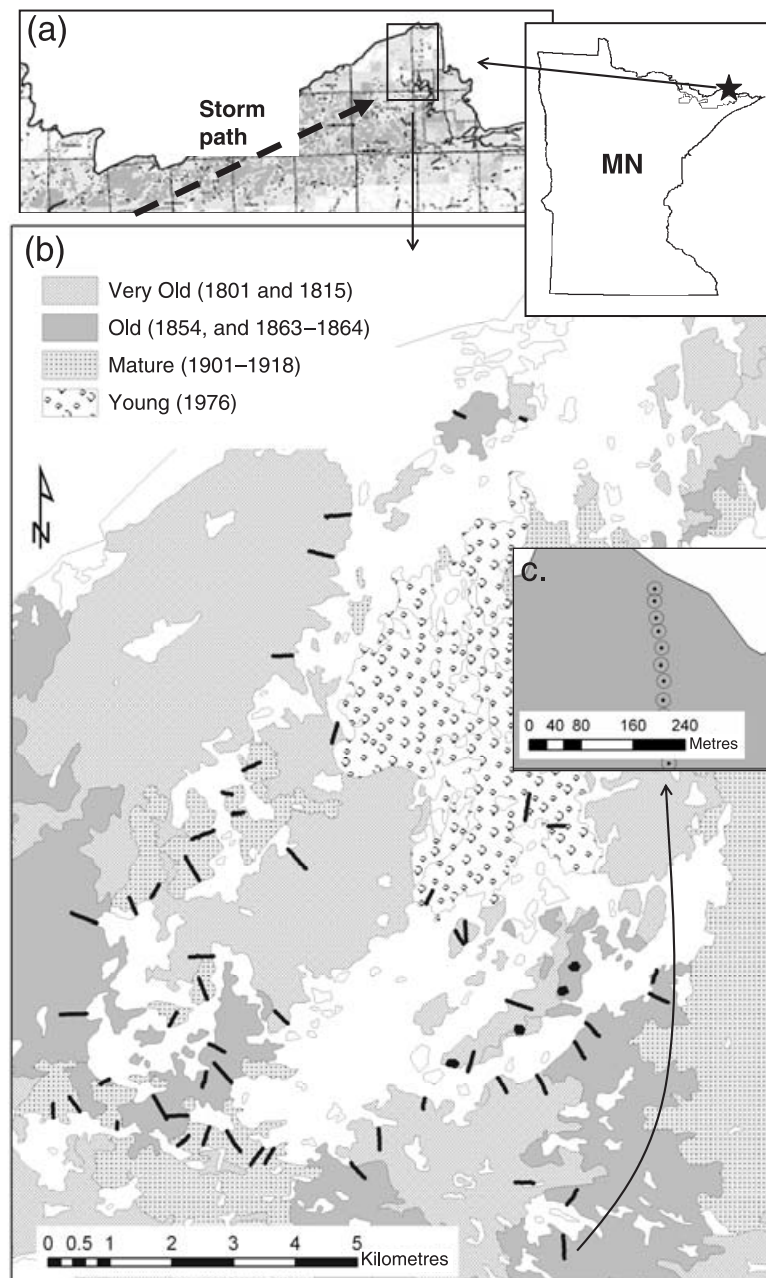
The role of stand age in influencing susceptibility to wind-throw is not well understood. Foster (1988) observed that wind damage to forest stands exhibits a positive linear relationship with age for stands up to 100 years of age. The reasons for increasing mortality may include increases in crown area, volume and tree height, and increases in disease or other structural weaknesses. The above suggests that as stands become more decadent, they will become more susceptible and thus the probability of mortality will be greatest within older stands. On the other hand, if late-successional species are less susceptible to windthrow, and are more prevalent in older stands, this may partially or totally compensate for the aforementioned structural changes.

As there is no single, simple expectation, we will test the null hypothesis that there will be no changes in tree mortality associated with stand age.

## Methods

### STUDY AREA

The study area (*c.* 14 400 ha) is centred at 90°56' W and 48°08' N, within the Boundary Waters Canoe Area Wilderness (BWCAW), a 400 000 ha federally designated wilderness area within the Superior National Forest in north-eastern Minnesota, USA (Fig. 1). Granitic bedrock of the Canadian Shield underlies the forests,



**Fig. 1.** Study area within the Boundary Waters Canoe Area Wilderness: (a) BWCAW area with wind damage from 1999 blowdown; (b) stand age map and study site locations (white areas represent lakes); (c) detail of transect with individual plots.

which are laced by a network of glacier-formed lakes. The area has low total relief (400–580 m a.s.l.), but has many hills and rock outcrops with 10–50 m of relief. The climate is cold-temperate continental with a frost-free season of 100 days. Summers are typified by hot and humid days sustained by tropical air masses from the Gulf of Mexico that are frequently interrupted by episodes of drier, cooler days sustained by Arctic air masses (Heinselman 1996). Average annual precipitation is 64 cm, ranging from 38 to 100 cm. The mean July temperature is 17 °C and the mean January temperature is –8 °C.

During the storm, 236 000 ha of near-boreal forest were damaged (FEIS 2001), including 193 000 ha of predominantly virgin, fire origin forests within the BWCAW. Wilderness area designation makes this area, to our knowledge, the largest tract of wind-damaged forest available for study where salvage logging was prohibited. Furthermore, this blowdown was superimposed on an existing mosaic of fire-origin stands with known fire histories (Heinselman 1973). The c. 14 400 ha study area was chosen because it included a gradient of wind disturbance severity from no damage to nearly complete canopy tree mortality.

#### SITE SELECTION AND FIELD METHODS

Windthrow impact was quantified across 741 plots on 52 transects during 2000 and 2001. As this forest had not been salvaged or burned at the time of fieldwork, it was possible to assess which trees had died during or after the 1999 windstorm.

The BWCAW has an extraordinarily high density of lakes; almost 80% of the land area is within 500 m of a lake in this physiographic area (Rich 2005). The main pattern of variation in forest communities is a gradient from lakeshore to ridge top. Therefore, to provide a representative sample of forest communities, individual field plots were spread along transects that began 5 m from a lakeshore and extended inland 250–400 m at an azimuth perpendicular to the lake edge (Fig. 1). Transect locations were determined before visiting or sampling the area by choosing shoreline locations on US Geological Survey 7-min topographic maps. Although the exact plot location was random, transects were distributed throughout the landscape with respect to forest stand age (Table S1 in Supplementary Material). Plots along each transect sampled a variety of hillslope and aspect combinations; in general, transect length was greater than the size of individual landscape topographic elements.

Nested fine-scale (3, 4 or 5 m radius) and coarse-scale (12 m radius) plots were placed every 25 m along each transect. At the fine scale, all trees rooted or uprooted greater than 2.5 cm d.b.h. were surveyed for species, d.b.h., canopy position, damage type and mortality. Given the potential for near term mortality, trees likely to die within 3 years were considered dead in our survey. Examples of this include conifers that had more than

50% crown damage or hardwood trees mostly severed from their root system, with diminutive leaf size, and living under severe stress (e.g. surviving from carbohydrates stored in the trunk). Individual fine-scale plot radius was increased to as much as 5 m to measure at least 15 trees per plot. For trees that were damaged during the windstorm, d.b.h. was measured at the point on the stem that would have been 1.4 m above the root crown prior to the windstorm. Individual trees on the fine-scale plots were determined to be part of the pre-wind disturbance canopy if they were at least 5 cm in diameter and existed in an open-light environment considering both the living and dead neighbouring trees rooted in the plot. Only living neighbours were considered for post-disturbance canopy membership. Coarse-scale plot (12 m radius) data were collected independently by tallying all trees rooted in the plot greater than 5 cm d.b.h. for species, size class and mortality status. There were two size classes: “pole” trees 5–15 cm d.b.h. and “large” trees over 15 cm d.b.h. (Table 1). Mortality status had three classes: alive, alive with damage, or dead. Alive and dead classes followed the same definition as the fine-scale plots. Alive with damage was defined as damage that dramatically altered the tree growth form.

For this study we grouped plots by stand age, defined as years since stand originating fires. All plots were within an area that has a known fire chronology and stand origin history (Heinselman 1973; Fig. 1, Table S1). 1 Very old stands, c. 188–200 years old, having originated after severe fires between 1801 and 1813. These stands were of uneven age although a few trees from the original post-fire cohort were still present prior to the windstorm.

2 Old stands, c. 126–137 years old, having originated after severe fires in 1864 or 1875. The post-fire cohort was still substantial in these stands, although some canopy break-up had started to occur prior to the windstorm, with recent younger cohorts starting to enter canopy gaps.

3 Mature stands, c. 90 years old, having originated after a severe fire in 1910. These stands had even-aged structural characteristics and were heavily dominated by the post-fire cohort.

#### INTENSITY INDEX

Disturbance intensity is the physical measure of disturbance, in this case wind force, over a given area (Frelich 2002). One cannot directly measure disturbance intensity at a given site without instrumentation in place during a disturbance. Hence, ecologists rely on surrogates for disturbance intensity such as disturbance severity, which is assumed to be correlated with intensity. Sometimes the percentage of total basal area wind-thrown in a stand is used as an index of wind intensity. Although this may be an adequate surrogate for intensity among sites that are biologically homogeneous or where only a rough indicator is needed, it may

**Table 1.** Pre- and post-wind disturbance distribution and mortality data for nine boreal species on 692 plots at fine (5 m) and coarse (12 m) scales

Species	Pre-wind living stems (5 m)	Post-wind living stems (5 m)	Mortality (%) (5 m)	Total stems sampled (%) (5 m)	Pre-wind mean d.b.h. (5 m)	Post-wind mean d.b.h. (5 m)
<i>A. balsamea</i>	654	426	34.9	18.3	9.6	8
<i>A. rubrum</i>	122	101	17.2	3.4	13	12.7
<i>B. papyrifera</i>	494	406	17.8	13.8	12.9	12.3
<i>F. nigra</i>	75	69	8	2.1	10.9	10.7
<i>P. glauca</i>	—	—	—	—	—	—
<i>P. mariana</i>	964	438	54.6	26.9	14.1	12.4
<i>P. tremuloides</i>	409	123	69.9	11.4	23.5	21.4
<i>P. banksiana</i>	461	81	82.4	12.9	23.3	22.3
<i>P. resinosa</i>	48	11	77.1	1.3	37.7	38
<i>P. strobus</i>	—	—	—	—	—	—
<i>T. occidentalis</i>	355	311	12.4	9.9	16.2	15.8
Total or mean	3582	1966	41.6		17.9	17.1

Species	Pre-wind living stems (12 m)*	Post-wind living stems (12 m)	Mortality (%) (12 m)	Total stems sampled (%) (12 m)	Total basal area sampled (%) (12 m)	Species used in intensity index	Number of plots with species occurrence (12 m)
<i>A. balsamea</i>	8508	6165	27.5	29	10.1	Y	672
<i>A. rubrum</i>	783	703	10.2	2.7	1.8	Y	147
<i>B. papyrifera</i>	4018	3331	17.1	13.7	11	Y	609
<i>F. nigra</i>	496	476	4.0	1.7	1	Y	35
<i>P. glauca</i>	157	117	25.5	0.5	0.8	Y	89
<i>P. mariana</i>	6797	3909	42.5	23.2	17.3	Y	645
<i>P. tremuloides</i>	2796	1048	62.5	9.5	20.9	N	397
<i>P. banksiana</i>	2769	511	81.5	9.4	21.2	N	401
<i>P. resinosa</i>	277	97	65.0	0.9	5.1	N	67
<i>P. strobus</i>	87	65	25.3	0.3	2.6	N	60
<i>T. occidentalis</i>	2646	2261	14.6	9	7.9	Y	248
Total or mean	29 334	18 683	36.3		99.7		

\*Includes trees that were classified as alive or alive and damaged.

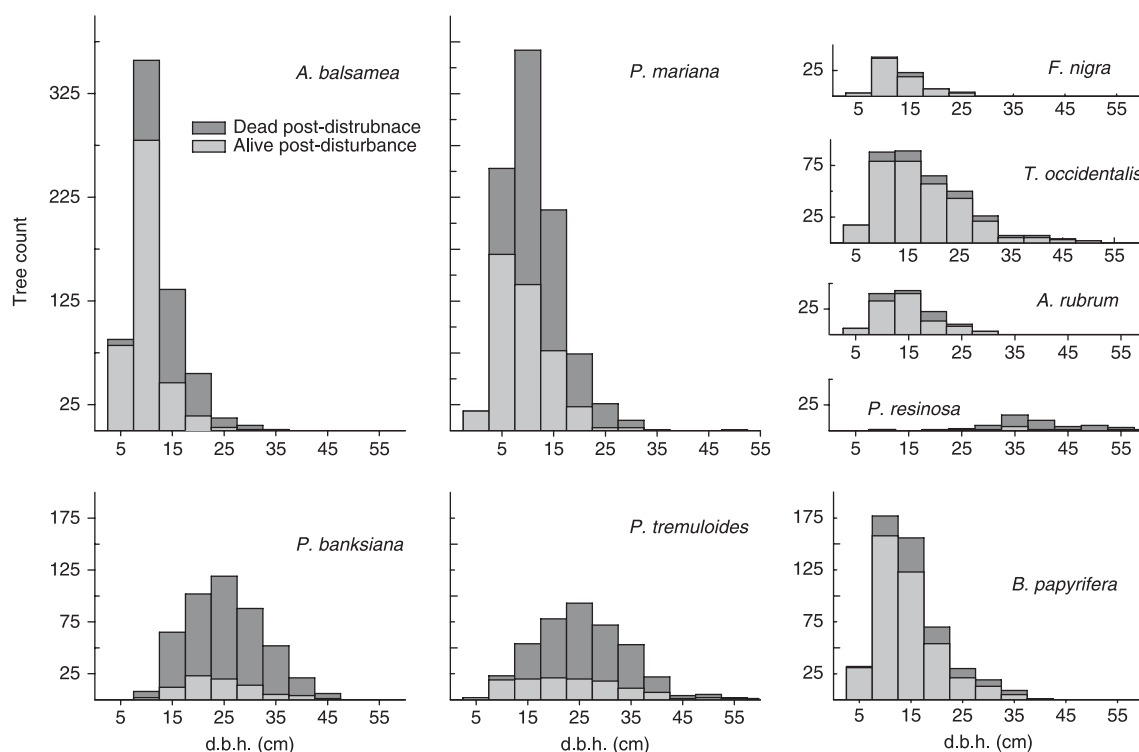
not be reliable in cases such as our BWCAW forests where there is compositional and structural heterogeneity. Two stands dominated by different species of the same d.b.h., or by the same species but of different d.b.h., may exhibit very different severities as measured by proportion of basal area blown down even if they experience the same wind intensity.

Establishing unbiased surrogates for disturbance intensity through empirical techniques has been gaining attention; for example, utilizing maximum likelihood modelling to simultaneously establish both severity and susceptibility without species biases (Canham *et al.* 2001). The ideal intensity measure would use common indicators, such as the same size and species trees at all sites, akin to the mechanical trees used in wind tunnel studies (Wood 1995). Therefore, we created an intensity index, based on standardization of severity using species of trees that are widespread across the landscape and have similar mean d.b.h. ANOVA comparison of mean diameter by species in our fine-scale plot data showed two distinct groups of species. *Populus tremuloides*, *Pinus banksiana*, *Pinus resinosa* and *Pinus strobus* had mean d.b.h. that was significantly larger than all other tree species (Tukey-Kramer

honestly significant difference test,  $P < 0.05$ , Fig. 2) and in some cases the species also were patchily distributed or infrequent across the landscape. As these species were dissimilar in size to the others and not uniformly distributed across the majority of plots, we did not include them in the calculation of the intensity indices. The index included the remaining species (*T. occidentalis*, *P. glauca*, *P. mariana*, *A. rubrum*, *B. papyrifera*, *F. nigra* and *A. balsamea*); these species have similar mean d.b.h. (range 9.6–14.10 cm) and occur in abundance on most plots (29433 trees used in the intensity index). We calculated the intensity index using coarse-scale data on a per plot basis as follows:

$$\text{Intensity Index} = \frac{\text{Total basal area killed of selected species}}{\text{Total basal area of selected species}}$$

Because coarse-scale (12 m) data were recorded by species and size class, it was necessary to use continuous data from the fine-scale plots to estimate the basal area for each species and size class. We calculated mean basal area and quadratic mean diameter (QMD), the diameter of a tree with mean basal area, for pre- and post-disturbance populations of individual species in



**Fig. 2.** Canopy tree size distributions across fine-scale (5 m) plots for trees dead vs. alive after the 1999 windstorm, separated by species. All trees with d.b.h. > 2.5 cm are included.

pole (5–15 cm) and large (> 15 cm) size classes using data from the fine-scale plots. For estimates of pre-disturbance mean basal area and QMD, we used all trees rooted in the plots (5140 stems). For the post-disturbance basal area and QMD, we only used stems living following the disturbance (2966 stems). These mean values were then used to assign a basal area to each tallied tree in the coarse-scale radius plots. (Table S2).

We calculated intensity in several ways using iterations of all seven remaining species or eliminating species that were the least abundant, such as *F. nigra*, *P. glauca* and *A. rubrum*. All of these indices were highly correlated with each other ( $R^2 > 0.90$ ,  $P < 0.0001$ ). We chose to proceed with an intensity index that included all seven of these species because removing further species did not change the index dramatically. The intensity index was only used on plots that had more than 10 trees present of the included species. Consequently, only 692 of the 741 plots were used in these analyses.

The method of using mean basal area estimates from the fine-scale plots to assign basal values to each tree in the coarse-scale plots moderated the tendency of larger trees to bias basal area-based indices because all trees in a similar size class used the same basal area value. The net result is a hybrid index that has properties of both stem and basal area indices. There was a strong correlation between percentage basal area killed vs. percentage of stems killed ( $R^2 = 0.85$ ,  $P < 0.0001$ , data not shown). In severity indices that use basal area only, plots with individual large trees often have higher disturbance severity compared with stem-based indices for the same plots (Canham *et al.* 2001). Not

surprisingly, severity and the intensity index are correlated ( $r^2 = 0.66$ ,  $P < 0.0001$ ) (Figure S2). Divergence in the indices is primarily due to plots with larger diameter trees having greater disturbance severity for a given disturbance intensity (Figure S2).

The resulting intensity index is intermediate between true wind intensity that would have been measured by anemometers if they had been present across the landscape, and severity using all species and sizes of trees. Although not perfect, because it ignores factors such as soil type, depth to bedrock and tree rooting depth, it is a better metric of intensity than severity alone, and hence useful to understanding responses to wind disturbance.

#### ANALYSIS METHODS

Multiple logistic regression was used to model the probability of tree mortality as a function of the continuous predictors  $\ln$  d.b.h. (cm) and *intensity index*, and categorical predictors *species* and *stand age*. Analysis and model fitting were completed and evaluated in both Arc v.1.0 (Cook & Weisberg 1999) and S-Plus 2000 (Mathsoft 2000). Mortality data from the fine-scale (5 m) plots was used as the response and coded 1 if an individual canopy tree was dead (success) or 0 if the tree was alive (failure). Thus, the probability function increases with mortality. Each species had to have at least 40 individuals in the fine-scale plots to be included in analyses.

Initial predictors of mortality were  $\ln$  d.b.h. (in cm), *intensity index* and *species*. To allow for differences in

response among individual species, individual indicator variables were coded to allow for interactions between predictors and individual species. We evaluated candidate models starting from the fully saturated model and considered all interactions using likelihood ratio tests (LRT) and Akaike's information criterion (AIC) to remove terms (Agresti 1996; Peng *et al.* 2002; Quinn & Keogh 2002). Candidate models also included models with and without a common intercept. Each successive model also was visually tested for lack of fit against a mean function and LOWESS smoothing of the data. The mean function is generated by applying the model function across the predictor data range using a moving average where mean predictor values are derived from overlapping slices of data. This technique is useful as it shows where the fitted response departs from the observed data (Cook & Weisberg 1999). Successful models matched the mean function throughout the range of responses and had no patterning in the residual plots. We also evaluated differences among species coefficients and generated 95% asymptote support limits to visually verify these results (Cook & Weisberg 1999; Cook & Weisberg 2004).

Stand age was addressed in a second, separate model; selection started with the main model for the other three variables as the base model. The starting model was fully saturated with respect to stand age variables. Species with fewer than 50 observations were not included in this model. Model fit was evaluated with the same methods as the main model using both visual and statistical lack of fit methods.

## Results

Across all plots, there was considerable variation in the pre-storm abundance and diameter distributions of the nine species examined (Fig. 2). No one species dominated this landscape. Six species each accounted for at least 9% of all stems and none more than 27% in the fine-scale plots; and six species each contributed at least 7% to total basal area and none more than 22% in the course-scale plots (Table 1). The seven most dominant species (by stem number) were: *P. mariana*, *A. balsamea*, *B. papyrifera*, *P. banksiana*, *P. tremuloides*, *T. occidentalis* and *A. rubrum*.

There were dramatic differences among species in the percentage of canopy trees killed by the windstorm (Fig. 2, Table 1). Percentage mortality ranged from 12 to 82% among the seven dominant pre-storm species. *F. nigra*, *T. occidentalis*, *A. rubrum* and *B. papyrifera* all had low mortality (< 20%). *P. mariana* and *A. balsamea* had intermediate mortality (35% and 55%, respectively). *P. tremuloides*, *P. resinosa* and *P. banksiana* had high mortality (70–82%) and also had the highest mean d.b.h. However, some species with smaller mean diameters (e.g. *P. mariana* and *A. balsamea*) had higher mortality than species with larger average size, such as *T. occidentalis* or *B. papyrifera* (Table 1). Over all plots, there was little concurrence between abundance and mortality rate.

**Table 2.** Coefficients and goodness of fit statistics for the logistic regression model. Each species factor used in the model has a separate intercept coefficient. *Abies balsamea* and *Picea mariana* have interactions with ln d.b.h. or intensity; all other species do not

Variable	Coefficient value	ASE	Wald statistic	P-value
ln d.b.h.*	0.755	0.151	25.146	< 0.0001
Intensity index*	4.789	0.28	292.561	< 0.0001
<i>P. banksiana</i> † <sup>HM</sup>	-2.562	0.48	28.54	< 0.0001
<i>P. resinosa</i> † <sup>HM</sup>	-3.203	0.657	23.751	< 0.0001
<i>P. tremuloides</i> † <sup>HM</sup>	-3.557	0.481	54.659	< 0.0001
<i>A. rubrum</i> † <sup>LM</sup>	-4.937	0.465	112.584	< 0.0001
<i>F. nigra</i> † <sup>LM</sup>	-5.079	0.569	79.581	< 0.0001
<i>B. papyrifera</i> † <sup>LM</sup>	-5.653	0.427	174.944	< 0.0001
<i>T. occidentalis</i> † <sup>LM</sup>	-5.798	0.46	158.825	< 0.0001
<i>A. balsamea</i> † <sup>CM</sup>	-9.674	0.699	191.73	< 0.0001
<i>A. balsamea</i> :ln d.b.h.‡	2.457	0.335	53.874	< 0.0001
<i>P. mariana</i> † <sup>CM</sup>	-7.963	0.652	149.006	< 0.0001
<i>P. mariana</i> :ln d.b.h.‡	1.452	0.271	28.796	< 0.0001
<i>P. mariana</i> : standardized severity‡	1.204	0.511	5.552	0.018

\*Required coefficients.

†Intercepts coded for species factors (will be zero except for modelled species).

‡Interaction coefficients for species-variable combination.

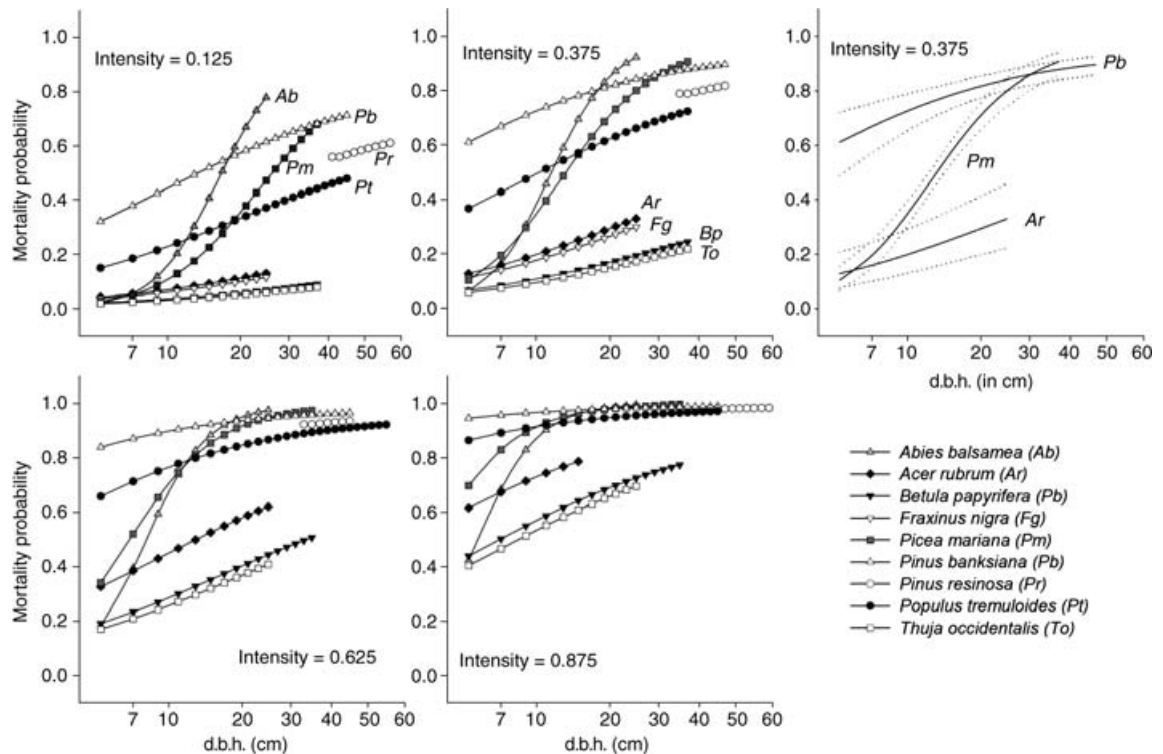
HM, CM or LM: high, changing or low mortality species. There are significant differences between individual species intercepts among these groups.

The regression models assessed how much of the variation in mortality among and within species can be explained by diameter, distribution of plots across the intensity index, distribution among stand age classes and species identity. Our analysis confirmed the following model (Table 2):

$$\begin{aligned} \text{Logit (individual canopy tree mortality)} = & 0.75 \ln \text{ d.b.h.} + 4.79 \text{ intensity} \\ & + \beta \text{ species} + \beta (A. \text{ balsamea} \times \ln \text{ d.b.h.}) \\ & + \beta (P. \text{ mariana} \times \ln \text{ d.b.h.}) + \beta (P. \text{ mariana} \times \text{intensity}) \end{aligned}$$

All four predictors were influential in describing canopy tree mortality (Table 2). Pearson's and  $G^2$  statistics showed no evidence of lack of fit (Pearson  $\chi^2 = 3642.94$ ,  $P = 0.81$ , and deviance = 3055.837,  $P = 1$ , 3568 d.f.). LRT statistic for the model against the saturated model showed that the model was highly significant ( $P < 0.0001$ ). Also, models that included fewer parameters had significantly worse fits. More complex models did not significantly affect model fit. Additionally, the selected model has a good visual fit when compared with a mean function and LOWESS smoothing of the data throughout the predictor range (Cook & Weisberg 1999). All coefficients included in this model were significant (Table 2).

Mortality increased with diameter for all nine species when intensity index was held constant (Fig. 3).



**Fig. 3.** Predicted mortality probability as a function of diameter with intensity index held constant. Mortality probability is only shown for diameter ranges present in data set for a given stated level of intensity. Asymptotic 95% confidence limits for three example species.

Seven of nine species were described by a simple asymptotic increase in mortality with increasing diameter and regression models had common coefficients for  $\ln$  d.b.h. and intensity index, but different intercept coefficients for each species. Thus, these seven species exhibited parallel response patterns across d.b.h. and wind intensity. Closer assessment shows these seven species fell into two groups whose asymptotic 95% support limits did not overlap and have significantly different coefficients. This was verified by modelling data subsets with all pairwise species groupings to directly test for significant differences between individual species intercepts (Table 2). The high mortality (HM) group included *P. banksiana*, *P. resinosa* and *P. tremuloides* (Fig. 3). The low mortality (LM) group includes *B. papyrifera*, *A. rubrum*, *F. nigra* and *T. occidentalis*. Across d.b.h., mortality risk for both groups increased between 15 and 30% across the range of tree sizes present in large numbers (*c.* 5 to *c.* 30 cm d.b.h.), except at high intensity ( $> 0.75$ ), where mortality for the HM group was near the maximum (*c.* 90%) even for the smallest trees (Fig. 3). The changing mortality (CM) group with *A. balsamea* and *P. mariana* had a mortality pattern that differed from the other species; there was an S-shaped increase in mortality with d.b.h. Their probability of mortality at small d.b.h. was low (similar to the LM group) but was high at larger d.b.h. (similar to the HM group). Thus, their risk of mortality across the range of d.b.h. present had a larger magnitude of change than species in the LM and HM groups (*c.* 60 to *c.* 80%).

When diameter was held constant mortality increased with intensity index for all species (Fig. 4). For 10 cm d.b.h. trees there was a large difference (*c.* 70%) in risk of mortality among species at high intensity index, whereas this difference was only *c.* 20% for trees in the 30 cm d.b.h. class. For the 40 cm d.b.h. class, differences in mortality risk among species at high intensity index were almost zero, but no species in the LM or CM groups were present at that size class (Fig. 4).

We used a second multiple logistic regression model to assess whether prior disturbance (fire) history influenced response to the windstorm (Table 3). In this model, mortality probability decreased with stand age, even after accounting for differences in species and diameter. There was little difference in model coefficients other than the inclusion of the nominal categorical *stand age* variable with three levels, between the first and second models. In this second model, the overall results showed that the mature class ( $\approx 90$  years old) was significantly more susceptible to canopy tree mortality than the old (126–137 years old) or very old (184–195 years old) classes (the mature forest factor was significant while the old forest factor was not against the very old forest base model, Table 3). For five of the six species included in the model, the very old class had the lowest mortality, but this trend was only significant for *P. tremuloides* (Fig. 5). For *P. mariana*, mortality was lowest in the old forest class, although differences among stand age classes were not significant.



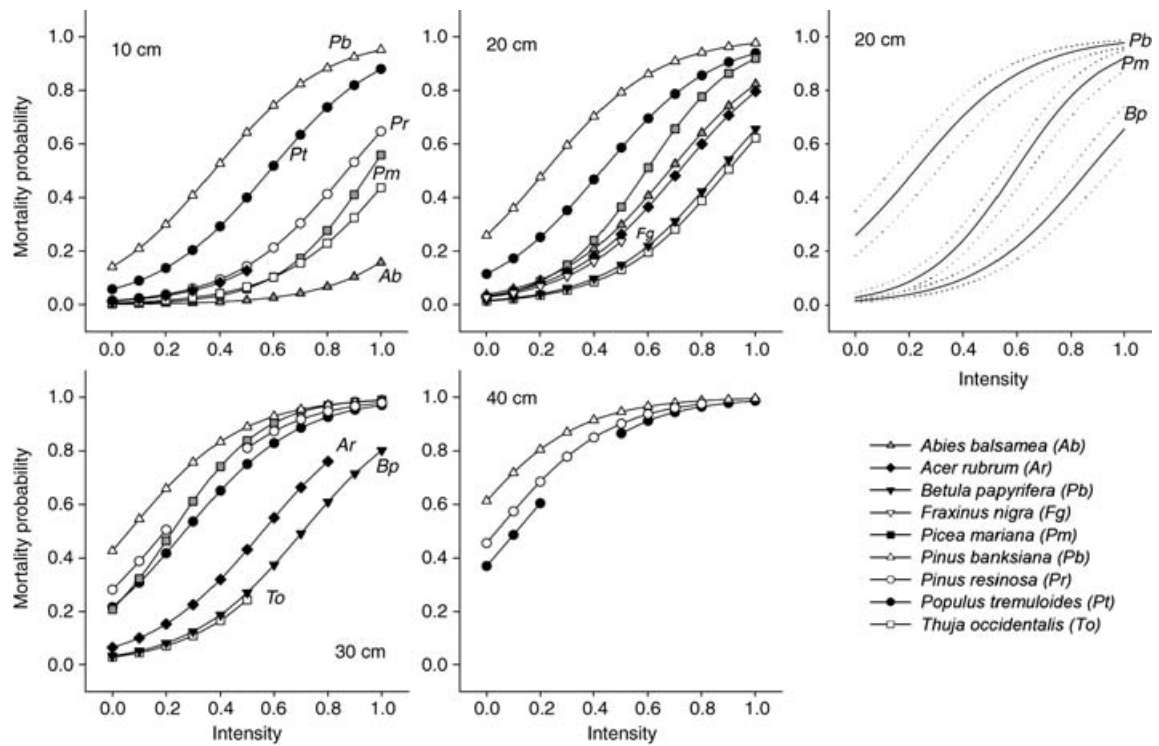


Fig. 4. Predicted mortality probability as a function of intensity index with diameter held constant. Mortality probability is only shown for intensity ranges present in data set for a given diameter. Asymptotic 95% support limits generated for three example species.

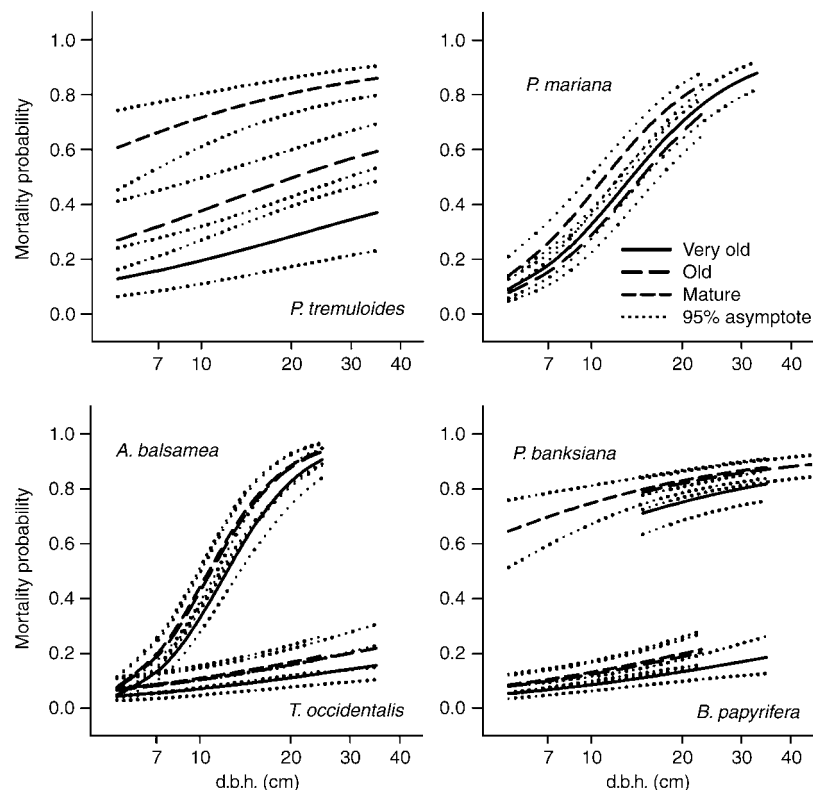


Fig. 5. Predicted mortality probability for six species using stand age model. Intensity index was held to 0.375. Asymptotic 95% support limits generated around each stand age class.

**Table 3.** Coefficients and goodness of fit statistics for the model including stand age. Stand ages include: mature, 90 years; old, 126–137 years; and very old, 188–200 years. Each species factor used in the model has a separate intercept coefficient. Interactions exist with stand age for *P. tremuloides* and *P. mariana* in addition to those from the first model

Variable	Coefficient value	ASE	Wald statistic	P-value
ln d.b.h.*	0.709	0.164	18.709	< 0.0001
Intensity index*	4.536	0.298	232.191	< 0.0001
Old – origin 1864 & 1865*§	0.325	0.448	0.526	0.4680
Mature – origin 1910*§	2.349	0.383	37.679	< 0.0001
<i>P. banksiana</i> †	–0.761	0.682	1.243	0.2650
<i>P. tremuloides</i> †	–4.162	0.63	43.648	< 0.0001
<i>P. tremuloides</i> : very old‡	–1.87	0.405	21.344	< 0.0001
<i>P. tremuloides</i> : mature‡	–1.368	0.331	17.054	< 0.0001
<i>B. papyrifera</i> †	–3.741	0.635	34.691	< 0.0001
<i>T. occidentalis</i> †	–3.949	0.651	36.739	< 0.0001
<i>A. balsamea</i> †	–7.972	0.83	92.196	< 0.0001
<i>A. balsamea</i> : ln d.b.h.‡	2.557	0.343	55.674	< 0.0001
<i>P. mariana</i> †	–6.871	0.748	84.478	< 0.0001
<i>P. mariana</i> : ln d.b.h.‡	1.562	0.28	31.185	< 0.0001
<i>P. mariana</i> : intensity‡	1.567	0.535	8.593	0.0030
<i>P. mariana</i> : old‡	–0.589	0.227	6.73	0.0090

\*Required coefficients.

†Intercepts coded for species factors (will be zero except for modelled species).

‡Interaction coefficients for species-variable combination (will be zero except interaction).

§Coefficients for stand age represent deviations from very old (origin 1801 and 1813) class, which is the default level for stand age.

## Discussion

This study shows that individual tree mortality from wind disturbance is a function of species, diameter and stand age, and that the magnitude of differences among species is also influenced by wind intensity. In combination, these attributes explained the observed patterns of canopy tree mortality, indicating how windstorms can apply a selective weeding process to the forest that removes or leaves behind trees with certain attributes.

This study specifically considers canopy tree mortality rather than susceptibility to wind-throw (trees standing vs. fallen). In the near-boreal ecosystem, a living tree still may have a large impact on its surroundings despite having partially fallen or broken. This system is characterized by a relatively low density of trees with a low canopy, a small range in diameter from juvenile to canopy trees, and strong persistence mechanisms such as resprouting (*Populus tremuloides*, *Betula papyrifera* and *Acer rubrum*) and replacement of lost leaders by lateral branches (*Thuja occidentalis*, *Abies balsamea*, *Picea mariana*, *P. tremuloides*, *A. rubrum*, *B. papyrifera* and *Fraxinus nigra*). These trees, if living despite having lost part of their canopy, will continue to occupy growing space and influence potential regeneration. The number of canopy trees that were classified as alive but no longer in the canopy was 104 of 1966 living trees, c. 5% of the data set. Of these trees, those with the largest percentage alive were *P. tremuloides* (11.3% of all remaining living stems), *P. resinosa* (9.1%) and *P. banksiana* (8.6%). Removal of all live but fallen trees from the model would reinforce the findings, maintain

the rankings of the current model and further separate these species from the others.

## SPECIES

We hypothesized that canopy tree susceptibility due to wind disturbance would be greater for shade-intolerant than tolerant species. The species fell into three windthrow mortality groups (Fig. 3): a high mortality group (HM), a low mortality group (LM), and a third group that changes from low to high mortality with increasing diameter (CM). The three members of the HM group, *Populus tremuloides*, *Pinus banksiana* and *Pinus resinosa*, have historically been the most abundant early successional species after large-scale fires (Heinselman 1996), are shade-intolerant (Fowells 1965) and had the highest overall mortality rates as well as higher mortality rates than the LM group for any comparable d.b.h. across the range of diameters present. The marked high percentage mortality (69–82%) in the HM group (as compared with 8–18% in the LM group), was the result of both higher mortality at a given diameter and larger mean diameter of trees (Table 1, Fig. 3). Species in LM groups do not strictly conform to shade tolerance rankings, but all were part of the late-successional group for this area (Frelich & Reich 1995). The LM group included *T. occidentalis* (very tolerant) and *A. rubrum* (tolerant), but also included *B. papyrifera* (intolerant, but persists and continues to reproduce in late-successional stands) and the most susceptible of the LM group, *F. nigra* (mid-tolerant). The CM group includes two shade-tolerant species (*A. balsamea* and *P. mariana*) that are also part of the

late-successional species group in the study area (Frelich & Reich 1995). Their overall mortality rates range from 34 to 56%, but these averages conceal rates that are close to the LM and HM groups for smaller and larger diameters, respectively.

#### DIAMETER

All nine species had positive slopes in the regression models (i.e. higher mortality with larger trees), confirming the hypothesis that larger trees were more susceptible to blowdown (Fig. 3). However, we also expected that diameter would have the same effect across all species. For all but two species (*A. balsamea* and *P. mariana*), ln d.b.h. could be modelled as a single coefficient, indicating that, for this group of seven species, the effect of increased diameter functions similarly with respect to wind disturbance. This is remarkable considering variations in growth form and mechanical attributes among these species. Separate slopes indicating a different functional response with diameter were necessary to model the response of the CM group, *P. mariana* and *A. balsamea* (Table 2). A plausible explanation is that they are the only spire-form conifers included in the study. They retain lower branches as understorey saplings, and then self-prune lower branches when they reach the canopy; thus they make a transition from a low to high centre of gravity as they mature, and end up with a small dense crown on top of a tall trunk. In contrast, *P. resinosa* and *P. banksiana* in the HM group self-prune lower branches at a young age, whereas *T. occidentalis* in the LM group retain more of the lower branches and a low centre of gravity throughout their lives.

With only a single coefficient for diameter, the influence of diameter on mortality was less variable than in Canham *et al.* (2001). However, the diameter range of our models, and the near boreal canopy trees in this landscape, is more restricted (5–55 cm), compared with 15–80 cm in the northern temperate forests. Tree d.b.h. at small diameters may be less confounded by differences in form than at larger diameters. Ln d.b.h. was a better predictor of mortality than d.b.h., indicating that diameter increase had less influence as trees became larger. This observation has two likely explanations: (i) tree height reaches a plateau while diameter continues to increase; and (ii) trees with very large d.b.h. may not carry the same foliage load as somewhat smaller trees due to the cumulative effect in relatively old and large trees of branch loss during low-severity windstorms and episodes of heavy wet snow that break off branches.

Similar to other studies, the mortality patterns summarized in the preceding paragraphs generally but incompletely support our hypotheses about mortality in relation to successional status, shade tolerance and tree size, and their integrated effects on acceleration of succession. Given their higher mortality at a given d.b.h. and their generally higher d.b.h., wind disturbance

did almost instantaneously shift the forest away from the dominant post-fire dominants, *P. tremuloides*, *P. resinosa* and *P. banksiana*, and towards the species that would increase in relative abundance without disturbance (Frelich & Reich 1995; Heinzelman 1996).

#### INTENSITY

We hypothesized that changes in disturbance intensity would affect all trees in the same manner. Thus, we expected to observe that the probability of mortality would increase as a single function of intensity for all species for any given diameter of trees. The single shared intensity coefficient shows that mortality differences at any given level of intensity are due to species differences rather than species  $\times$  intensity interactions. Mortality patterns across the gradient in wind intensity index, holding diameter constant, are similar to those across the diameter gradient in that the species fall in the same rank order with *Pinus banksiana* (highest mortality) and *Thuja occidentalis* (lowest mortality) bracketing the nine species (Fig. 4). However, the species do not fall into three clearly separated groups as they did across the d.b.h. gradient (Figs 3 and 4). One exception, *P. mariana*, is more susceptible at higher disturbance intensities as compared with the other species (as indicated by the interaction term in the model). Thus, in areas with higher wind intensity, we would expect to see acceleration in the proportion of *P. mariana* killed.

#### STAND ORIGIN AGE

Windthrow mortality was hypothesized to increase with stand age as suggested by Foster (1988), and this was tested in the second logistic regression model. Contrary to expectation, our results showed the probability of tree mortality was significantly higher in mature (90 years old) than old (126–137 years) or very old (188–200 years) stands, with the latter two categories about equal (Table 3, Fig. 5). These findings suggest that a tighter linkage exists between canopy mortality and stage of forest development than canopy mortality and stand age. The mature stands probably had higher mortality because pioneer tree species that were established at the time of stand initiation were reaching the end of their life span, and stands were thus about to start the transition to an uneven-aged stage of development. This transition had already occurred in the old and very old stands, so that they had a higher proportion of less susceptible late-successional species, as well as high numbers of smaller trees that were filling gaps left by the demise of the post-fire cohort. Another contributing factor may be that the few remaining trees from the post-fire cohort in the old and very old stands have existed as emergent trees since the surrounding trees of their own cohort died, and thus had some time to adapt to wind exposure, and some trees in the very old stands may have grown more slowly to reach

an equivalent size, giving them narrower rings and stronger wood.

In contrast to our model, Canham *et al.* (2001) found second growth forest to be less susceptible than old growth stands. They attributed this finding to the combination of species abundance and diameter distribution differences among community types. In part this is true of the findings here also as the mature forest had higher abundance of high mortality species in susceptible size classes. Together, these findings reinforce the need to take into account stem distribution along with relative susceptibility or mortality probability.

Among species, only *P. tremuloides* had a significantly different mortality response among stand ages; mortality for this species was higher in mature stands than old or very old stands (Fig. 5). This response makes sense in that the mean size of *P. tremuloides* was lower in very old stands, perhaps because the above-ground portion of the post-fire regenerated trees had died and new sprouts had arisen from the root system (mean d.b.h. of *P. tremuloides* canopy trees was 23.5 cm, 25.4 cm and 19.6 cm in mature, old and very old stands, respectively, with the 19.6 cm mean from very old stands significantly different from the other two by Tukey-Kramer HSD,  $P < 0.05$ ). Stand age differences had the least influence on mortality as compared with the other model variables.

## Conclusions

The observed canopy mortality patterns generally support the disturbance-mediated accelerated succession hypothesis among canopy trees, and partially support two related hypotheses: that shade tolerant and late-successional tree species are less susceptible to windthrow. The earliest successional and most shade-intolerant species (*Pinus banksiana*, *Pinus resinosa* and *Populus tremuloides*) suffered the most canopy-level mortality. This outcome is the result of the confluence of their higher mortality for a given diameter tree and pre-storm diameters that were larger than later successional species in most cases. Under the current landscape conditions, species capable of persisting indefinitely in the absence of large-scale disturbance (late-successional) had lower windthrow mortality across the range of diameters present and across the wind intensity gradient. One critical exception to this was larger diameter *Abies balsamea* and *Picea mariana*, which experienced similar mortality to shade-intolerant species. Also, *Betula papyrifera* is an ambiguous species because it is intolerant of shade, but can persist for long periods via gap-phase dynamics and had low mortality from windthrow.

Differences in mortality among canopy trees have several implications for near-boreal forest dynamics. The loss of early successional trees from the canopy due to large-scale disturbances could lead to profound shifts for the boreal ecosystem. With the observed loss of pioneer species, the propagule pool has been shifted

decidedly towards later-successional species, which is different from the case over the last 400 years, when large fires were the dominant type of disturbance. Therefore, even if the forest burns again, it may not be able to return to the historic species composition typical of central North America (dominated by *Pinus banksiana* and *Populus tremuloides*). The combination of a century of fire exclusion followed by selective removal of the remaining pioneer tree species by a large windstorm may make these forests more similar to the boreal forests of Labrador and New Brunswick in eastern Canada, as well as northern Scandinavia, where later successional species occupy a relatively large proportion of the canopy. If, as expected in a warmer climate, wind becomes a more important disturbance type in these southern boreal forests, the results presented here point to a further shift in canopy composition towards the least susceptible species, including *B. papyrifera*, *T. occidentalis*, *A. rubrum* and *F. nigra*.

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