Plant Ecology **129:** 121–134, 1997.

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Wind disturbance in remnant forest stands along the prairie-forest ecotone, Minnesota, USA

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Received 2 January 1996; accepted in revised form 11 September 1996

Key words: Disturbance: windthrow, Forest dynamics, Overbrowsing: deer, Storm: damage, Succession.

Abstract

Strong winds are an important disturbance agent in northern Minnesota forests. On June 19, 1994, strong winds (>160 km h^{-1}) associated with a tornado damaged forested areas within the Rydell National Wildlife Refuge, situated in Polk County Minnesota along the prairie-forest boundary. Field sampling was conducted immediately following the storm to quantify the type and extent of damage in four different community types, and to project future composition based on the nature of the storm damage and current understory characteristics, including the impact of overbrowsing by deer. Basal area in six sampled remnant forest stands was reduced by 33.5%, although the damage was heterogeneous; basal area in one stand was reduced by 68.1%. The overall effect of the storm was the removal of early- successional species (primarily *Populus tremuloides*) in larger size classes. Trees situated at stand edges were not more susceptible to snapping or uprooting than interior trees. Projections of future stand composition indicate that wind disturbance, unlike other agents of disturbance such as fire, may accelerate succession on the Refuge, such that early-successional stands will assume a later-successional character, while *Acer-Tilia* stands should maintain their late-successional character. Overbrowsing and preferential foraging by deer may significantly alter stand recovery patterns.

Introduction

Along the prairie-forest ecotone, the role of fire in influencing forest extent and composition has long been recognized (Upham 1895; Daubenmire 1936). European settlement of the Plains resulted in a cessation of prairie fires, and a sequential invasion by woodland species (Winchell 1884). Increasingly, wind is being recognized as an important agent of disturbance affecting forest dynamics (Canham and Loucks 1984; Foster 1988; Runkle 1990). Unlike fire, there is little opportunity for humans to alter wind disturbance regimes directly, although by altering stand characteristics the impact of wind may be changed.

The forest response to damaging wind is very different from that of fire. Wind damage usually is concentrated in the canopy, and generally only a portion of the trees are damaged (Glitzenstein and Harcombe 1988; Matlack et al. 1993; Veblen et al. 1989). There is more variation in microsite colonization sites, as snapping and uprooting by wind action deposit some length of bole on the forest floor (Peterson and Pickett 1991); uprooting also mixes the upper soil, exposes the buried seed bank, and creates pit and mound topography (Dunn et al. 1983; Foster 1988; Peterson and Pickett 1991). Although the response to wind damage is different from that of fire, downed trees also may increase the risk of subsequent fire or pest infestation.

A first objective of this study was to quantify wind damage to stands representing different forest community types in a National Wildlife Refuge along the prairie-forest boundary in northwestern Minnesota, USA. On June 19, 1994, a tornado with rotational winds in excess of 320 km h^{-1} passed within 2 km north of the Refuge (pers. comm., Regional Weather Information Center, University of North Dakota 1994). The damage to the forest stands resulted from straight line wind (>160 km h^{-1}) inflow to the tornado vortex. Although the return interval for tornadoes in this region is approximately 1500 years (Thom 1963), strong winds are very common. Wind speeds as high as those that damaged the forest stands have a return period of approximately 100 years (Baker 1983). Sampling was conducted in the months following the storm to (a) quantify the amount of downed basal area, (b) identify the type of damage (e.g., snapping, uprooting), (c) determine any tree size- or species- specific susceptibilities to windthrow, and (d) determine if trees along stand edges were more susceptible to windthrow than interior trees due to their more exposed position.

A second objective was to project future stand composition based on the nature of the damage and the status of current regeneration. Of special consideration in this regard is the exceptionally high density of whitetail deer (*Odocoileus virginianus* Zimmerman) on the Refuge, where predators are absent and hunting had not occurred for over 25 years. The overwintering population on the Refuge in 1993–1994 was estimated at approximately 41 deer km^{-2} (pers. comm., Minnesota Department of Natural Resources 1994), and saplings in most Refuge stands were either heavily browsed, or absent entirely. It was hypothesized that overbrowsing may influence recruitment into the canopy.

Methods

Study site

Rydell National Wildlife Refuge, 48° N 96° W, occupies 859 ha adjacent to Maple Lake in Polk County, Minnesota. The region experiences a humid continental climate, and the area is relatively flat: elevation varies from 357 to 373 m. Glacially-derived soils are principally fine sandy loams. The Refuge contains a complex of wetlands, old fields, conifer plantations, a bog, and stands of mesic deciduous forest. Early vegetation records indicate that the Refuge is situated at the prairie-forest boundary (Marschner 1974; Upham 1896), and represents the furthest northwestern extent of mesic deciduous forest in North America (McAndrews 1966).

An interview with a long-term resident of the present Refuge, whose family was one of the original settlers in the 1880s, indicated that the current stands of mesic deciduous forest were never clearcut, although selective cutting may have occurred especially for aspen. Cattle generally were fenced out of wooded areas, although some grazing in the stands occurred during the dry years of the 1930s. Fires were suppressed by residents, and most were confined to the litter layer and typically did not directly affect the overstory.

Six stands representing four different forest community types (Minnesota Department of Natural Resources 1993) were sampled in the present study (Figure 1): an Aspen stand (14 ha), an Oak stand (7 ha), a Lowland Hardwood stand (9 ha), and three Maple-Basswood stands (6, 11, and 20 ha). Tree species sampled, in order of shade tolerance (from Bakuzis and Hansen 1959), are *Acer saccharum* Marsh., *Ostrya virginiana* (Mill.) K. Koch, *Tilia americana* L., *Ulmus americana* L., *Quercus rubra* L., *Acer negundo* L., *Populus grandidentata* Michx., *Quercus macrocarpa* Michx., *Populus balsamifera* L., *Fraxinus pennsylvanica* Marsh., *Prunus virginiana* L., *Populus tremuloides* Michx. and *Betula papyrifera* Marsh. (Plant nomenclature follows Ownbey and Morley (1991) Vascular Plants of Minnesota: a Checklist and Atlas.) Common names of the four community types are used throughout this paper. Aspen communities are early successional, maintained by fire or windthrow, and occur primarily on sites with wet, poorly-drained soils and high water tables. In mesic stands of the Oak community type, *Quercus rubra* and *Quercus macrocarpa* are dominant, and in the absence of fire appear to be successional to the Maple-Basswood community type. Lowland Hardwood communities represent a wet-mesic forest type, on sites with a seasonally high water table (within the tree rooting zone). Prior to the introduction of Dutch elm disease (*Ophiostoma ulmi* (Buism) Nannf.), dominant trees historically included *Ulmus americana*, but most stands now contain a mixture of species including *Tilia americana*, *Quercus macrocarpa*, *Fraxinus pennsylvanica*, *Populus tremuloides*, and *Betula papyrifera*. Stands usually occur in fire-protected areas, and often contain late-successional species. Few stands contain old canopy trees, however, presumably because of windthrow and killing floods. The Maple-Basswood community is a mesic, late-successional forest type, occurring on protected sites where catastrophic fires were historically rare. Dominant trees are *Acer saccharum*, *Tilia americana*, and formerly *Ulmus americana*. The understory is patchy and multi-layered, composed of seedlings and saplings of the canopy trees (especially *Acer*), along with *Ostrya virginiana*, *Cornus alternifolia* L. f., and *Dirca palustris* L.

Woodside Township (T148N, R43W), which encompasses the Refuge, and adjoining Townships

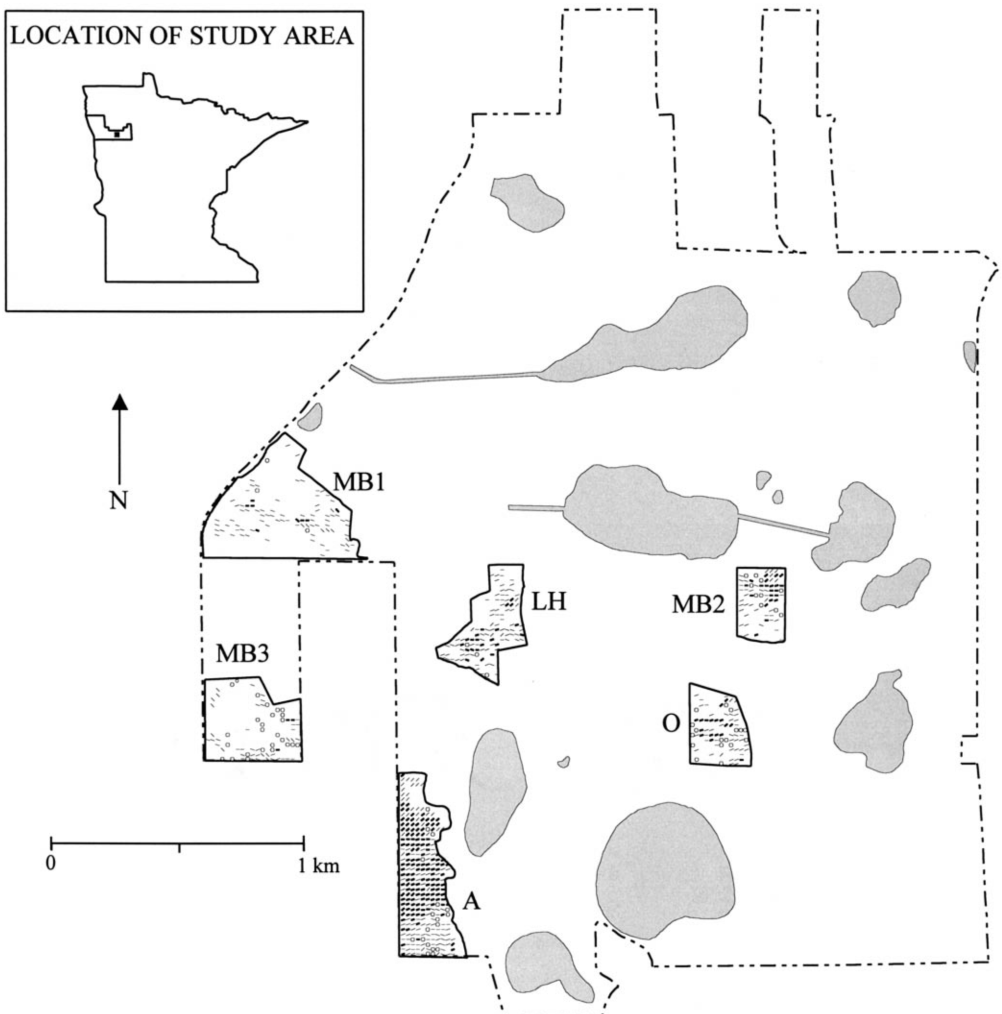

Figure 1. Map of Rydell National Wildlife Refuge, indicating the pattern of wind damage. Heavy lines represent ≥50% canopy loss within a cell, lighter lines indicate <50% canopy loss. Circles indicate a wind-damaged cell in which the principal direction of tree fall could not be ascertained from air photos. Community types are as follows: A = Aspen Stand, O = Oak Stand, LH = Lowland Hardwood Stand, and MB = Maple-Basswood Stands. Shaded areas represent water bodies.

were surveyed in 1872 (before European settlement) as part of the Public Land Survey authorized by the U.S. Congress (Stewart 1935). These records were consulted to ascertain disturbance histories of the study area.

Field procedures

Depending on stand shape, 1–5 transects were established and divided into equal sections in each of the six forest stands. Sample points were randomly located within each section. A total of 132 sample points were established, with a minimum of 20 sample points in each forest stand.

At each sample point, trees ≥10 cm dbh were inventoried using a point-centered quarter (PCQ) survey. Species, dbh, and distance from sample point were recorded for each tree. If the sample tree had been damaged in the 1994 windstorm, the type of damage was noted: snap, uproot, partial uproot (roots not exposed), pin (crushed by a larger stem; lower bole vertical, upper bole not vertical), or partial pin (upper bole bent by larger stem). Damage could be ascribed to the windstorm with a high degree of certainty, since foliage was still green on the damaged individuals. Additionally, the distance from the sample point to the damaged tree's original position was estimated in order to characterize pre-storm conditions. Post-storm sprouting of windthrown trees was noted; no distinction was made between root, epicormic, or coppice sprouting. To characterize post-storm conditions, the nearest undamaged tree was measured in each quadrant which had a windthrown sample tree. For expediency, if no undamaged tree was located within 5 m of the sampling point, the quadrant was listed as empty, and Warde and Petranka's (1981) correction for empty quadrants was used to prevent statistical biases (Peterson and Pickett 1991).

Arborescent saplings, that is, species which could be expected to attain the 10 cm dbh criterion for trees, were sampled using 25 m^2 circular quadrats located at each sampling point. Density by species was noted for two classes of saplings: large saplings ($<$10 cm dbh but $>$2 m in height), and small saplings ($\geq$0.5 and $\leq$2 m in height). Small saplings were not counted in the Aspen stand due to the extensive windthrow damage that occurred there. In one Maple-Basswood stand (MB3), large saplings were sampled using a separate PCQ procedure, and small saplings were sampled using a 10 m^2 circular quadrat at each sampling point.

Aerial photography

Forest stand boundaries were transferred from pre-storm air photos onto a 1:24 000 topographic map using a zoom transfer scope. This base map was then digitized, and a 20 $\times$ 20 m grid was superimposed over this new map. To evaluate the extent, severity, and pattern of windthrow across the Refuge, post-storm aerial slides at a nominal scale of 1:24 000 then were projected onto the gridded map, and a line drawn in each damaged 20 $\times$ 20 m cell in the principal direction of windthrow. Two weights of line were used to indicate severity of disturbance: $\geq$50% canopy loss, and $<$50% canopy loss (Figure 1).

Statistical analyses

Descriptive statistics were calculated for each community type and for the Refuge as a whole. These included relative density (number of stems for a particular species as a percentage of all stems sampled), relative basal area, and relative frequency. Importance values also were computed, which equally weighted these three relative values.

Differences in mean dbh of windthrown trees vs. undamaged trees were tested with a t-test as was the difference in mean dbh of windthrown trees that had sprouted vs. those that had not. Goodness-of-fit G-tests (Sokal and Rolf 1981) were used to test for significant departures from expected ratios of snapping and uprooting within species and within size classes. To examine simultaneously the effect of size and species on windthrow damage, a logistic regression was employed (Grizzle et al. 1969) using the CATMOD Procedure in SAS (SAS Institute 1987).

Projection of future stand composition

In order to explore the effect of windstorm damage on future stand composition, tree replacement scenarios were developed for each forest stand. It was assumed that every sampled windthrown tree created a canopy gap, that each gap would be filled by a single tree, and that the most likely replacement tree could be identified (Brewer and Merritt 1978). Gap size was not considered for this part of the analysis. The replacements would be drawn, in order of likelihood, from (1) a neighboring canopy tree in the same quadrant as the windthrown tree (extension growth into the gap), (2) a large sapling (release into the gap), or sprouting of the damaged tree (if noted in the field), or (3) a small sapling (release). Candidate saplings occurred anywhere in the circular quadrats. If no candidate tree existed in one category, the next category was searched for the replacement tree. If no candidates existed in any category, a replacement projection was not performed for that damaged tree. Additionally, when more than one candidate existed within a replacement category, and included a candidate of the same species as the damaged tree, 'Minimum Diversity' and 'Maximum Diversity' scenarios were generated. In the Minimum Diversity scenario, the selected replacement was of the same species as the windthrown tree, and with the Maximum Diversity scenario a different species was selected. Finally, in those instances where more than one species of replacement stems existed in a given category, consideration was given to a particular species' abundance relative to the others for that particular canopy gap (a greater number of stems inferred a greater likelihood of replacement probability), and to the relative growth rates of the different candidate species. These considerations usually led to the selection of *Acer saccharum* as the replacement tree, although *Prunus virginiana* was also selected on a few occasions.

Results

Overview of storm damage

Of 523 trees sampled (excluding the 17 undamaged trees closest to windthrown sample trees), 137 were affected by the storm (due to the random placement of points, 5 of 528 trees were sampled at two separate points). Twenty-three trees were affected by the storm, but may survive indefinitely; these include pinned trees (n=10), partial pins (n=4), and partial uproots (n=9). This analysis will focus on the 114 trees (21.8% of the sample) which experienced more severe damage (hereafter referred to as windthrown trees): uproots (n=63, 12.0%) and snaps (n=51, 9.8%).

Three species experienced more uproots than snaps: *Populus tremuloides* (51 vs 32), *Populus balsamifera* (3 vs 0), and *Tilia americana* (2 vs 1). Although the small sample size of damaged individuals of the latter 2 species precludes any definitive statement, it may be that saturated soil conditions contributed to the greater percentage of uproots to snaps with these species, especially in the larger size classes (>30 cm dbh). The June 19 storm was accompanied by heavy rains, and precipitation totals since the first of the month were well above normal June values across the region. Of the six other species which experienced windthrow, snapping was more common than uprooting (18 vs 7). Uprooting and snapping generally resulted in the death of the tree, although seven of the snapped trees experienced breakage of one of multiple boles and thus may survive indefinitely. In all cases when a multiple-stemmed tree was uprooted, all boles were downed. Total stand density in the six forest stands was reduced 29.6%, from 538 to 379 trees ha^{-1}, and total basal area was reduced 33.5%, from 40.9 to 27.2 m^2 ha^{-1}. Although basal area declined in all species after the storm, the early- successional *Populus tremuloides* showed the most notable decrease. (*Tilia americana*, which characteristically is multiple-stemmed with very large basal areas, also experienced a large decrease in basal area through the loss of only three individuals.) This general pattern also emerges with changes in Importance Values for the stands; all sites revealed a marked decrease in early-successional species, notably *Populus tremuloides*, and a corresponding increase in Importance Values for more mid- and late-successional species (see Figure 2).

Trees located at stand edges were not more susceptible to windthrow. Of trees identified at sample points within 30 m of a stand edge, 15.6% (12 of 76) were snapped or uprooted, compared to 24.4% of trees located at interior sample points.

Snapped trees broke 0–12 m ($\bar{x}$ = 4.3 m, sd = 3.3 m) above the ground. The average size of snapped boles was 24.7 cm dbh, and ranged from 8.6–41.1 cm. There was no significant relationship between snap height and species or dbh size class.

Mean dbh of windthrown trees was 29.9 cm, significantly larger than the 25.0 cm of surviving trees (t=2.72, df=521, P<0.01). When individual boles of multiple-stemmed trees are treated separately, the mean dbh of windthrown boles is 26.0 cm, again significantly greater than the 17.8 cm mean for surviving boles (t=8.73, df=706, P<0.001). Figure 3 presents type of fall (snap or uproot) by size class of individual boles. G-tests confirm there was a significant departure from randomness (P<0.001) regarding tree damage (snap and/or uproot) with respect to tree size. Small size classes (<20 cm dbh) which constitute 59% of the ‘pre-storm’ sample, are underrepresented in terms of percentage of windthrown boles (26.2%). The intermediate size classes (20–40 cm dbh) are overrepresented (37.9% of all boles, but 68.3% of windthrown boles). Of all windthrown boles in the intermediate size class, 61.1% were *Populus tremuloides*. The larger size classes (≥40 cm dbh) were downed in proportion to their number in the sample pool. Table 1 provides windthrow data by size class for each species.

Figure 4 presents type of fall by species, and reveals a pronounced species-specific susceptibility to windthrow. Over 52% of all *Populus tremuloides* sampled were downed in the storm, and 72.8% of all windthrown trees were *P. tremuloides*. Of the 159 *P. tremuloides* sampled, 51 were uprooted and 32 were snapped. G-tests confirm the significant departure from randomness (P<0.001) regarding tree damage with respect to species. The percentage of trees which were windthrown (excluding species which comprised < 2% of the sample), combined for all sites yields: *Populus tremuloides* (52.2% downed) > *Quercus rubra* (20.0%) > *Acer saccharum* (10.4%) > *Tilia americana* (7.1%) > *Quercus macrocarpa* (6.3%) > *Fraxinus pennsylvanica* (5.1%) > *Ulmus americana* = *Ostrya virginiana* (0%), although there was spatial variability between stands. The absence of windthrown *Ulmus americana* and *Ostrya virginiana* may be attributable to the secondary canopy position occupied by these species.

Since there is a relationship between species and size class, a logistic regression was performed to investigate the influence of one factor while controlling

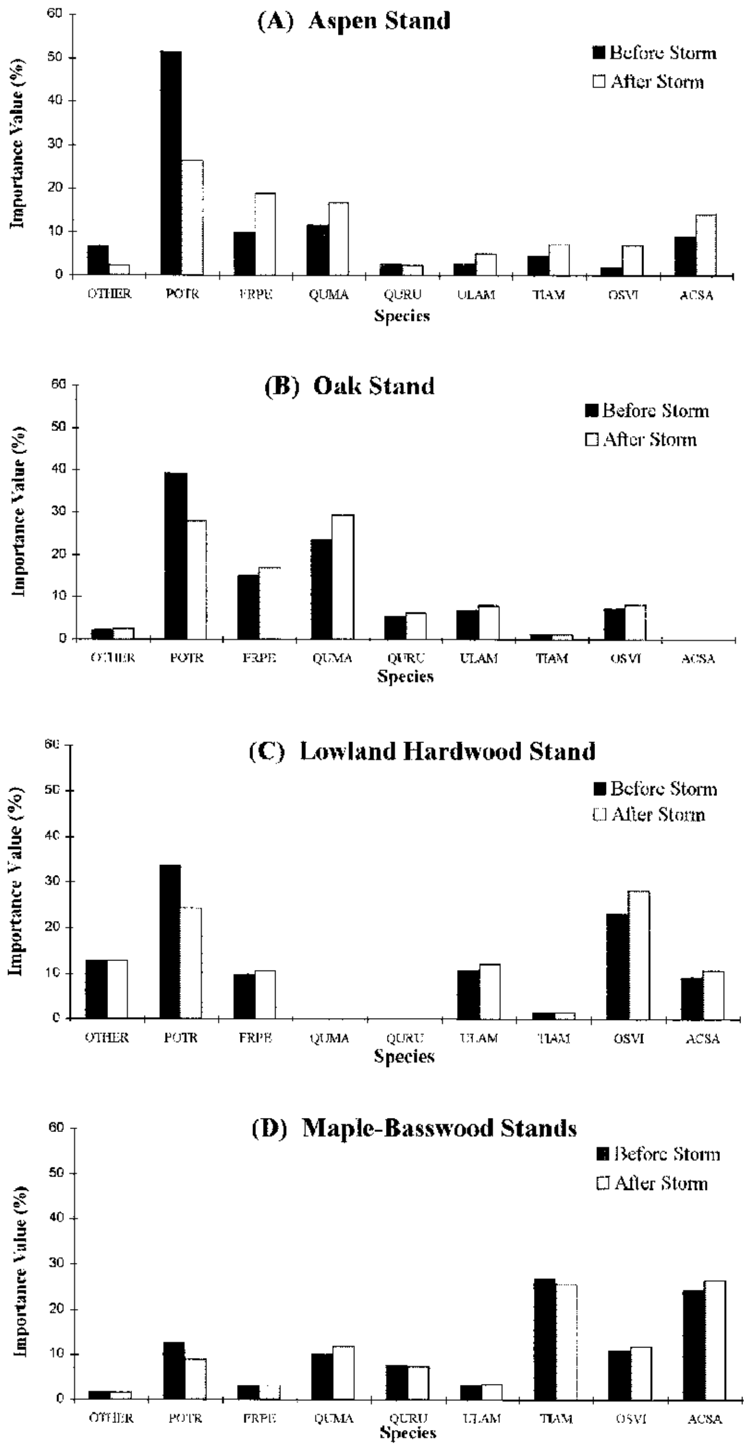

Figure 2. Change in Importance Values by stand. Values have been combined for the three Maple-Basswood Stands. Species are presented in order of increasing shade tolerance; species acronyms are as follows: POTR=*Populus tremuloides*, FRPE=*Fraxinus pennsylvanica*, QUMA=*Quercus macrocarpa*, QURU=*Quercus rubra*, ULAM=*Ulmus americana*, TIAM=*Tilia americana*, OSVI=*Ostrya virginiana*, ACSA=*Acer saccharum*. 'OTHER' refers to species comprising $<2\%$ of the sample, and includes *Betula papyrifera* (BEPA), *Populus balsamifera* (POBA), *Acer negundo* (ACNE), and *Populus grandidentata* (POGR).

Table 1. Percent of trees in each size class that experienced windthrow, by species. See Figure 2 for species acronyms

Species	Total sampled (n)	Percent windthrow by DBH (cm) 10.0 -14.9	15.0 -19.9	20.0 -24.9	25.0 -29.9	30.0 -34.9	35.0 -39.9	>40.0
BEPA	(7)	100.0	100.0	.	.	.	.	.
POTR	(159)	47.4	29.6	46.9	55.6	68.0	80.0	60.0
FRPE	(39)	6.3	.	.	.	33.3	.	.
POBA	(3)	.	.	100.0	100.0	.	.	.
QUMA	(48)	.	.	.	.	16.7	.	22.2
ACNE	(6)	.	.	.	.	.	.	.
POGR	(3)	.	.	.	50.0	.	.	.
QURU	(25)	.	16.7	.	.	66.7	.	50.0
ULAM	(29)	.	.	.	.	.	.	.
TIAM	(42)	11.1	.	.	.	.	.	10.5
OSVI	(66)	.	.	.	.	.	.	.
ACSA	(96)	.	4.2	.	50.0	22.2	.	20.0
TOTAL	(523)	9.8	11.4	20.3	36.4	41.1	34.8	25.0

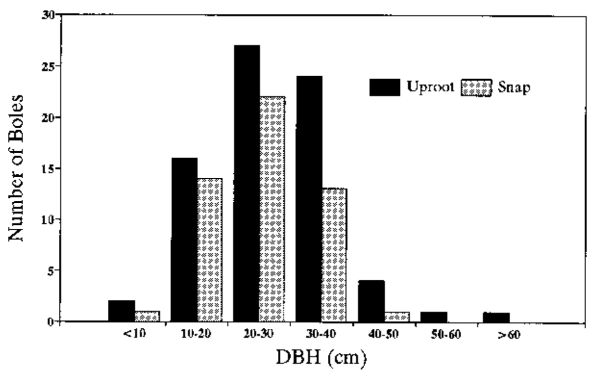

Figure 3. Distribution of type of tree fall among 10-cm DBH classes of trees at Rydell National Wildlife Refuge, Minnesota.

for the other. The resulting analysis-of-variance table revealed that the additive effect of both size and species is significant in the model, indicating that both species and size class independently influence a tree's susceptibility to windthrow.

Patterns of response in individual stands

Figure 1 presents a map showing each sampled stand on the Refuge, depicting the pattern and extent of storm damage using a 20 m × 20 m grid overlay. Table 2 provides stand data for pre- and post-storm density and basal area. It is clear from Figure 1 and Table 2 that certain stands experienced greater windthrow damage than others. To a large extent a stand's susceptibility to windthrow can be explained by the percentage of *Populus tremuloides* in the stand (stands are listed in Table 2 in decreasing order of percentage of *P. tremuloides*). Two stands do not fit this general pattern, however. The Oak Stand experienced less windthrow damage, and one Maple-Basswood Stand (MB2) more windthrow damage than expected based on the percentage of *P. tremuloides* in each.

Average size of *P. tremuloides* in the stands, percentage of trees of intermediate size (20–40 cm dbh), and stand density were not useful predictors of a stand's susceptibility to windthrow. Since this area is relatively flat, with only 15 m difference between the highest and lowest points across all sampled stands, topographic position was not a contributing factor to wind exposure. And although not systematically noted, fungal heart rot did not appear to play a role in susceptibility to windthrow; sound trees were being downed. Thus species composition partially explained a stand's susceptibility to windthrow, but local storm dynamics also played a role.

Figure 2 presents changes in Importance Values by stand. In all stands, the effect of the windstorm was a decrease in Importance Value of early-successional species (notably *P. tremuloides*), and a corresponding increase in Importance Value of mid-successional (e.g., *Fraxinus pennsylvanica*) and late-successional species (e.g., *Ostrya virginiana, Acer saccharum*).

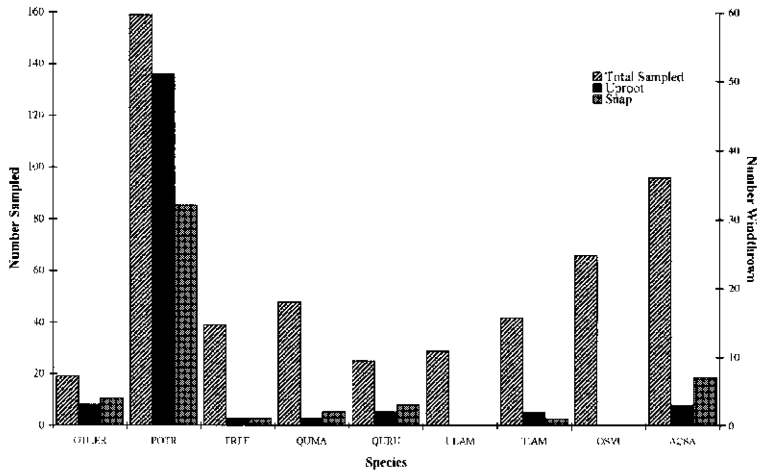

Figure 4. Distribution of number of trees sampled (left axis) and type of tree fall (right axis) by species at Rydell National Wildlife Refuge, Minnesota. See Figure 2 for species acronyms.

Table 2. Compositional characteristics by stand, before and after the wind storm.

Stand	Snapped or uprooted trees (%)	Pre-storm density of quaking Aspen (%)	Pre-storm density (stems ha^{-1})	Post-storm density (% remaining)	Pre-storm basal area (m^2 ha^{-1})	Post-storm basal area (% remaining)
Aspen (n=80)	61.3	60.0	461	36.2	27.9	31.9
Oak (n=90)	20.0	42.2	432	73.4	26.4	70.5
Lowland Hardwood (n=80)	21.3	35.0	636	71.5	43.8	72.1
Maple-Basswood (1) (n=84)	11.9	27.4	688	80.1	43.2	80.6
Maple-Basswood (2) (n=77)	22.1	18.2	487	70.0	59.9	58.4
Maple-Basswood (3) (n=112)	2.7	7.1	592	98.6	47.5	92.2
All Stands	21.8	30.4	538	70.4	40.9	66.5

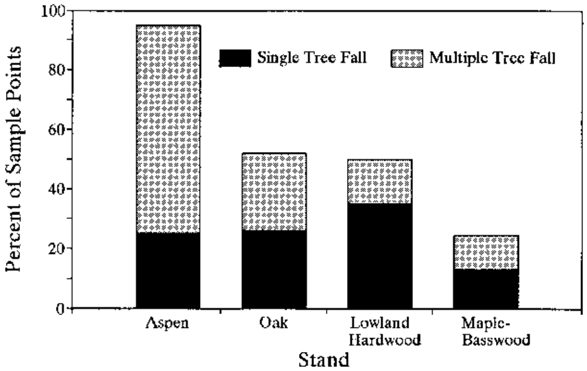

Figure 5. Percent of sample points that experienced windthrow of one or more sample trees, by stand. Values have been combined for the three Maple-Basswood Stands.

In general, the more early-successional stands (i.e., non-Maple-Basswood stands) had more snapping or uprooting of sample trees, and more windthrow of multiple sample trees (Figure 5). The more severely damaged Maple-Basswood stand (MB2) was more similar to the early-successional stands in this regard.

Regeneration: saplings and sprouting

It is likely that multiple-tree falls will produce larger canopy gaps than single-tree falls. Whereas single-tree falls may result in release and radial expansion of existing canopy trees into gaps, multiple-tree falls may increase the importance of growth into the canopy of existing sapling trees. In this regard, the make-up of the sapling layer at sites with large canopy gaps is potentially critical in terms of regeneration. In the Oak stand, 50% (3 of 6) of multiple-tree fall sites had no large (>2 m) saplings in the 25 m^2 quadrat located at the site; in the other early- successional stand, the Aspen stand, 36% (5 of 14) of multiple-tree fall sites had no large saplings.

Table 3 presents density of large saplings (<10 cm dbh and >2 m height) and small saplings ($\leq$2 m height) for each stand. In the early-successional Aspen Stand and Oak Stand, the two stands with the lowest canopy tree density (Table 2), shade-intolerant species (*Populus tremuloides*, *Prunus virginiana*) are regenerating. There is very little early-successional species regeneration occurring in the Maple-Basswood stands. Instead, compositional maintenance is suggested, with the large-sapling stratum being dominated by late-successional *Acer saccharum* and *Ostrya virginiana*, with some *Tilia americana*.

A striking characteristic evident in Table 3 is the very low density of the small-sapling stratum in all stands. Three stands had small sapling densities less than 500 stems ha^{-1}, and one stand (MB2) had a small-sapling density of only 40 stems ha^{-1}.

As with the large saplings, early- successional species are regenerating in the Oak Stand, although the later-successional *Ostrya virginiana* is the dominant species in the small-sapling stratum; (no *Acer saccharum* individuals were sampled in any stratum in this stand, although infrequent occurrences were noted in the field). In the Maple-Basswood stands, the late-successional *Acer saccharum* and *Ostrya virginiana* are dominant in the small-sapling stratum, but again overall densities are low.

Of all trees that had either snapped or uprooted, 45% had sprouted in the 4 months following the storm. A greater percentage of uprooted trees sprouted (68%) compared to snapped trees (16%). The majority of trees (88%) that sprouted were *Populus tremuloides* (54% of windthrown *P. tremuloides* sprouted), and most of these sprouted from the roots. There was no significant difference in tree size between those trees that sprouted and those that did not.

Although the potential survivorship of sprouts is unknown, sprouting could play a significant role in regeneration, especially in the Aspen stand. Over 81% of the sample trees that were uprooted in this stand were *Populus tremuloides*, and 81% of these uprooted *P. tremuloides* trees had sprouted. In each of the Aspen, Oak, and Lowland Hardwood Stands, over 50% of windthrown trees (snapped or uprooted) had sprouted. Table 4 provides data on sprouting by species, by size class, and by stand.

Projected changes in composition

Sixty of the 132 sample points (45.5%) incurred snapped or uprooted trees. Twenty-three of these 60 sample points (38.3%) had no large (>2 m) saplings or undamaged tree within 5 m of the sample point in the same quadrant as the windthrown tree. Whereas projections of future composition are always conjectural, this is especially true when so many of the sites are 'open.'

When pre-storm relative densities are compared with either the Minimum or Maximum Diversity scenarios (Figure 6), a significant decrease is evident with the early- successional species, notably *Populus tremuloides*. A corresponding increase is seen in the later-

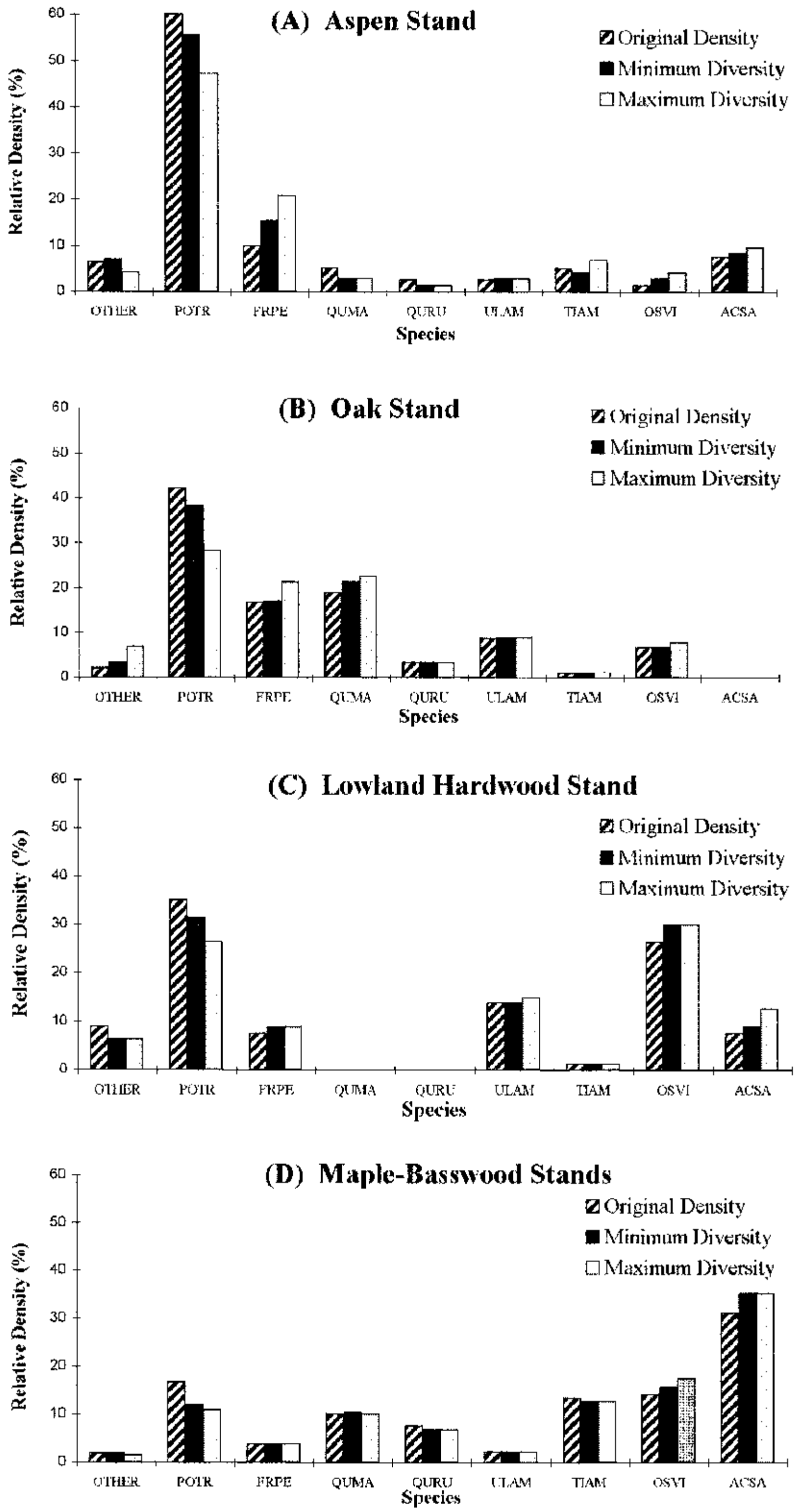

Figure 6. Original and projected relative density values by stand. Values have been combined for the three Maple-Basswood Stands. See Figure 2 for species acronyms.

Table 3. Total density and individual species densities (stems ha^{-1}) by stand, for large saplings ($<$10 cm dbh and $>$2 m height) and small saplings ($\geq$0.5 and $\leq$2.0 m in height). PRVI=*Prunus virginiana*; see Figure 2 for remaining species acronyms

STAND	TOTAL	POTR	PRVI	FRPE	POBA	QUMA	ACNE	POGR	ULAM	TIAM	OSVI	ACSA
(a) Large saplings												
Aspen	540	220	20	160	.	.	.	.	.	80	20	40
Oak	678	17	296	209	.	17	122	.	17	.	.	.
Lowland Hardwood	1080	20	.	60	.	.	60	.	220	.	220	500
Maple-Basswood (1)	1867	57	.	38	.	19	.	.	19	114	743	876
Maple-Basswood (2)	820	.	60	.	.	40	.	.	.	.	160	560
Maple-Basswood (3)	1371	.	.	13	.	.	.	.	13	75	747	523
(b) Small saplings												
Oak	1780	300	260	100	.	.	.	.	20	.	1100	.
Lowland Hardwood	400	180	.	80	.	.	60	.	.	.	60	20
Maple-Basswood (1)	1181	57	.	.	38	19	.	19	.	.	914	133
Maple-Basswood (2)	40	.	.	.	.	.	.	.	.	.	40	.
Maple-Basswood (3)	393	.	.	.	.	.	.	.	.	.	214	179

successional species, notably *Ostrya virginiana* and *Acer saccharum*.

Changes in the Aspen Stand reveal a decrease in *Populus tremuloides*, with an increase in *Fraxinus pennsylvanica*, *Ostrya virginiana*, and *Acer saccharum*. The stand is still dominated by *P. tremuloides*, however. The decrease in *P. tremuloides* in the Oak Stand is offset by an increase in mid-successional species, especially *Quercus* (with no indication of *Acer saccharum* recruitment into the canopy). A projected increase in late-successional *Ostrya virginiana* and *Acer saccharum* is anticipated in the Lowland Hardwood Stand following a loss of *P. tremuloides*. The Maple-Basswood Stands also are expected to experience an increase in later-successional species, but mostly these stands are maintaining their predisturbance composition. This maintenance reflects the fact that these stands experienced less storm damage overall compared to the other stands, and also that the current shade-tolerant canopy is regenerating in the understory.

Discussion

Overall patterns of damage

Strong winds associated with inflow to the tornado of June 19, 1994 caused significant damage to forest stands in Rydell National Wildlife Refuge in northwestern Minnesota. Overall basal area across six separate stands was reduced by 13.7 m^2 ha^{-1}; within the Refuge damage was heterogeneous, however, and some stands were more seriously impacted than others. Basal area in the Aspen Stand was reduced by 19.0 m^2 ha^{-1}.

Size was an important determining factor in tree susceptibility to wind damage up to a point, as was the case in other studies (Glitzenstein and Harcombe 1988; Peterson and Pickett 1991; Webb 1988, but see Matlack et al. 1993). Intermediate size classes were most severely affected by both snapping and uprooting, in accord with the results of Peterson and Pickett (1991); however, in our study the ratio of snapping to uprooting did not increase with tree size (Figure

Table 4. Number of trees that sprouted (n=51, 45% of windthrown trees) vs. number that did not sprout (n=63, 55% of windthrown trees), by species, by size class, and by stand. See Figure 2 for species acronyms. Values have been combined for the three Maple-Basswood Stands in (c).

Species	Sprouting (n)	No sprouting(n)
(a) By Species		
BEPA	0	3
POTR	45	38
FRPE	0	2
POBA	3	0
QUMA	0	3
POGR	1	0
QURU	0	6
TIAM	1	2
ACSA	1	9
(b) By size class		
DBH (cm)		
10.0-14.9	3	9
15.0-19.9	3	9
20.0-24.9	8	8
25.0-29.9	14	14
30.0-34.9	9	14
35.0-39.9	8	0
>40.0	6	9
(c) By stand		
Stand		
Aspen	28	21
Oak	11	7
Lowland Hardwood	9	8
Maple-Basswood	3	27

3). The largest size classes were not disproportionately downed, although it is likely that the larger-sized trees occupied a dominant position in the canopy, and therefore would be exposed to the highest wind velocities (Brewer and Merritt 1978; Foster 1988; Veblen et al. 1989) since wind speeds increase logarithmically with increased height above the canopy (Matlack et al. 1993). Perhaps the largest trees have extensively developed root systems which 'anchor' them against wind damage. Alternatively, the largest trees (and edge trees) may be wind-trained, having experienced prior exposure to strong winds which strengthens the tree against subsequent damage (Peterson and Pickett 1991).

Uprooting was more prevalent than snapping among sample trees, which is attributed primarily to the increased incidence of uprooting vs. snapping in *P. tremuloides*, and secondarily to high soil moisture at the time of the wind storm. Thirty-two percent of all *P. tremuloides* in the sample were uprooted, and 20% were snapped. This species-specific response, wherein *P. tremuloides* were downed preferentially, perhaps can be explained in one of two ways. First, at this study site *P. tremuloides* were generally taller, dominant canopy trees and therefore subject to greater wind stress. Tree height was not measured, but this reasoning is supported using basal area as a surrogate for canopy dominance. However, canopy position alone would not account for the disproportionate wind damage experienced by *P. tremuloides*. A second explanation therefore could be wood properties of the windstruck trees. With the exception of *Betula papyrifera*, which is known to snap more than uproot in high winds (Burns and Honkala 1990), *Populus tremuloides*, with its shallow lateral roots, is the only sampled species which is not considered windfirm based on rooting habit (Burns and Honkala 1990). Of the sampled species, *P. tremuloides* also has the lowest maximum tensile strength (230 Psi), a measure of resistance to forces which tend to split the wood (Forest Products Laboratory 1987).

The pattern of wind damage on the Refuge was heterogeneous, both between and within stands. This suggests that although tree size and species influenced a tree's susceptibility to windthrow, local storm dynamics produced inexplicable patterns of damage. The response to this damage also will be patchy, and subsequent differences in recovery therefore may increase landscape diversity (Foster 1988).

Successional trends

Fire has played an important role in shaping ecotonal characteristics along the continental prairie-forest boundary; prairie fires were common along the forest boundary prior to European settlement. With the suppression of prairie fires, eastern forests have expanded westward (Grimm 1981; McAndrews 1966). Fire certainly has had an influence in the region; original surveyor notes for the forested townships in the vicinity of the Refuge indicate that much burnt land existed in 1872. However, the dominance of mature *Acer saccharum* and *Tilia americana* at several stands within the Rydell Refuge and nearby sites, located leeward of a large lake situated at the prairie-forest boundary, suggests that certain mesic sites may have been sheltered from fire and had a lower fire frequency before settlement occurred in the 1880s (McAndrews 1966).

Several studies have indicated that at certain sites wind may be a more important agent of disturbance than fire in affecting forest composition. Based on wind data from the Great Lakes region, Frelich and Lorimer (1991) have suggested that wind speeds of 140–180 km hr^{-1} would cause moderate to moderately-heavy disturbance once or twice during the life span of a cohort of trees. Due to the flatter topography and more open cover characteristic of the western part of Minnesota, extreme wind events would be expected to be as common if not more frequent than in the eastern portion of the state. Wind speeds across the Refuge associated with inflow to the tornadic storm of June 19, 1994 were estimated at over 160 km hr^{-1}; at Fargo North Dakota, approximately 100 km south-southwest of the study site, the predicted extreme wind velocity for a 100-year return period is 153 km hr^{-1} (Baker 1983). It would seem then, that wind could be an important disturbance agent in this region. Downed logs in one stand at the Refuge suggested previous wind damage, and residents of the area recalled a windstorm in the 1940s which caused extensive forest damage. In addition, Public Land Survey records from 1872 describe extensive areas in windfall for Woodside Township, and the adjacent township to the south.

The size of canopy openings resulting from the wind storm ranged in size from single-tree falls, to over 65% canopy loss in one stand. In general, small canopy openings are closed quickly, especially through encroachment of existing canopy trees. Larger gaps are more persistent, and favor the establishment of new trees (Dunn et al. 1983; Oliver and Stephens 1977; Veblen et al. 1989; Webb 1989). Although a significant number of windthrown canopy trees had initiated sprouts and root suckering, sprouts are subject to heart rot, and sprouts of large trees are less likely to survive than smaller trees (Putz and Brokaw 1989), again favoring the establishment of new trees in large gaps (Peterson and Pickett 1991). The establishment of large gaps through multiple-tree falls in many stands may result in significant changes in stand composition, and highlights the role of release of the existing sapling stratum over the radial expansion of existing canopy trees.

Overall densities for large (>2 m) and small ($\geq$0.5 and $\leq$2 m) saplings were low, presumably from intense browsing pressure by white-tail deer. Significantly lower deer densities than the estimated 41 deer km^{-2} virtually eliminated trees <2.1 m at Itasca State Park, approximately 90 km southwest of the study site, and prevented saplings from growing larger than 2.1 m (Ross et al. 1970). In addition to reducing the advance regeneration from the stands, successional changes also may be affected by preferential browsing pressure on the part of the deer. Of the tree species sampled, deer prefer to browse the early-successional *Populus tremuloides*, which was significantly affected by the windstorm and which now is sprouting in abundance; mid- and later-successional species are not browsed as heavily (Burns and Honkala 1990). *Ostrya virginiana* in particular, which has the highest small sapling density and the second highest large sapling density on the Refuge, is only incidentally browsed by deer (Burns and Honkala 1990). Thus the deer are having a direct effect by removing biomass, but their selective foraging also may have an indirect effect. Higher densities of their non-preference browse may inhibit regeneration of other species in gaps formed by canopy tree fall.

Conclusions

The main effect of the wind storm on the forest stands at Rydell National Wildlife Refuge was the preferential removal of early-successional species in large size classes. Projecting future stand composition based on present understory characteristics indicates that the disturbance may accelerate succession. Traditionally disturbance has been seen as setting back succession. However, disturbance that removes a canopy dominated by early-successional species may result in the release of advance regeneration of shade-tolerant species (Abrams and Scott 1989). Based on canopy losses and understory composition, it would appear that the early- successional stands on the Refuge (Aspen, Oak, and Lowland Hardwood Stands) will assume a later-successional character, whereas the Maple-Basswood Stands will maintain their later-successional character. These findings are consistent with other studies that have explored the role of wind damage on forest succession (Glitzenstein and Harcombe 1988, Veblen et al. 1989, Webb 1989).

Acknowledgements

We would like to thank Troy Winter and Tom Feiro for their assistance in the field. The U.S. Fish and Wildlife Service granted permission and provided financial assistance to conduct the field work.

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