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Changes in two Minnesota forests during 14 years following catastrophic windthrow

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Abstract. We monitored damage, forest structure and tree species composition following a catastrophic windthrow in permanent plots in an oak forest and a white pine forest in central Minnesota. *Quercus borealis* and *Populus grandidentata* dominated the oak forest, and *Pinus strobus* and *Betula papyrifera* dominated the white pine forest prior to the storm. The storm removed 60% of the basal area and 40% of the density of trees in the oak forest, against 80% of the basal area and 60% of the density in the white pine forest. 14 yr after the storm, the basal area of the oak forest was 80% of the basal area before the storm and density increased 65%. At the same time, the white pine forest's basal area was just 43% of that before the storm and the density increased 5%. The number of tree species remained the same in the oak forest, but increased in the white pine forest. Ordination of tree species composition revealed a shift from earlier successional species to later successional species, both as a direct effect of the storm as well as during recovery following the storm. The net effect of the disturbance was to accelerate the successional processes, removing earlier successional species and providing few opportunities for other tree species to become established.

Keywords: Basal area; Convergence; Density; Disturbance; LTER; Succession

Introduction

Windstorms are an important kind of disturbance in forests (Perry 1994). Catastrophic winds are increasingly under investigation because global climate models predict an increase of severe winds in mid and high latitudes (thunderstorms and tornadoes) and in the tropics (hurricanes) (Overpeck et al. 1990). Wind disturbances offer opportunities to study regeneration of devastated areas as well as effects on forest dynamics (Webb 1988, 1989; Glitzenstein & Harcombe 1988; Abrams & Scott 1989).

Disturbances are reported in general as accelerators of successional processes due to the elimination of earlier successional species and creating new open spaces for other species to become established (Abrams & Scott 1989). In more advanced successional forests, medium-high frequency level of disturbance creates a mosaic of patches of different and successional status, resulting in an increase of vegetation diversity (Pickett & White 1985).

The NE USA have a low rate of extremely strong winds, where return interval of catastrophic winds (hurricanes and tornadoes) is between ca. 1200 (Canham & Loucks 1984) and 1500 yr (Thom 1963). Due to that, windthrows, with a rate of once every 100-150 yr (Moore 1988), represent a basic element in the understanding of forest structure and dynamics (Foster 1988).

We monitored changes in basal area, density and tree species composition in two Minnesota forests. The objectives of the study are to document trends in forest structure, composition, and diversity, and to interpret these trends in light of the successional status of the forests.

Material and Methods

Study site

We conducted our study in the Cedar Creek Natural History Area (CCNHA), which is one of the U.S. National Science Foundation's Long Term Ecological Research (LTER) sites, located in Anoka and Isanti Counties, Minnesota. CCNHA is located on the Anoka sand plain. On July 3, 1983, straight-line winds caused substantial mortality in a number of forests throughout CCNHA. We established permanent plots in two different sites: an oak forest dominated by *Quercus borealis*, *Q. alba*, *Q. macrocarpa* and *Populus grandidenta*, and a pine forest dominated by *Pinus strobus*. Since *P. strobus* typically colonizes oldfields, and since the white pine forest has the appearance of an even-age structure, we believe this site is of an earlier successional stage than the oak forest. Neither of the sites had any clear signs of cutting or other major recent anthropogenic disturbance.

Sampling

Two weeks after the storm, we established a 50 m × 50 m plot in the oak forest, and a 60 m × 50 m plot in the pine forest. We mapped the locations of all living and dead stems > 2.5 cm DBH, by species. We also counted, but did not map, saplings (individuals > 1.3 m in height but < 2.5 cm DBH) in each quadrat. Since it was usually obvious when the dead trees were killed during the windstorm, we were able to reconstruct pre-storm, as well as post-storm, forest structure. We remapped the plots in 1990, 1993 and 1997.

Data analysis

We used Detrended Correspondence Analysis (DCA, Hill & Gauch 1980) to examine whether species composition changed through time, whether the two sites behaved similarly, whether the initial effect of the disturbance was to accelerate succession, and whether the two sites converged in composition through time. We performed separate analyses for the two sites using tree basal area.

We performed all multivariate analyses with CANOCO (ter Braak 1987). Except where otherwise noted, statistical methods followed Zar (1984).

Table 1. Basal area (m^2/ha) and densities (ind/ha) of trees in the Oak forest along 14 yr of succession. Total values are also indicated.

	1983 before storm		1983 after storm		1990		1993		1997	
	B.a.	Dens.	B.a.	Dens.	B.a.	Dens.	B.a.	Dens.	B.a.	Dens.
Acer negundo	0.0137	8.00	0.0137	8.00	0.0944	48.00	0.1539	48.00	0.1646	28.00
Acer rubrum	0.1513	56.00	0.1430	48.00	0.8200	360.00	1.5777	600.00	2.5384	708.00
Amelanchier spec.	0.1088	64.00	0.0835	48.00	0.1166	64.00	0.1056	60.00	0.0516	16.00
Betula papyrifera	2.4433	128.00	0.7307	48.00	0.8997	64.00	0.5844	64.00	0.6832	64.00
Cornus alternifolia	-	-	-	-	0.0049	8.00	0.0053	8.00	-	-
Corylus americana	-	-	-	-	-	-	0.0036	4.00	-	-
Fraxinus nigra	0.8024	172.00	0.6828	148.00	1.3811	292.00	1.9584	384.00	2.3362	376.00
Ilex verticillata	-	-	-	-	-	-	-	-	0.0023	4.00
Pinus banksiana	4.6468	64.00	-	-	-	-	-	-	-	-
Pinus resinosa	0.6448	8.00	-	-	-	-	-	-	-	-
Pinus strobus	1.5808	24.00	0.1606	8.00	0.4344	8.00	0.5504	8.00	0.7285	8.00
Populus grandidentata	4.0061	120.00	0.2314	36.00	0.4505	132.00	0.6892	128.00	0.8368	92.00
Prunus serotina	0.4184	68.00	0.3188	56.00	0.8222	236.00	0.8775	212.00	1.1066	180.00
Prunus virginiana	0.0388	36.00	0.0164	16.00	0.0337	20.00	0.0257	16.00	0.0247	16.00
Quercus alba	0.2238	40.00	0.2238	40.00	0.3700	44.00	0.4895	60.00	0.5881	60.00
Quercus ellipsoidalis	12.9681	248.00	8.7360	160.00	10.9118	164.00	11.9369	188.00	13.5847	172.00
Quercus macrocarpa	0.8755	64.00	0.8755	64.00	1.0485	92.00	0.6762	96.00	0.7602	92.00
Vitis riparia	-	-	-	-	-	-	-	-	0.0076	12.00
Ulmus americana	0.0491	4.00	0.0491	4.00	0.0725	4.00	-	-	-	-

Results

The pre-storm basal area and the density of the oak forest were 28.97 m^2/ha and 1104.00 ind/ha respectively. In the oak forest the dominant species were *Quercus borealis*, *Populus grandidentata* and *Pinus banksiana*. The pre-storm basal area and density of the white pine forest was 41.94 m^2/ha and 1069.20 ind/ha. The dominant species was *Pinus strobus*, and with much less importance (Tables 1 and 2).

The two forests differed in their initial response to disturbance, and their recovery following disturbance (Fig. 1). The oak forest lost 60% of the basal area and recovered 40% during the succession, while the pine forest lost 80% of the basal area and recovered only 20% (Fig. 1a). Tree density in the oak forest quickly increased to well above the initial values, and experienced a slight decline from 1993 to 1997. In contrast, in the pine forest, tree density approximately returned to pre-storm levels by 1993 (Fig. 1b). The sapling density decreased after 6 yr of succession in the oak forest, due to mortality as well as recruitment to tree size classes; we did not observe this pattern in the pine forest (Fig. 1c).

The two forests also differed in how species richness changed through time. Tree species richness following the storm was unchanged in the oak forest while it increased by five species in the pine forest (Table 1 and 2). Prior to the storm, *Q. borealis* was the dominant species of the oak forest and it remained dominant immediately after the storm and after 14 yr of succession. The basal area of *Q. borealis* was reduced by 37% in the oak forest with similar basal area in the 1997 sampling compared to before the storm. The most numerous species in the oak forest prior to the storm

Table 2. Basal area (m^2/ha) and densities (ind/ha) of trees in the Pine forest along 14 yr of succession. Total values are also indicated.

	1983 before storm		1983 after storm		1990		1993		1997	
	B.a.	Dens.	B.a.	Dens.	B.a.	Dens.	B.a.	Dens.	B.a.	Dens.
Acer negundo	0.0202	9.90	0.0202	9.90	0.1679	42.90	0.2810	49.50	0.4544	49.50
Acer rubrum	0.0540	13.20	0.0330	9.90	0.1664	49.50	0.3248	62.70	0.6053	62.70
Amelanchier sp.	-	-	-	-	0.0020	3.30	0.0052	6.60	0.0039	3.30
Betula papyrifera	5.1361	128.70	1.5327	39.60	1.5672	39.60	0.6404	56.10	0.8339	85.80
Cornus alternifolia	0.0146	9.90	-	-	0.0022	3.30	0.0114	13.20	0.0120	9.90
Fraxinus nigra	0.1902	89.10	0.1623	79.20	0.6029	155.10	0.9235	165.00	1.2070	161.70
Ilex verticillata	0.0034	3.30	-	-	0.0058	9.90	0.0080	13.20	0.0048	6.60
Pinus strobus	36.2622	640.20	10.1999	178.20	11.5766	204.60	12.8287	214.50	12.8419	207.90
Populus grandidentata	0.0354	9.90	0.0317	6.60	0.0573	9.90	0.0756	6.60	0.0630	3.30
Prunus pensilvanica	0.0134	3.30	0.0134	3.30	0.0325	3.30	0.0496	6.60	0.0545	3.30
Prunus serotina	0.1851	135.30	0.1067	85.80	0.4652	184.80	0.7511	194.70	0.9240	141.90
Prunus virginiana	0.0068	6.60	0.0041	3.30	0.0117	6.60	0.0127	3.30	0.0228	6.60
Quercus alba	-	0.00	-	-	0.0313	26.40	0.0721	36.30	0.1284	36.30
Quercus ellipsoidalis	0.0027	3.30	0.0027	3.30	0.0727	56.10	0.2016	135.30	0.5283	231.00
Quercus macrocarpa	0.0062	3.30	0.0062	3.30	0.0342	13.20	0.0530	19.80	0.0876	19.80
Rhamnus cathartica	-	-	-	-	-	-	0.0062	6.60	0.0145	9.90
Rhamnus frangula	-	-	-	-	-	-	0.0022	3.30	0.0062	6.60
Rhus typhina	-	-	-	-	0.0251	26.40	0.0565	33.00	0.0668	23.10
Ulmus americana	0.0152	9.90	0.0059	6.60	0.1360	42.90	0.3382	49.50	0.3423	33.00
Vitis riparia	-	-	-	-	-	-	0.0128	19.80	0.0157	16.50
Zanthoxylum americanum	0.0018	3.30	0.0018	3.30	0.0043	6.60	0.0071	9.90	0.0114	13.20
Total	41.94	1069.20	12.12	432.30	14.96	884.40	16.66	1105.50	18.22	1131.90

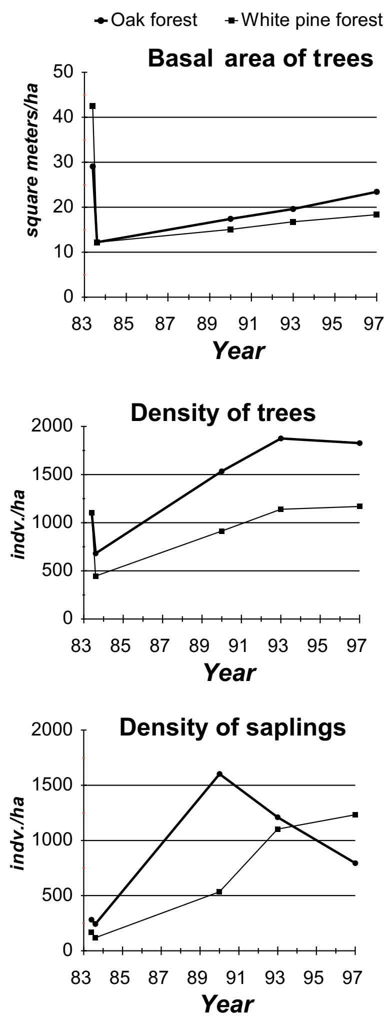


Fig. 1. Tree basal area (**a**), tree density (**b**) and sapling density (**c**) as a function of time since the windstorm. The initial decline in 1983 represents the direct effects of the storm.

were *Q. borealis* and *P. grandidentata*. *Acer rubrum* and *Fraxinus nigra* have replaced them after the storm (Table 1).

In the pine forest *P. strobus* was the dominant species in terms of basal area. It also remained dominant immediately after the storm and throughout the study. *P. strobus* lost 60% of its basal area during the storm. After 15 yr the basal area of *P. strobus* did not recover its pre-storm levels. *P. strobus* remained numerous, but *Prunus serotina* and *Q. borealis* had similar densities (Table 2).

Codominant species (*B. payrifera*, *P. grandidentata* and *P. strobus* in the oak forest and *B. papyrifera* in the pine forest) were more affected and did not recover their codominance after 15 yr.

Ordination of both sites through time (based on basal area) showed a strong site effect on the first axis, with species typical of the pine forest on the left, and species typical of the oak forest on the right (Fig. 2). The second axis appeared to be a temporal effect, with species that increased through time at the top, and those which decreased at the bottom. Note that the initial effects of the disturbance (i.e. comparing the 1983 site scores before and after the storm) are in the same direction as the change in later years. This means that the best-surviving species also grew well following the storm.

Discussion

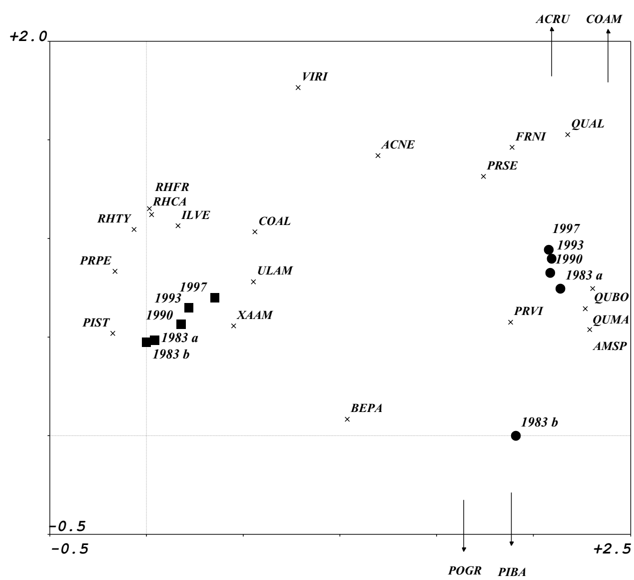
Although tree species richness did not change much in the oak forest, it increased in the secondary pine forest. Tree richness tends to reach a low point in the middle of secondary forest succession, and then increase as the forest enters a steady-state (Bormann & Likens 1978, but see Perry 1994). It is possible that by releasing juveniles that were competitively suppressed by the canopy, the windstorm accelerated the inevitable increase in diversity.

In the oak forest, the two most shade-tolerant species, *Quercus borealis* and *Acer rubrum* almost recovered or even increased their basal area after 14 yr, and also *A. rubrum* has the greatest basal area after 14 yr. *A. rubrum* has

Fig. 2. Species and site scores for the DCA axes based on tree basal area (eigenvalues 0.731 and 0.053; cumulative % variance of species data of both axes was 82.7%). Circles indicate the oak forest and squares the white pine forest (indicating the sampling year; b = before the storm; a = after). Axis 3 (not shown) did not reveal interpretable patterns for species of sites; its eigenvalue = 0.009.

Abbreviations for species names:

ACNE	*Acer negundo*	ACRU	*Acer rubrum*
AMSP	*Amelanchier* spec.	BEPA	*Betula papyrifera*
COAL	*Cornus alternifolia*	COAM	*Corylus americana*
FRNI	*Fraxinus nigra*	ILVE	*Ilex verticillata*
PIBA	*Pinus banksiana*	PIST	*P. strobus*
PRPE	*Prunus pensylvanica*	PRSE	*P. serotina*
PRVI	*P. virginiana*	POGR	*Populus grandidentata*
QUAL	*Quercus alba*	QUBO	*Q. ellipsoidalis*
QUMA	*Q. macrocarpa*	RHCA	*Rhamnus cathartica*
RHTY	*Rhus typhina*	ULAM	*Ulmus americana*
VIRI	*Vitis riparia*	XAAM	*Zanthoxylum americanum.*



a high rate of asexual regeneration that may explain its high density. Canham & Marks (1985) considered *A. rubrum* to be a climax species that depends on pulses of resources produced by small-scale disturbance.

Although *Pinus strobus* decreased dramatically after the storm in the white pine forest, and recovered very little, it continued being the dominant species in the pine forest. However, the current rapid increase in *Prunus serotina*, *Q. borealis*, and other more shade-tolerant species, implies that *P. strobus* will soon be replaced.

In the late successional oak forest, disturbance did not cause an extreme change in the structure. In the white pine forest, however, changes are more dramatic and the recovery of basal area and density is slower. Physiognomy, structure (age, height and density), and compositional characteristics of the vegetation mosaic explains the difference between the later and earlier successional stand.

The net effect of the disturbance was to accelerate succession by removing large early successional trees, at least in the white pine forest. Windthrows could provide establishment opportunities for other tree species, especially in earlier successional stands. This point of view has been strongly supported in various studies (Dyer & Bair 1997; Glitzenstein & Harcombe 1988; Abrams & Scott 1989; Glitzenstein et al. 1986), and is contradictory to Clements' (1916) paradigm, according to which disturbance largely interrupts and reinitiates seral development.

The study of successional convergence is greatly affected by temporal and spatial scale as well as the sampling design (Lepš 1991). It is therefore difficult to know whether our observation of a slight successional convergence between the two forests is a general phenomenon. It is not possible to untangle whether the convergence between our sites would have occurred without the disturbance.

This study offers some information about the effect of wind disturbance in the vegetation and a secondary succession analysis. If the global warming models are confirmed, the boreal forest dynamics could be altered by the beginning of the next century (Overpeck et al. 1990) due to these kind of disturbances. The accumulation of information about wind disturbances could be essential for the preservation of certain forests.

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