

Intermediate disturbance in a late-successional hemlock-northern hardwood forest

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Summary

1 An old-growth mesic forest in northern Michigan, USA, experienced an unusually intense storm in July 2002. Permanent inventory plots and a 2.9-ha mapped stand allow comparison of effects of this rare disturbance with patterns of ‘baseline’ mortality.

2 Tree mortality attributable to immediate effects of the storm was of similar magnitude to mortality over the previous decade, amounting to about 9% of basal area and 7% of stem density (mean of 88 inventory plots).

3 Storm mortality differed from baseline mortality in patterns related to species and size. *Tsuga canadensis* suffered little mortality of either type. *Betula alleghaniensis* had high baseline mortality in all size classes, but very low storm mortality. *Acer* spp. and *Fagus grandifolia* showed similar overall levels of baseline and storm mortality, but storm mortality was higher for larger stems.

4 Spatial patterns of mortality differed between baseline and storm-caused disturbance, with storm mortality patterns related to composition and to substrate variation over the stand. Baseline canopy mortality was hyperdispersed at local scales, but mortality due to the storm was strongly clustered at distances up to 30 m.

5 Properties of rare, intermediate disturbances cannot be predicted by simply scaling up patterns due to frequent, less intense, events. They may have distinctive influences on community dynamics, countering trends towards dominance by shade-tolerant species, generating demographic and spatial structure in the canopy, and distinctively affecting understorey environment.

6 These results suggest that climate change may induce changes in forest ecosystems by changing disturbance patterns even when species are not close to limits of physiological tolerance. Forest management for natural regeneration may need to take the effects of rare, intermediate disturbance into account.

Key-words: *Acer saccharum*, *Betula alleghaniensis*, canopy gaps, climate change, disturbance ecology, *Fagus grandifolia*, forest management, forest succession, long-term studies

Journal of Ecology (2004) **92**, 464–476

Introduction

Patterns of canopy-tree mortality shape forest stand structure and dynamics through effects on tree regeneration and replacement. Mortality patterns are rooted in interactions among environmental disturbance factors, stand demographic and structural properties, and condition of individual trees. There is strong potential for feedback effects between disturbance patterns and stand properties; for example, stand structure both influences mortality risks for trees and, at the same time, is influenced by mortality patterns. In the absence of human influence, wind appears to be the primary

agent of canopy disturbance in mesic temperate forests of north-eastern North America (henceforth ‘northern hardwood forests’). In these forests, intensity and frequency of wind disturbance should interact with stand composition, structure and demography to shape stand structure and dynamics (Romme *et al.* 1998; Frelich & Reich 1999; Peterson 2000; Seymour *et al.* 2002).

At one end of the spectrum of wind disturbances in late-successional forests, small gaps are opened frequently by blowdown of scattered individuals or small groups of canopy trees. Studies in several stands comparable with those studied here suggest that about 5–20% of canopy trees (depending on size and species) die per decade, many of them due to windthrow, creating gaps of tens to a few hundred square metres (for example, Runkle 1982, 2000; Payette *et al.* 1990; Tyrrell

& Crow 1994; Parshall 1995; Woods 2000a, 2000b). Small gaps are most frequently filled by lateral in-growth of existing canopy trees or through release of suppressed individuals of shade-tolerant species; successful occupation by more light-demanding species is infrequent. Disturbance regimes dominated by small gaps have traditionally been associated with late-successional mesic forests, and resulting tree-replacement patterns have been implicated as producing stability of composition and structure at the stand scale (Woods 1984; Poulson & Platt 1989, 1996; Frelich & Graumlich 1994).

At the opposite extreme, rare, catastrophic blowdowns can kill > 90% of canopy trees over tens to thousands of hectares. Such events are associated, in northern hardwood-dominated regions, with tornados, down-burst thunder-storms (ranging from relatively small events to super-cell 'derecho' events covering hundreds of km²), and the most severe hurricanes, where winds can approach or exceed 200 km h⁻¹ (Foster *et al.* 1998; Peterson 2000). Such disturbances have been documented directly (Dunn *et al.* 1983; Peterson & Pickett 1995) and, because they leave persistent and long-lasting 'signatures' on the landscape (Foster *et al.* 1998), can be reconstructed from historical records and stand analysis (Canham & Loucks 1984; Frelich & Lorimer 1991; Zhang *et al.* 1999). Canopy destruction of this sort, both spatially extensive and severe in terms of mortality rate, should produce strongly cohort-structured stands at hectare scales and larger, and is likely to be important in permitting persistence of light-demanding species in the landscape (Peterson & Pickett 1995). However, in the western Great Lakes region of North America, stand-initiating blowdowns are rare, even in the time-frame of dominant tree species; estimates of expected return times range from one to several millennia (Canham & Loucks 1984; Frelich & Lorimer 1991; Zhang *et al.* 1999). As rotation periods are several times canopy-tree life expectancies of 200–300 years, it follows that, without human interactions, most of the landscape, most of the time, would be in later stages of succession, with mixed-age canopy and increasing importance of shade-tolerant species (Frelich & Lorimer 1991b).

A wide range of intermediate wind disturbances (single events killing, say, 10–50% of canopy trees in a stand, potentially opening canopy gaps of 100 s to 1000 s of square metres) remains substantially undocumented (Seymour *et al.* 2002; but see Batista & Platt 2003 for a study in a mixed hardwood forest in south-eastern USA). Such disturbance might appear as patchy but severe canopy damage, or as widely dispersed, moderate canopy damage. Events of this sort are difficult to study, as they are too infrequent for dependable occurrence in stand-monitoring studies, but not of sufficient magnitude for quantitative assessment from historical or survey records (but see Henry & Swan 1974; Foster & Boose 1992). They must be presumed to occur at frequencies greater than catastrophic events; return-times for disturbance of this magnitude, estimated for mesic forests

in north-eastern North America (Frelich & Lorimer 1991a,b; Seymour *et al.* 2002) are in the range of from one to five centuries, with higher frequencies in hurricane-prone coastal areas (Boose *et al.* 2001). Intermediate disturbances may have distinctive effects on forest patterns and processes. In addition to simple quantitative differences, intermediate disturbances may differ qualitatively from more frequent, gap-type disturbance through distinctive interaction with tree species or size, or through different spatial patterns of disturbance. For example, stand simulations (Pacala *et al.* 1996) and long-term plot studies (Woods 2000a, 2000b) suggest that, under a pure gap-type disturbance regime, the most shade-tolerant species (here, *Tsuga canadensis* and *Fagus grandifolia*) may eventually attain complete canopy dominance. However, this may take several generations of canopy trees; intervening intermediate disturbances, if they created relatively large canopy openings, might permit persistence of less-tolerant species, as has been suggested for *Betula alleghaniensis* (Woods 2000a, 2000b) without completely resetting the successional clock.

On 21 July 2002, an unusually intense, local thunder-storm, generating winds of approximately 150 km h⁻¹, passed over a remnant of original, late-successional forest in northern Michigan. Long-term, permanent-plot monitoring (Woods 2000b) at the site permits assessment of the effects of the storm and comparison with 'baseline' mortality patterns over the previous decade. I use data on direct, storm-caused mortality, mortality patterns over the previous decade, and multidecade compositional trends to address the following questions:

1. Are spatial patterns of storm-caused tree mortality different from patterns of baseline (i.e. small-gap-dominated) mortality over the previous decade?
2. Do species and size effects on chance of death differ between storm mortality and baseline mortality?
3. What are the implications of observed patterns for long-term stand dynamics?

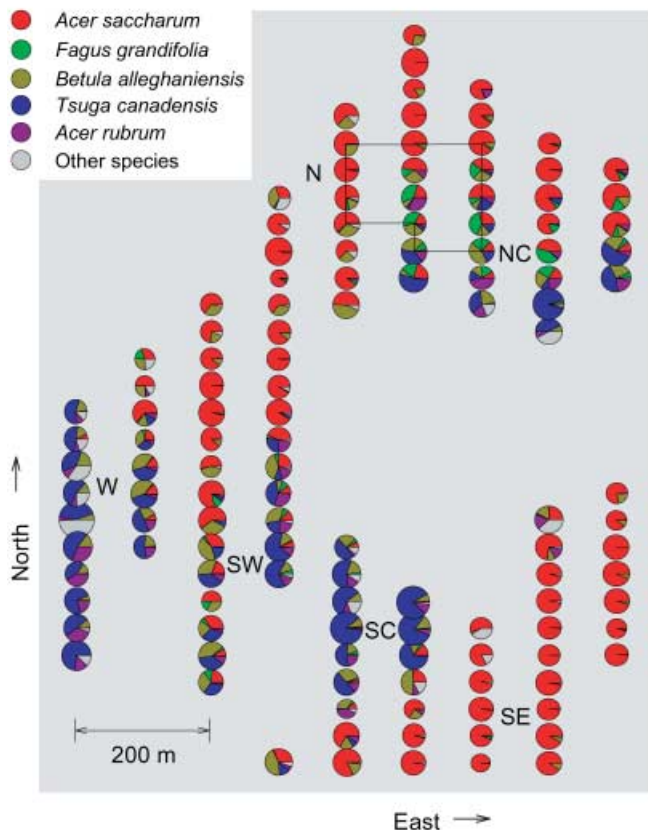
Materials and methods

STUDY SITE AND BASELINE DATA

The 100-ha Dukes Research Natural Area (RNA) is part of the Hiawatha National Forest in Marquette County, Michigan, USA. At 46° 25'N, 87° 10' W, it is 12 km from the shore of Lake Superior at an elevation of about 330 m (Lake Superior mean surface elevation is 183 m) (Fig. 1). Climate is cool-temperate and continental (although influenced by the proximity of Lake Superior). Catastrophic, stand-initiating windstorms are thought to be very infrequent in this area (Frelich & Lorimer 1991a,b; Peterson 2000), with return times in excess of 2000 years.

Anecdotal reports suggest that a few large *Pinus strobus* may have been removed from the Dukes site *c.* 100 years ago, but there is no other evidence or suggestion of logging within the RNA. Upland stands are uneven-aged, with tree ages exceeding 300 years (K. D. Woods,

(a) 1992 Composition



(b) Mortality

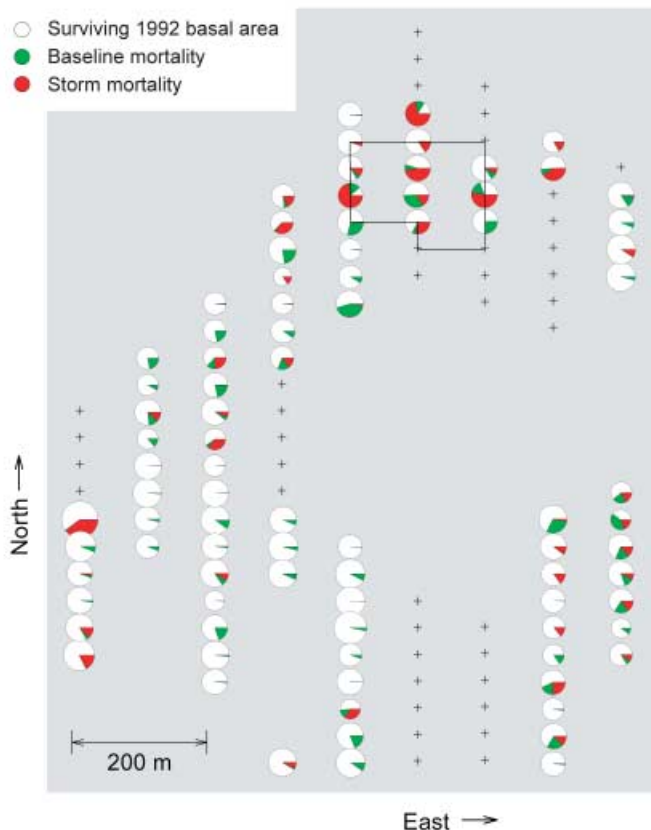


Fig. 1 Overall composition and mortality patterns. Blue star in inset map shows location of the Dukes RNA study site within the Upper Great Lakes region of Canada and the USA. (a) Each upland forest plot is represented on stand-map by a pie graph with total area proportional to 1992 total basal area for the plot (range = 21.6–86.3 m² ha⁻¹). ‘Other species’ includes *Abies balsamea*, *Fraxinus americana*, *Fraxinus nigra*, *Ostrya virginiana*, *Picea glauca*, *Pinus strobus*, *Quercus rubra*, *Tilia americana*, *Thuja occidentalis* and *Ulmus americana*. The mapped stand in the northern portion of the RNA is outlined. ‘Stand sectors’ are indicated by letter codes. (b) Plots re-measured after the 2002 storm are shown as pie graphs, as in (a), with area proportional to 1992 basal area; coloured slices represent basal area lost to either ‘baseline’ mortality, 1992–2002, or to July 2002 storm. Small crosses are plots that were not re-measured following the storm.

unpublished data). Compositionally, stands are dominated by shade-tolerant species (*Tsuga canadensis*, *Fagus grandifolia*, *Acer saccharum*), with significant representation of two less tolerant species (*Betula alleghaniensis*, *Acer rubrum*).

A grid of 240 circular 0.2-acre (809 m²) permanent inventory plots (about 130 of these are in upland, hemlock-hardwood forests; the remainder are in wetland forests) was established over the RNA in 1935, and these plots have been re-measured several times, with regular re-measurement on a staggered 5-year cycle since 1989. Woods (2000b) summarizes compositional patterns (Fig. 1a) and long-term trends for upland stands. From 1935 to the 1990s *Fagus grandifolia* increased dramatically in basal area (particularly in the NC sector, Fig. 1a), *Acer saccharum* saw modest increases, and *Betula*

alleghaniensis showed large declines throughout the stand. Total basal area increased slightly on average. There is no evidence, prior to the 2002 storm, of disturbance other than scattered, small gaps.

Soil properties measured for the top 20 cm of mineral soil, covary with composition (Woods 2000b). Areas dominated by *Acer saccharum* (N and SE sectors, Fig. 1a) have higher Ca concentrations and pH, and areas with significant *Fagus grandifolia* (particularly the NC sector) have pronounced hard-pan development at around 25–30 cm depth. *Tsuga* dominance (W and SC) is correlated with strong development of spodosols and a mor humus layer.

In 1993–94, I created a stem map for a 2.9-ha area (Figs 1 and 2), mapping all stems > 2 cm d.b.h. Independent re-measurements suggest that > 90% of stems

are mapped with < 1 m error, with maximum locational error of about 1.5 m. All stems were re-measured in 1999, with detailed notes on mortality. For analysis of pre-storm mortality patterns and rates I established a 1993 'baseline'. For portions of the mapped stand established in 1994, I used condition of dead stems to judge whether trees were alive in 1993, and used 1994–99 growth to extrapolate 1993 d.b.h. (in most cases this differed from 1994 to 1995 measurements by less than 0.2 cm, which is similar to measurement error).

STORM-EFFECTS DATA

Beginning about 3 weeks after the 21 July 2002 storm, we re-measured 88 of the 0.2-acre inventory plots (Fig. 1b). Last measured in 1997, these plots were distributed across the upland areas of the RNA, and represent the full range of composition and substrate variation in the stand. All mortality since 1997 was recorded, the nature of mortality (tip-up, break, or dead standing) was noted, and approximate year of death estimated from the condition of the tree. Trees killed in the 21 July storm were easily identified, as they retained green, unwilted leaves, and direction of fall was strongly constrained to ESE ($110 \pm 20^\circ$ E of N); it is possible that some trees blown down within a week or two prior to the storm were misclassified as storm-caused mortality, but trees dying earlier in the 2002 growing season were generally recognizable by wilted or browned leaves and, often, significant differences in direction of fall.

For storm-affected trees, 'mortality' was defined conservatively; only trees completely broken below the lowest branch, or fully uprooted (trunks resting directly on the ground or on other broken or fully uprooted trees) were recorded as killed. Many trees were damaged, either by loss of large proportions of crown, or by partial uprooting. While even fully uprooted trees may maintain some root connections, partially leafing out in subsequent growing seasons, past observations in the same stand suggest that their death is nearly certain within 1–2 years (informal observations in July 2003 suggest that less than one-third of fully uprooted trees produced foliage in that growing season). Analyses presented here do not take damaged trees into account, and so address only what Everham & Brokaw (1996) term 'compositional damage', underestimating eventual total canopy destruction ('structural damage' of Everham & Brokaw). Further, some damaged trees are likely to die within the next few years (Everham & Brokaw 1996). Consequently, assessments of direct and indirect effects of the 2002 storm are certainly underestimates.

All stems > 15 cm d.b.h. in the 2.9-ha mapped stand (about 900 stems) were censused in August 2002, but not re-measured. The 15-cm threshold was partly due to time constraints, but also recognizes that smaller trees are never in the canopy in this stand (typically, canopy trees are > 30 cm d.b.h.). All mortality since the 1999 measurement was recorded and assigned to approximate year of death, with information about the nature

of death and condition of the tree. Mortality resulting from the 21 July storm was distinguished as described above. In addition, I assessed whether storm-downed trees had been broken or uprooted. 'Secondary mortality', due to falling trees (rather than direct effects of wind) was recognized where possible. This category was assigned conservatively, as it is often impossible to ascertain unambiguously. Most trees in this category were subcanopy trees with shattered, sound boles and clearly associated with (usually beneath) a larger fallen tree (no such breakage was otherwise observed in subcanopy trees with sound boles). In some cases, larger or tipped-up trees with extensive scraping damage associated with other fallen trees were assigned to the secondary mortality category as well. While this assignment retains some ambiguity, errors of omission (i.e. failure to appropriately assign trees to secondary mortality category) are probably more frequent than errors of commission. I also recorded trees with heavy damage (partially uprooted or > 50% crown loss by subjective judgement).

ANALYSES

For purposes of analysis of spatial variation across the entire RNA, plots were assigned to six stand sectors based on compositional similarity and proximity (Fig. 1a, Table 1; Woods 2000b). I used logistic regression to assess the influence of species, stem diameter, and their interaction on the risk of mortality to individual trees within the mapped stand and in inventory plots. Separate analyses allowed comparison of storm-caused and baseline mortality. I added stand sector as a categorical independent variable to analyses of mortality in the 88 inventory plots measured in 2002. Contingency table analyses were used for more detailed assessment of effects of species and stand sector and their interactions. Influences of storm, stand sector, initial composition and total basal area on plot-level mortality patterns were explored using analysis of (co)variance and χ^2 analyses of two-way classification tables.

I used Ripley's-K analyses, with edge-correction, to compare spatial patterns of baseline and storm-caused mortality in the mapped stand (about 0.4 ha of the mapped stand was dropped as this analysis calls for a regular rectangular or circular map). Ripley's-K analysis permits simultaneous testing for spatial contagion at all scales up to a distance equal to the shorter dimension of the stand (here 120 m).

Results

MAPPED STAND

Total basal area (for stems > 15 cm d.b.h.) in the 2.9-ha mapped stand decreased from 35.9 m² ha⁻¹ in 1993 to 34.7 m² ha⁻¹ in 1999. From 1993 to 2002 prior to the storm, total mortality, including pre-storm mortality noted in the 2002 survey (henceforth 'baseline mortality'),

Table 1 General stand properties and mortality patterns

Stand sector	Number of plots*	Basal area of dominant species (1992 for plots, 1999 for mapped stand)						Storm mortality \pm SD ($m^2 ha^{-1}$)	Baseline mortality \pm SD ($m^2 ha^{-1}$)	1997 basal area \pm SD ($m^2 ha^{-1}$)	1992 basal area \pm SD ($m^2 ha^{-1}$)
		<i>Acer rubrum</i> ($m^2 ha^{-1}$)	<i>Acer saccharum</i> ($m^2 ha^{-1}$)	<i>Betula alleghaniensis</i> ($m^2 ha^{-1}$)	<i>Fagus grandifolia</i> ($m^2 ha^{-1}$)	<i>Tsuga canadensis</i> ($m^2 ha^{-1}$)					
Inventory plots											
W	14	9.5	1.7	8.8	0.2	27.4	4.2 \pm 2.2	2.3 \pm 2.1	50.1 \pm 16.5	49.8 \pm 15.3	
SC	8	5.9	1.2	8.6	1.1	26.8	1.2 \pm 2.8	2.7 \pm 1.1	48.1 \pm 13.8	47.1 \pm 13.8	
SW	13	3.0	14.2	12.1	2.3	11.6	0.7 \pm 2.3	2.4 \pm 1.1	48.9 \pm 9.2	47.2 \pm 9.2	
NC	11	4.8	13.7	9.4	8.0	8.4	9.2 \pm 1.1	5.1 \pm 1.1	46.6 \pm 8.1	47.7 \pm 7.6	
SE	18	1.0	33.2	2.6	0.1	0.2	3.4 \pm 0.9	4.8 \pm 0.9	39.1 \pm 7.6	38.1 \pm 8.2	
N	24	0.1	31.2	4.6	0.6	0.1	8.0 \pm 1.5	4.5 \pm 1.1	38.2 \pm 6.8	37.8 \pm 7.0	
Mapped stand	–	2.9	19.0	5.1	7.8	2.7	8.6	4.8	34.7	35.8	

*Including inventory plots re-measured in 2002 only; see Fig. 1(b).

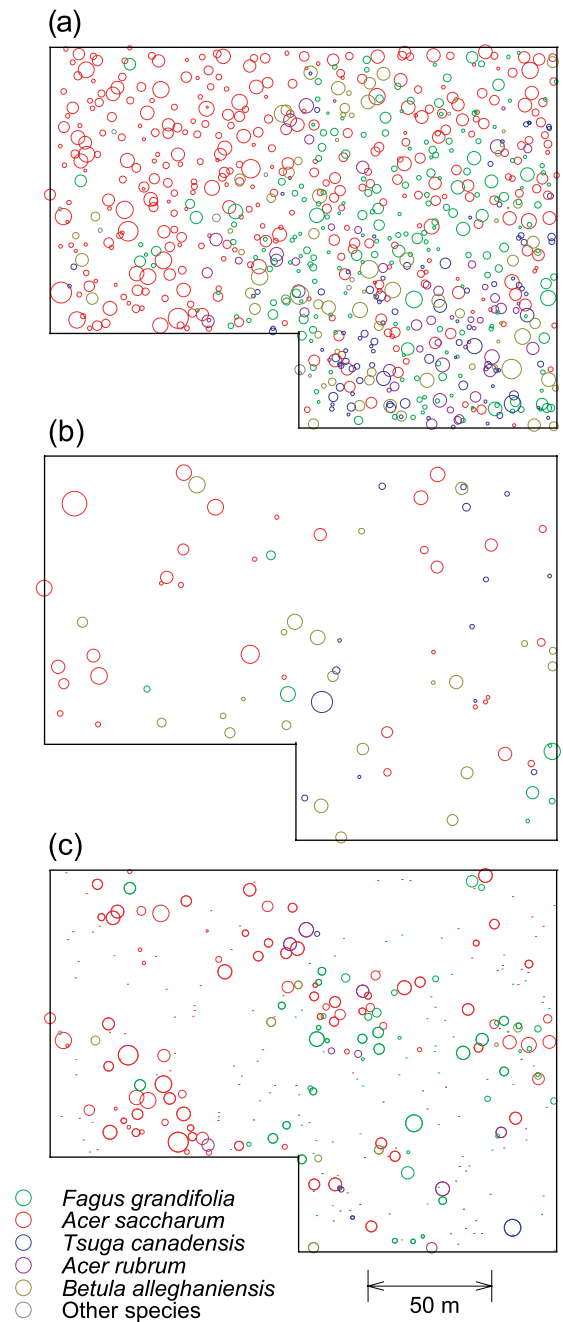


Fig. 2 2.9-ha mapped stand within Dukes RNA. (a) All living stems > 15 cm d.b.h. immediately before July 2002 storm are represented by circles with area proportional to basal area of stem in 1999. ‘Other species’ includes *Abies balsamea*, *Ostrya virginiana*, *Picea glauca* and *Quercus rubra*. (b) Stems > 15 cm d.b.h. that died from 1993 to 2002 prior to storm, symbols as in (a). (c) Stems > 15 cm d.b.h. killed by July 2002 storm.

amounted to 4.8 $m^2 ha^{-1}$ (based on 1993 d.b.h.), or about 13% of 1993 basal area. Total stem density in 1993 was 292.8 ha^{-1} , and baseline mortality was 27.1 ha^{-1} , amounting to a mortality rate of about 1.0% $year^{-1}$ (approximate because exact span of period of record is variable or imprecise). In 1999, trees 15–40 cm d.b.h. were hyperdispersed (i.e. distances between near neighbours greater than expected under random distribution) at all scales

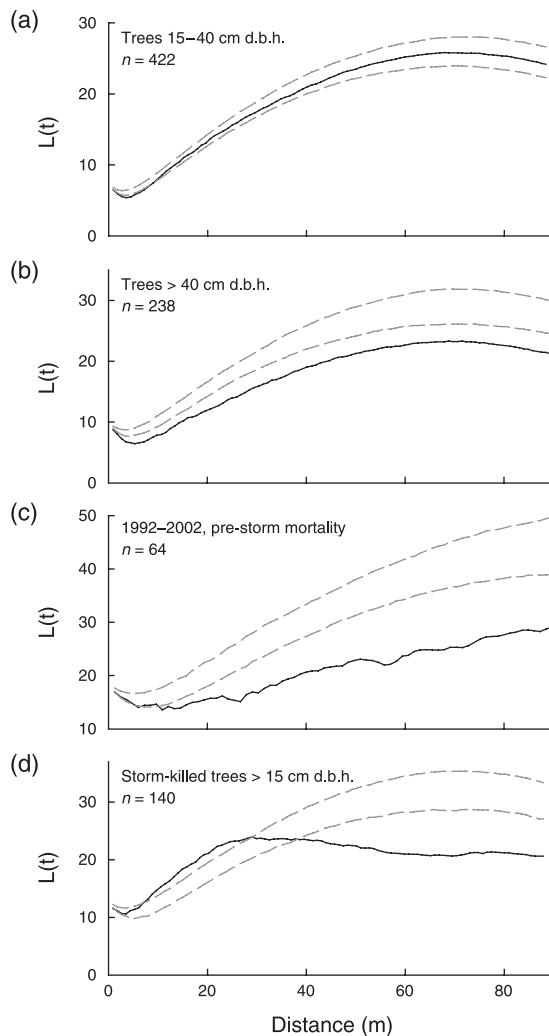


Fig. 3 Results of Ripley's-K analyses. Solid lines show calculated values for $L(t)$ for all distances analysed, while dashed lines indicate 95% confidence envelope for random distribution. Values above the envelope indicate clustering, while values below envelope indicate hyperdispersion for (a) subcanopy and small canopy trees (15–40 cm d.b.h.), (b) canopy dominants (> 40 cm d.b.h.), (c) baseline mortality 1992–2002, and (d) trees killed by July 2002 storm.

< 10 m and apparently randomly dispersed at larger distances. Trees > 40 cm d.b.h. were hyperdispersed at all scales (Fig. 3). Storm-caused direct mortality averaged $8.5 \text{ m}^2 \text{ ha}^{-1}$ (based on 1999 d.b.h.), or 24.5% of total 1999 basal area, and amounted to 18.8% of stems alive in 1999, or 19.5% of those alive immediately before the storm.

Baseline mortality was not uniform spatially, or across species or size classes. Over all species, larger stems were subject to greater risk of mortality (Fig. 4, $P < 0.001$ for χ^2 test using 10-cm d.b.h. classes). For stems > 45 cm d.b.h., 1993 density was 81.8 ha^{-1} and baseline mortality 12.4 ha^{-1} or, assuming constant mortality rate, about 1.6% year⁻¹. For stems 15–45 cm d.b.h. in 1993, density was 211.0 ha^{-1} , and baseline mortality was 14.8 ha^{-1} or about 0.8% year⁻¹. Mortality for *Betula*

alleghaniensis, analysed separately, showed no size-dependency. Baseline mortality was hyperdispersed at all scales above 10 m (Ripley's-K analysis, Figs 3 and 2b).

Storm-caused mortality showed different patterns with respect to space, species and stem size. Again, mortality was higher for larger size classes (Fig. 4, $P < 0.001$ for χ^2 test over 10-cm d.b.h. classes). 'Primary' mortality was much lower for small trees; the majority of dead trees < 35 cm d.b.h. were broken by other trees falling on them. Size-related storm mortality was similar for *Acer saccharum* and *Fagus*, and these species constituted the large majority of dead stems, especially in smaller size classes. *Betula* and *Tsuga* display strikingly different patterns (Fig. 4). No *Betula* > 55 cm d.b.h. were killed, and mortality in the smallest size classes was entirely secondary; only four (of 72) *Betula* trees were directly broken or uprooted. Of 93 *Tsuga*, only five were killed. It is difficult to interpret patterns for the fifth most common species, *Acer rubrum*, due to small sample size. Storm-caused mortality was significantly clustered (Ripley's-K analysis, $P = 0.05$) at scales of 6–28 m, and hyperdispersed only at scales > 37 m (Figs 2c and 3).

No results changed when severely damaged (partially tipped-up, or with > 50% canopy loss) trees were included with storm-killed trees.

PERMANENT INVENTORY PLOTS

Inventory plot basal area, for the 1992–94 re-measurement cycle, averaged $42.5 \text{ m}^2 \text{ ha}^{-1}$ (range 21.6 – $86.3 \text{ m}^2 \text{ ha}^{-1}$). Systematic differences are associated with composition and area within the stand (Fig. 1a, Woods 2000b); *Acer*-dominated areas average about 30% lower basal area than *Tsuga*-dominated areas. Two of the six stand sectors (Fig. 1a; SE and N) are *Acer*-dominated; two (W and SC) have high *Tsuga* dominance, and two (NC and SW) are mixed hardwood-hemlock with significant *Fagus*. This subdivision of the stand is crude; compositional variation is continuous and some plots in each group depart from group 'norms'. However, 'stand sector' may be treated as a complex variable incorporating site properties, community composition and (potentially) variation in storm intensity. *Betula* and *Acer rubrum* are present throughout the stand, but more abundant in mixed and *Tsuga* areas.

Over the entire stand, baseline mortality was about 1% of basal area per year, and total baseline and storm-caused mortality were similar, each amounting to about 9% of initial basal area (Table 1). In density terms, total baseline mortality was 7% of 1992 live stems (about 0.8% per year), and storm-caused mortality was about 6% of pre-storm living stems. Storm mortality and baseline mortality had different size-dependent effects. Baseline mortality rates were statistically similar for trees > 35 cm d.b.h. (most trees of this size are in the canopy) and trees 5–35 cm d.b.h. (mostly subcanopy). Storm-caused mortality was significantly higher for

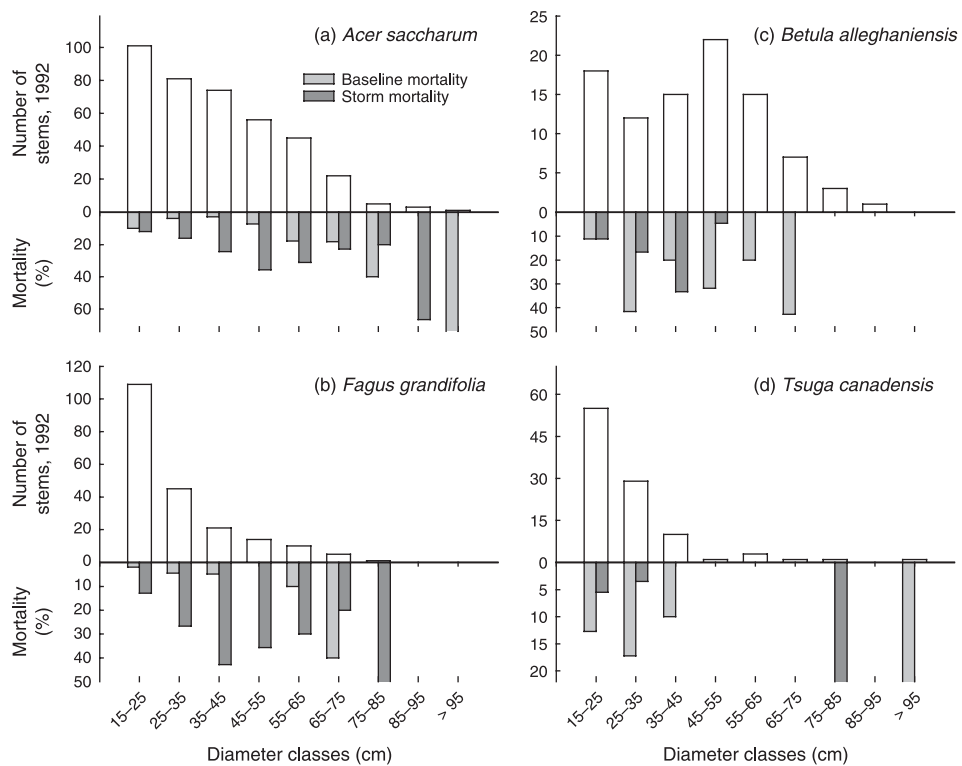


Fig. 4 Size structure, by species, for population and for baseline and storm-caused mortality, in 2.9-ha mapped stand. Ascending bars show distribution of live trees in 10-cm d.b.h. classes in 1992. Descending bars show mortality as percentage of size class; lighter shading indicates baseline (1992–2002) mortality, darker shading indicates mortality due to July 2002 storm (open-ended bars extend beyond graphed range).

Table 2 Effects of stand sector, species and d.b.h. on mortality in inventory plots. Where trends are given for particular sector, species or size class, overall effects of that category are significant (Pearson χ^2 for two-way frequency table, $P = 0.01$)

Category of effect	Class of mortality	
	Baseline (1992–2002)	Storm (July 2002)
Stand sector**	<i>SE</i> ↑ SC, SW ↓*	<i>NC</i> , <i>N</i> , <i>SE</i> ↑ SC, SW, <i>W</i> ↓
Species***	<i>Beal</i> , <i>Acsa</i> ↑ <i>Acru</i> , <i>Fagr</i> , <i>Tsca</i> ↓ (not significant)	<i>Acsa</i> , <i>Other</i> ↑ <i>Tsca</i> , <i>Beal</i> ↓
d.b.h. class (1992)		
d.b.h. class (1997)		d.b.h. > 45 cm ↑ d.b.h. < 25 cm ↓

*Plain text: value for sector, species or d.b.h. class departs from expectation by 1–2 standard deviations; italics, by 2–4 standard deviations; bold, by > 4 standard deviations. Arrows indicate direction of difference from expectation.

**See Fig. 1(a) and Table 1 for sector locations and properties.

*** *Acru* = *Acer rubrum*; *Acsa* = *Acer saccharum*; *Beal* = *Betula alleghaniensis*; *Fagr* = *Fagus grandifolia*; *Tsca* = *Tsuga canadensis*; other species listed in caption for Fig. 1.

canopy trees than for subcanopy stems (χ^2 test, $P < 0.001$). Chi-squared tests showed that stand sector, species and diameter all had highly significant effects on chance of storm-caused mortality (Table 2) (results of logistic regressions were consistent). Only stand sector and species were significant variables influencing likelihood of mortality during the baseline period.

Baseline mortality for *Betula* was high compared with mortality over all species (Tables 1 and 2), while

Fagus had significantly lower baseline mortality. Species differences were more complex for storm mortality; *Betula* and *Tsuga* manifested lower mortality rates over the stand, while *Fagus* and *Acer saccharum* mortality was higher. Statistical assessments were not possible for minor species, but storm mortality was particularly high for the few large canopy trees of *Pinus strobus*, accounting for loss of about 30% of basal area in one plot at the western edge of the stand.

While baseline mortality varied significantly among stand sectors, only the high mortality in the SE (*Acer*-dominated) sector departed from overall mortality rates by more than two standardized deviates (Table 2). Spatial variation in storm mortality was more pronounced (Fig. 1b, Table 2). N (*Acer*-dominated) and NC (mixed) sections experienced relatively high mortality, while mortality in SC (*Tsuga*-dominated) and SW (mixed) sections was lower. In sector W (*Tsuga*-dominated) storm mortality was predominantly emergent *Pinus strobus*; with exclusion of *Pinus* from analysis, mortality in this section is also low.

Chi-squared tests constructed separately for species and diameter effects within each stand sector and for stand sector and diameter effects within each species suggested several interactions among influences on mortality risks. Species effects on baseline mortality were not significant in *Tsuga*-dominated stand sectors (W and SC), or in the strongly *Acer*-dominated SE sector. Diameter class did not, in general, influence baseline mortality, but the relatively few larger individuals of *Fagus* had higher than expected mortality. While storm mortality was, overall, much higher for larger diameter classes, this was not the case for sectors SC and SW where general storm mortality was also low. In analyses by species, diameter effects on storm mortality were strong for *Acer* and *Fagus*, but were not significant for *Betula* and *Tsuga*.

Discussion

In mature, northern-hardwood forests, the immediate effects of intermediate wind disturbances are not predicted by simply magnifying the effects of 'baseline' gap-scale disturbances (Romme *et al.* 1998). Baseline mortality from 1992 to 2002 occurred at rates comparable with those documented in several previous studies. The single storm-disturbance of 21 July 2002 caused canopy mortality comparable in magnitude with one to three decades of baseline mortality. In addition, spatial patterns of mortality differed, as did the relationships between mortality and the size and species of trees. Consequently, community and population dynamics following such events are likely to differ from those observed in the context of smaller, more frequent gap-type disturbances. These results reflect only immediate post-disturbance mortality; distinctiveness of storm-caused mortality patterns may be reduced or magnified by delayed, storm-linked mortality (Everham & Brokaw 1996).

DIFFERENCES IN EFFECT OF TREE SIZE

Sub-canopy stems were less vulnerable to storm-caused mortality compared with baseline mortality. Batista & Platt (2003) observed similar patterns in a south-eastern USA mixed-hardwood forest (with substantially different species composition) following a major hurricane, in a study that included both immediate and delayed

effects of the storm. At Dukess, over half of baseline mortality of subcanopy stems was recorded as 'standing dead' (an underestimate, as some dead stems surely fell prior to plot re-census), suggesting death due to physiological or biological stresses rather than structural damage; shade suppression is a likely factor in many of these deaths. Sub-canopy stems killed by the storm were destroyed predominantly by falling canopy trees. Many additional small trees were damaged severely by falling trees, some pinned to the ground. However, many undamaged saplings remain as candidates for canopy recruitment, even in areas with intense storm damage. Foster & Boose (1992) note that stand-level damage following a 1938 hurricane in New England northern-hardwood forests increased rapidly with canopy height and was positively correlated with stem size and wind damage; similar patterns have been reported for a variety of forest types (Everham & Brokaw 1996).

DIFFERENCES IN SPATIAL PATTERN OF DISTURBANCE

In the 2.9-ha mapped stand, hyperdispersed baseline mortality produced small canopy gaps. Over 90% of gaps measured during this period had areas less than 80 m² (K. D. Woods, unpublished data), and gap-size distribution was similar to that described by Runkle (1981, 1982) for a range of eastern US forests. Storm-killed trees were clustered at scales up to about 30 m, creating canopy openings of several hundred m². Permanent inventory plots (diameter 32 m) do not permit quantitative assessment of gap formation at this scale, but observations suggest that storm-caused gaps typically involved several trees and were larger than baseline gaps. This difference may be due to 'secondary' mortality during the storm, due to direct impact by trees falling on others, or to increased exposure of trees immediately adjacent to downed trees. At least 20% of trees dying in the decade before the storm died standing (K. D. Woods, unpublished data), reducing the likelihood of subsequent, secondary mortality of adjacent trees.

A 30-m gap in a forest canopy 30 m high exposes, from gap centre, about 50° of sky compared with about 20° for a large single-tree gap of 10 m diameter; corresponding duration of exposure to direct sunlight at the forest floor is more than doubled for the larger gap. Single-tree gaps are typically filled within one to a few decades (Runkle 1982; K. D. Woods, unpublished data) by ingrowth of suppressed saplings and lateral growth of neighbour trees. In gaps as large as 30 m, canopy closure must be primarily through ingrowth of seedlings or saplings; where large suppressed saplings are lacking, this could take several decades, further increasing the likelihood of canopy entry for less shade-tolerant species. Increased insolation alters temperature and moisture regimes in large gaps (Runkle 1982); 2 weeks after the storm, understory vegetation in large gaps (particularly *Acer saccharum* seedlings and *Dryopteris* spp.) displayed substantial leaf mortality, apparently from heat stress.

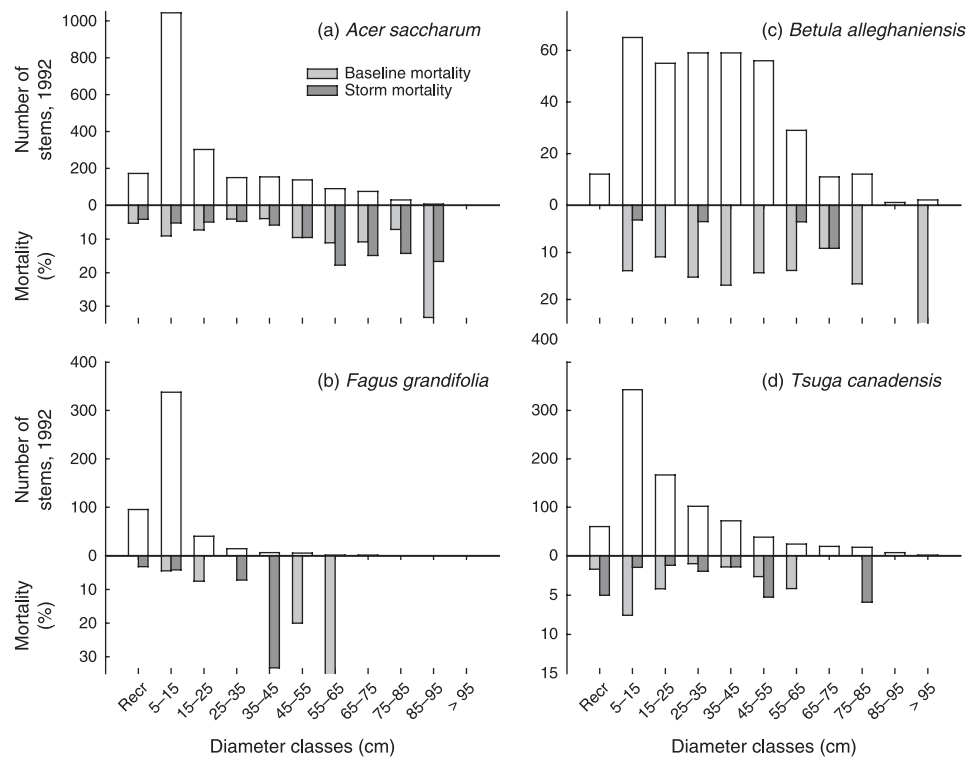


Fig. 5 Size structure, by species, for population and for baseline and storm-caused mortality for all inventory plots. ‘Recr’ category includes stems reaching 5 cm between 1992 and 2002. See Fig. 4 for further explanation.

DIFFERENCES IN MORTALITY PATTERNS AMONG SPECIES

Storm-caused mortality was distributed differently among species as compared with baseline mortality (Fig. 5). Most notably, while *Betula* constituted a disproportionate amount of baseline mortality throughout the stand, *Betula* mortality due to the storm was very low in comparison with other hardwoods (3.7% for *Betula* > 35 cm d.b.h. in inventory plots, compared with 9.4% for other species combined). Storm-caused *Betula* deaths were primarily small stems, many of which appeared to have been shattered by falling canopy trees. In contrast, *Betula* populations declined substantially in the Dukes stand over recent decades (Woods 2000b), possibly in a successional process; mortality patterns and size distributions are consistent with a *Betula* population dominated by one or a few ageing cohorts, perhaps dating to some major disturbance. Most baseline *Betula* deaths were recorded as ‘died standing’ (K. D. Woods, unpublished data), consistent with mortality due to physiological stress. Statistical models (Canham *et al.* 2001), fitted for a catastrophic blowdown in old-growth northern hardwood forests in northern New York, suggest that canopy *Betula* have lower windthrow vulnerability than any other species, except for *Acer saccharum* at storm intensities more extreme than experienced at Dukes; *Betula* is unique in this study in that large trees do not have higher windthrow probability than mid-size canopy individuals. Differences in structural strength may be implicated in species

differences; *Betula*, in some size classes, has wider-spreading roots than *Acer saccharum* (Tubbs 1977), and showed relatively low canopy breakage (compared with *Acer* and *Fagus*) in a severe ice-storm (Hooper *et al.* 2001). Resistance to windthrow or breakage might be adaptive in a species dependent on regeneration in large openings following severe disturbance.

Tsuga mortality was low in both the baseline period and the storm. Canham *et al.* (2001) found large *Tsuga* to be more vulnerable to blowdown than other species, but their model was fitted for a more severe storm. *Tsuga* is not a frequent canopy tree (and is even less frequent in large size-classes) in the portions of the Dukes stand where windthrow was most frequent; low mortality may be due in part to variation in storm intensity, which cannot be directly assessed here.

For the shade-tolerant hardwoods, *Fagus* and *Acer saccharum*, total baseline and storm-caused mortality were similar, but storm-caused mortality was more concentrated in larger size classes (Fig. 5). However, the *Fagus* population is concentrated in portions of the stand where general blowdown intensity was highest. It is difficult to assess whether this pattern is due to local site effects (particularly, a well-developed hard-pan), higher local wind-speeds, or higher intrinsic vulnerability of *Fagus* to high wind.

Among minor species, *Pinus strobus* showed particularly distinctive response to the storm. No mortality was observed among a small number of canopy individuals during the baseline period, but 50% were blown down during the storm. All *Pinus* in the upland forests

at Dukes were emergent, with maximum heights approaching 40 m. Stands with *P. strobus* were also particularly vulnerable to hurricane damage in Massachusetts (Foster & Boose 1992).

VARIATION IN STORM DAMAGE OVER THE STAND

Over the entire study area, variation in storm-caused mortality is correlated with canopy composition and substrate. Storm mortality was generally highest in the north-central part of the stand (Fig. 1b), where beech is most abundant and where there is a well-developed, shallow hardpan. The distribution of beech may be related to inhibited drainage due to the hardpan (Woods 2000b). Consequent shallow rooting may also increase vulnerability to windthrow; most windthrows in this area were tip-ups, typically with comparatively large, thin root-plates (occasionally, several trees were carried on a single tip-up root-plate). Damage was also relatively high in some strongly *Acer saccharum*-dominated areas (SE and NW; Fig. 1b) where hardpans are present but variable. Damage was comparatively light in areas with high *Tsuga* basal area (W and SC sectors; Fig. 1b); most of the basal area loss was due to mortality of emergent *Pinus*.

These patterns suggest that: (i) hardwood-dominated canopy may be more susceptible to wind damage; and (ii) reduced rooting depth may lead to increased damage in intense windstorms. However, it is impossible to reject the possibility that variation in damage across the stand was simply a result of differences in wind intensity or demographically related variation in vulnerability to windthrow (Peterson 2000). While variation in within-storm windspeed at relevant scales (tens to a few hundreds of metres) cannot be assessed from direct measurement in comparable storms, it could be a critical factor in shaping patterns of wind damage. Differential effects of terrain on windspeed (Foster & Boose 1992), however, are likely to be minimal at the Dukes site; slopes are very gentle and the entire study area varies in elevation by less than 10 m.

Within the 2.9-ha mapped stand, substrate properties are relatively uniform. Windthrow from the 2002 storm, however, is strongly patterned (by contrast, baseline mortality is spatially random). A modest compositional trend across the mapped stand (SE to NW) appears unrelated to windthrow patterns. Here, spatial structure of storm mortality may be due to: (i) variation in wind intensity; (ii) spatial patterns in canopy vulnerability to windthrow due, for example, to stem age or stand history; or (iii) feedback effects resulting, for example, from increased risk of blowdown for canopy trees immediately down-wind of initial blowdown. Intense blowdown appears to occur in diagonal bands across the mapped stand; while the area is too small to allow rigorous assessment of this pattern, the trend is consistent with wind direction and direction of fall of most trees (approximately ESE). This pattern is consistent

with at least the first and third of the hypotheses enumerated above.

IMPLICATIONS FOR STAND DYNAMICS AND INTERPRETATION OF STAND HISTORY

Directional change in stand composition over the previous six decades, most notably declines in *Betula* and increases in *Fagus*, may be successional (Woods 2000b). Multi-decade trends in comparable forests (Woods 2000a,b) and simulation models (Pacala *et al.* 1996) suggest gradually increasing dominance by the most shade-tolerant species (*Fagus* and *Tsuga*) under a regime of diffuse, small-gap mortality (comparable with the baseline period in this study). While the Dukes stand appears to have been free of stand-initiating disturbance for at least several centuries, these trends suggest that current frequencies of *Betula* and other intolerant or mid-tolerant species (particularly *Acer rubrum*) are due to more recent intermediate disturbance.

While events comparable with the 2002 storm may tend to counter the successional replacement of *Betula* and other species in late-successional northern hardwoods, this is not necessarily a general model. Everham & Brokaw (1996) suggest that post-disturbance dynamics may depend on whether canopy re-establishment is primarily *via* regrowth of surviving trees (including resprouting from stumps or roots), establishment of new seedlings in gaps, or release of suppressed, subcanopy stems. While lateral growth of surviving trees can fill small gaps within a few years, storm-caused gaps at Dukes are too large for lateral closure. Root- or stump-sprouts can be produced by several of the hardwood species at Dukes, but have been observed only very rarely in the c. 100 gaps produced by canopy tree deaths since current studies began in 1989. *Fagus* can be a prolific producer of root-sprouts, but relative importance of seedlings and root-sprouts shows great geographical variation (Ward 1961; Held 1983), and sprouts have been observed only rarely since 1989 in the Dukes stand (K. D. Woods, unpublished data).

Released saplings and subcanopy trees can dominate canopy openings, potentially to the exclusion of new seedling establishment, thus preventing establishment of new seedlings of less tolerant species. Webb (1989) and Webb & Scanga (2001) report such a scenario following wind disturbance in a Minnesota USA forest, suggesting that wind disturbance might, in fact, advance successional trends by removing early or mid-successional canopy species that are replaced by released saplings. A comparable scenario may apply in a small portion of the Dukes stand, where emergent *Pinus strobus* suffered particularly high mortality and are likely to be replaced by subcanopy *Tsuga*, but parallels between the Dukes blowdown and the Minnesota study are limited. At the Dukes stand, canopy mortality was highest for shade-tolerant *Fagus* and *Acer saccharum*. Storm-caused gaps were much smaller (primarily single-tree gaps) in the Minnesota study and did not form light-gaps at the

forest floor. Surviving subcanopy individuals are present in the large gaps formed at the Dukes stand, but they do not form a closed stratum, and the forest floor experienced sustained high light intensity (evidenced by extensive light-induced damage to foliage of herbaceous species and small seedlings).

The storm-caused gaps at the Dukes stand, then, may be well suited for seedling establishment of less shade-tolerant species. Because storm-caused mortality was spatially contagious, gaps are much larger than those typically created by baseline, and large gaps should favour seedlings of light-demanding species. Large tip-up mounds and abundant rotting logs may provide appropriate microsite conditions for seedling establishment. Patchy, intermediate disturbance in mesic, northern-hardwood forests could particularly benefit species of intermediate shade-tolerance, here *Betula alleghaniensis* (Peterson & Pickett 1995; Webster & Lorimer 2002), and perhaps *Acer rubrum*. Batista & Platt (2003) report greatly increased recruitment of shade-intolerant canopy species (particularly *Liquidambar styraciflua* and *Pinus glabra*) following hurricane disturbance, with mortality comparable with that caused by the Dukes storm, in a Florida, USA, forest.

Seedling regeneration in the large gaps caused by the storm may generate long-lasting demographic and spatial structure in the form of small, even-aged patches of canopy trees (Henry & Swan 1974). There is some evidence that existing *Betula* in old-growth stands are cohort-structured (K. D. Woods, unpublished data; Willis & Coffman 1975), perhaps showing the signature of past intermediate disturbances. Cook (2000) reports a parallel cohort structuring of *Quercus rubra* canopy stems in an *Acer saccharum*-dominated forest in Wisconsin, USA, and attributes the pattern to a prehistoric 'moderately intense' wind disturbance. Trees in even-aged patches may become simultaneously vulnerable to blowdown, thus propagating and reinforcing the patchy disturbance pattern. Parshall (1995) documented canopy openings on a similar scale through tree-ring-based reconstruction of disturbance history for a similar stand (although lacking *Fagus*) in northern Michigan. He attributes mortality, in this instance, to severe drought in the 1930s, but wind as a proximal factor is not excluded. This disturbance gave rise to small, even-aged groups of *Acer saccharum*, which appears to have replaced the more shade-tolerant *Tsuga*.

CLIMATIC CONTROLS AND INTERACTIONS

The general importance of intermediate events depends on their frequency, which is not readily reconstructed, and is likely to vary among stands and with climate change over time. Models based on land-survey data (Frelich & Lorimer 1991a) suggest that intermediate disturbances in northern Michigan might have a return time of one to a few centuries, an interval much less than half of typical estimates for catastrophic blowdowns and comparable with the life expectancies of most canopy

tree species. However, meteorological records are not of sufficient length or spatial resolution to confidently estimate stand-level frequency of storms comparable with the one studied here.

Past climate changes appear to be associated with population expansions and declines of forest tree species (Davis *et al.* 1986; Spear *et al.* 1994; Jackson & Booth 2002). It is possible that some of these population responses were mediated through changed patterns and frequencies of wind-caused disturbance. For example, there may be a threshold frequency of intermediate wind-disturbances below which species of modest shade-tolerance, such as *Betula alleghaniensis*, cannot sustain a substantial presence in the landscape. Typically, climate-change effects on community composition are taken to be due to direct physiological stress as temperature or moisture availability approach or pass species tolerances (but see Overpeck *et al.* 1990). However, changed disturbance dynamics might provide a mechanism for induction of community change even when climate change is moderate and does not directly stress trees.

Conclusions

Extrapolation from long-term observations in a single stand and observations of the effect of a single storm is risky. However, results reported here suggest several patterns that may be important in understanding and managing late-successional, northern-hardwood forests:

1. Relatively rare, intermediate disturbances may have distinctive, long-lasting effects on stand properties, in terms of species dominance and demographic structure.
2. Spatial pattern of intermediate disturbances may be distinctive and important in establishment and landscape maintenance of long-lived, shade-intolerant species like *Betula alleghaniensis*.
3. Intermediate disturbances affect understorey environment in ways that may have long-lasting consequences for composition and dynamics of the herbaceous community as well as for tree seedlings.
4. Climate change may produce changes in forest communities and landscape properties through changes in disturbance patterns even when species' temperature and moisture tolerances are not approached.
5. Forest management imitating natural disturbance regimes so as to foster natural patterns of tree regeneration may require incorporation of the effects of rare, intermediate disturbance.

Acknowledgements

This research has been supported financially by the Andrew Mellon Foundation, the National Science Foundation, and the United States Forest Service. The work would not have been possible without the establishment of inventory plots by Forest Service researchers and their generosity with information about the plots.

Personnel of the Hiawatha National Forest have supported the work logistically and with information about the stand. Many Bennington College students have assisted in data collection and data entry. Suggestions from Chris Peterson and an anonymous reviewer were helpful in revision of the manuscript.

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Received 30 July 2003

revision accepted 2 February 2004

Handling Editor: Frank S. Gilliam