

Changes in two Minnesota forests during 14 years following catastrophic windthrow

Arévalo, José Ramón^{1*}; DeCoster, James K.²; McAlister, Suzanne D.³; & Palmer, Michael W.³

¹Universidad de La Laguna, Departamento de Ecología, E-38206, La Laguna, Islas Canarias, Spain; ²Louisiana State University, Department of Biological Sciences, Life Sciences Building #508, Baton Rouge, LA 70803, USA;

³Oklahoma State University, Department of Botany, Stillwater, OK 74078-3013, USA;

*Corresponding author; Fax +34922318311; E-mail jarevalo@ull.es

Abstract. We measured tree damage and mortality following a catastrophic windthrow in permanent plots in an oak forest and a pine forest in central Minnesota. We monitored changes in forest structure and composition over the next 14 years. Prior to the storm, the oak forest was dominated by *Quercus ellipsoidalis*, and the pine forest by *Pinus strobus*. The immediate impacts of the storm were to differentially damage and kill large, early-successional hardwoods and pines. Subsequent recovery was characterized by the growth of late-successional hardwoods. In both forests the disturbance acted to accelerate succession. Ordination of tree species composition confirmed the trend of accelerated succession, and suggested a convergence of composition between the two forests.

Keywords: Convergence; Forest dynamics; LTER; Succession; Tree damage; Tree mortality; Wind disturbance.

Nomenclature: Kartesz (1994).

Introduction

Windstorms is one of the most important kind of disturbance in forests, after anthropogenic disturbances and fire (Perry 1994). In the Upper Midwest, moderate wind damage (20–50% canopy removal) has been calculated to occur once or twice in the life span in a cohort of trees (Frelich & Lorimer 1991). Furthermore, global climate models predict increased frequencies of thunderstorms and tornadoes in mid and high latitudes (Overpeck et al. 1990), suggesting that wind disturbance will become an even more important force impacting the structure and dynamics of the forests in this region. A number of models have been proposed to describe the impact of disturbances on forest dynamics. The classic succession model of Clements (1916) viewed disturbance as interrupting succession and re-initiating seral development. More recently, disturbance models have described disturbances as creating a heterogeneous mosaic of patches of different successional status, resulting in an increase of vegetation diversity (Pickett & White 1985). In several

studies, disturbance has acted to accelerate succession by removing early-successional species, allowing for a more rapid growth of late-successional species (Lorimer 1980; Abrams & Scott 1989; DeCoster 1996).

While many studies have examined the immediate impacts of windstorms on forest vegetation, few have examined post-storm changes beyond several years, and consequently have not been able to evaluate these forest dynamic models with respect to wind disturbance. In 1983 we established permanent plots in two forests immediately following a catastrophic windstorm in Cedar Creek Natural History Area, Minnesota. Our objective is to document the immediate impacts of the storm, and the changes in forest structure and composition in the 14 years following the storm.

Material and Methods

Study site

We conducted our study in the Cedar Creek Natural History Area (CCNHA), one of the U.S. National Science Foundation's Long Term Ecological Research (LTER) sites, located in Anoka and Isanti Counties, Minnesota, USA. CCNHA is located on the Anoka sand plain, with relatively nutrient-poor and well-drained soils (Tilman 1988). On July 3, 1983, straight-line winds caused substantial mortality in a number of forests throughout CCNHA. We established permanent plots in two sites: an oak forest dominated by *Quercus ellipsoidalis* (the CCNHA population is apparently a genetic mixture of *Q. ellipsoidalis* and *Q. rubra*; Swain 1972), and a pine forest dominated by *Pinus strobus*. Since the pine forest has the appearance of an even-age structure and *P. strobus* typically colonizes oldfields, we believe this site is of an earlier successional stage than the oak forest. Neither site had any signs of cutting or other major recent anthropogenic disturbance, although the presence of pines in the oak forest suggests disturbance in the past century.

Sampling

Within two weeks following 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. For each living and dead stem greater than 1 cm diameter, we collected the following data: diameter at breast height (DBH; measured at 1.4 m), species, damage type and mortality. Damage types (noted for both living and dead trees) included undamaged, snapped, uprooted, and light damage (trees that were leaning, pinned, or with crown or bark damage). In instances of multi-stem trees, stems were included if they originated from the main stem below 1.4 m in height. During the first sampling, we were able to distinguish between trees that were killed during the windstorm and trees that were dead at the time of the storm, and thus we were able to reconstruct both pre-storm and post-storm forest structure. We resampled the plots in 1990, 1993, and 1997 to assess subsequent growth, mortality, and establishment of new stems.

Data analysis

We used multiple logistic regression (statistics were implemented using SAS (Anon. 1990) to determine the factors contributing to tree damage and tree mortality. Logistic regression uses the logit function to allow prediction of probabilities from a linear function of independent variables (Hosmer & Lemeshow 1989). We performed three logistic regressions: one that examined the effects of tree characteristics on mortality, a second that examined the effects of damage type on mortality, and a third that examined the effects of diameter and species on damage. In the first regression, we examined whether or not a tree was killed immediately following the storm as a function of tree diameter and species. The seven most abundant species ($n > 25$) were entered as dummy variables, with each species being compared to the combined unspecified species. In the second regression, we examined tree mortality as a function of damage type, with diameter included as a covariate. The three damage types were entered as dummy variables, and were compared to undamaged trees. In the third regression, we examined whether or not a tree sustained any type of damage (including trees that died from their damage) as a function of tree diameter and species. As with the first multiple regression, the seven most abundant species were entered as dummy variables and compared to undamaged trees. We tested all three models for interactions and quadratic functions. No interactions were significant in the second mortality model and in the damage model, and hence such terms were excluded from these. We did not include a site variable in the regression models because species

composition varied so much between the forests, and therefore might obscure a species effect. Nevertheless, some patterns may result from site differences.

Ordination techniques help to explain community variation (Gauch 1982) and can be used to evaluate trends through time as well as space (Franklin et al. 1993; Arévalo et al. 1999; ter Braak & Šmilauer 1998). We used Detrended Correspondence Analysis (DCA; Hill & Gauch 1980, CANOCO package; ter Braak & Šmilauer 1998) to examine how species composition changed through time, and whether the two sites behaved similarly. We performed separate analyses using tree basal area and tree density. Ordinations were run using a data set consisting of the two sites (pine and oak) at five different time intervals: 1983 – before the storm, 1983 – after the storm, 1990, 1993, and 1997.

Results

The forests differed in pre-storm structure and composition. The pre-storm basal area and the density (for stems with dbh > 2.5 cm) of the oak forest were 28.97 m²/ha and 1104.00 individuals/ha respectively (Table 1). The dominant species was *Quercus ellipsoidalis*, although *Populus grandidentata* and *Pinus banksiana* also had high basal area. The pre-storm basal area and density of the pine forest was 41.94 m²/ha and 1069.20 individuals/ha (Table 2). *Pinus strobus* dominated, while the remaining species contributed a small portion of the basal area.

The first logistic regression model of mortality shows that the probability of being killed varied with respect to species and diameter (Table 3). The range of diameter used was all stems higher than 2.5 cm dbh. All but two species (*Acer rubrum* and *Prunus serotina*) were significantly ($p < 0.05$) different from the unspecified species either as main effects or interactions. The relative susceptibility to mortality for each species varied with diameter, with species generally increasing in susceptibility with size, although two species (*Pinus strobus* and *Quercus ellipsoidalis*) showed significant decreases in susceptibility (Table 3, Fig. 1a). A univariate model of diameter showed that when considered by itself, mortality increases with diameter (Wald $\chi^2 = 11.454$, $p = 0.0007$), with no significant quadratic effect (Wald $\chi^2 = 1.149$, $p = 0.2838$).

The second logistic regression shows that the probability of a tree dying varied with respect to damage type. All damage classes showed significantly higher mortality than undamaged trees (Table 4). Diameter was not significant, indicating that within damage types, mortality did not vary with size. Not surprisingly, snapped and uprooted trees had higher mortality than trees with

Table 1. Basal area and densities of trees (stems > 2.5 cm DBH) in the oak forest during 14 years of succession; b.s. = before storm; a.s. = after storm.

Species	Basal area (m ² /ha)					Density (individuals/ha)				
	1983 b.s.	1983 a.s.	1990	1993	1997	1983 b.s.	1983 a.s.	1990	1993	1997
<i>Acer negundo</i>	0.01	0.01	0.09	0.15	0.16	8.00	8.00	48.00	48.00	28.00
<i>Acer rubrum</i>	0.15	0.14	0.82	1.58	2.54	56.00	48.00	360.00	600.00	708.00
<i>Amelanchier spec.</i>	0.11	0.08	0.12	0.11	0.05	64.00	48.00	64.00	60.00	16.00
<i>Betula papyrifera</i>	2.44	0.73	0.90	0.58	0.68	128.00	48.00	64.00	64.00	64.00
<i>Cornus alternifolia</i>	-	-	+	0.01	-	-	-	8.00	8.00	-
<i>Corylus americana</i>	-	-	-	+	-	-	-	-	4.00	-
<i>Fraxinus nigra</i>	0.80	0.68	1.38	1.96	2.34	172.00	148.00	292.00	384.00	376.00
<i>Ilex verticillata</i>	-	-	-	-	+	-	-	-	-	4.00
<i>Pinus banksiana</i>	4.65	-	-	-	-	64.00	-	-	-	-
<i>Pinus resinosa</i>	0.64	-	-	-	-	8.00	-	-	-	-
<i>Pinus strobus</i>	1.58	0.16	0.43	0.55	0.73	24.00	8.00	8.00	8.00	8.00
<i>Populus grandidentata</i>	4.01	0.23	0.45	0.69	0.84	120.00	36.00	132.00	128.00	92.00
<i>Prunus serotina</i>	0.42	0.32	0.82	0.88	1.11	68.00	56.00	236.00	212.00	180.00
<i>Prunus virginiana</i>	0.04	0.02	0.03	0.03	0.02	36.00	16.00	20.00	16.00	16.00
<i>Quercus alba</i>	0.22	0.22	0.37	0.49	0.59	40.00	40.00	44.00	60.00	60.00
<i>Quercus ellipsoidalis</i>	12.97	8.74	10.91	11.94	13.58	248.00	160.00	164.00	188.00	172.00
<i>Quercus macrocarpa</i>	0.88	0.88	1.05	0.68	0.76	64.00	64.00	92.00	96.00	92.00
<i>Vitis riparia</i>	-	-	-	-	0.01	-	-	-	-	12.00
<i>Ulmus americana</i>	0.05	0.05	0.07	-	-	4.00	4.00	4.00	-	-
Total	28.97	12.27	17.46	19.63	23.41	1104.00	684.00	1536.00	1876.00	1828.00

(+) indicating very low presence of the species

light damage (Fig. 1b).

The third logistic regression focused on damage, including both living and dead trees. The probability of damage varied with respect to diameter and species (Table 5). Species varied in their damage probabilities, creating a hierarchy of relative susceptibilities (Fig. 1c). *Betula*

papyrifera, *Pinus strobus* and *Populus grandidentata* showed significantly higher damage probabilities than trees of unspecified species. Damage probability also increased with diameter. A univariate model of damage as a function of diameter was also highly significant (Wald $\chi^2 = 24.453, p = 0.0001$), although a quadratic term

Table 2. Basal area and densities of trees (stems > 2.5 cm DBH) in the pine forest during 14 years of succession (b.s. = before storm; a.s. = after storm).

Species	Basal area (m ² /ha)					Density (individuals/ha)				
	1983 b.s.	1983 a.s.	1990	1993	1997	1983 b.s.	1983 a.s.	1990	1993	1997
<i>Acer negundo</i>	0.02	0.02	0.17	0.28	0.45	9.90	9.90	42.90	49.50	49.50
<i>Acer rubrum</i>	0.05	0.03	0.17	0.32	0.61	13.20	9.90	49.50	62.70	62.70
<i>Amelanchier spec.</i>	-	-	+	0.01	+	-	-	3.30	6.60	3.30
<i>Betula papyrifera</i>	5.14	1.53	1.57	0.64	0.83	128.70	39.60	39.60	56.10	85.80
<i>Cornus alternifolia</i>	0.01	-	+	0.01	0.01	9.90	-	3.30	13.20	9.90
<i>Fraxinus nigra</i>	0.19	0.16	0.60	0.92	1.21	89.10	79.20	155.10	165.00	161.70
<i>Ilex verticillata</i>	+	-	0.01	0.01	+	3.30	-	9.90	13.20	6.60
<i>Pinus strobus</i>	36.26	10.20	11.58	12.83	12.84	640.20	178.20	204.60	214.50	207.90
<i>Populus grandidentata</i>	0.04	0.03	0.06	0.08	0.06	9.90	6.60	9.90	6.60	3.30
<i>Prunus pensylvanica</i>	0.01	0.01	0.03	0.05	0.05	3.30	3.30	3.30	6.60	3.30
<i>Prunus serotina</i>	0.19	0.11	0.47	0.75	0.92	135.30	85.80	184.80	194.70	141.90
<i>Prunus virginiana</i>	0.01	+	0.01	0.01	0.02	6.60	3.30	6.60	3.30	6.60
<i>Quercus alba</i>	-	-	0.03	0.07	0.13	0.00	-	26.40	36.30	36.30
<i>Quercus ellipsoidalis</i>	+	+	0.07	0.20	0.53	3.30	3.30	56.10	135.30	231.00
<i>Quercus macrocarpa</i>	0.01	0.01	0.03	0.05	0.09	3.30	3.30	13.20	19.80	19.80
<i>Rhamnus cathartica</i>	-	-	-	0.01	0.01	-	-	-	6.60	9.90
<i>Rhamnus frangula</i>	-	-	-	+	0.01	-	-	-	3.30	6.60
<i>Rhus typhina</i>	-	-	0.03	0.06	0.07	-	-	26.40	33.00	23.10
<i>Ulmus americana</i>	0.02	0.01	0.14	0.34	0.34	9.90	6.60	42.90	49.50	33.00
<i>Vitis riparia</i>	-	-	-	0.01	0.02	-	-	-	19.80	16.50
<i>Zanthoxylum americanum</i>	+	+	+	0.01	0.01	3.30	3.30	6.60	9.90	13.20
Total	41.94	12.12	14.96	16.66	18.22	1069.20	432.30	884.40	1105.50	1131.90

(+) indicating very low presence of the species.

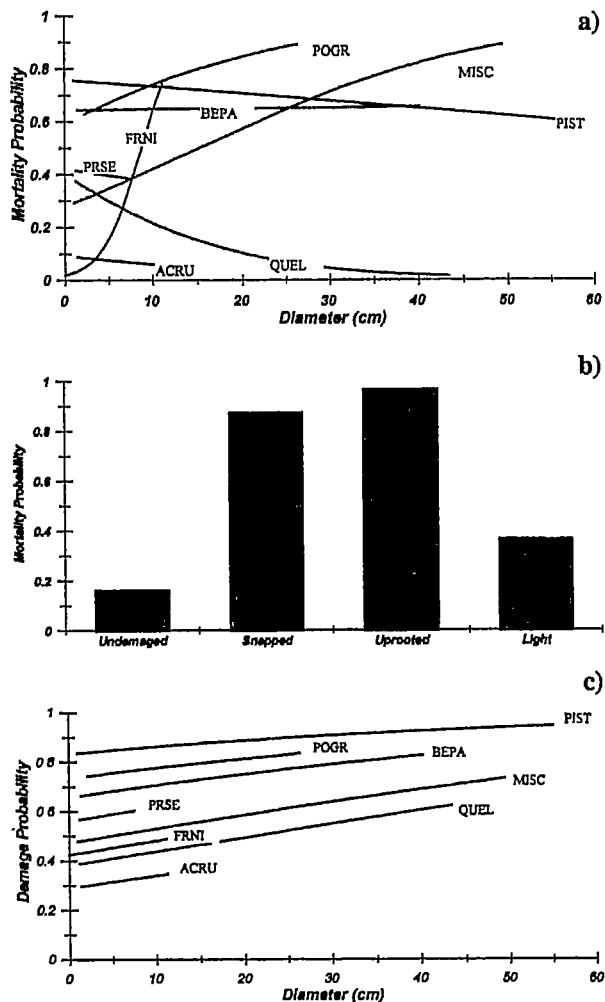


Fig. 1. Logistic models for mortality and damage probability. **a.** Mortality probability as a function of diameter for seven species (> 25 individuals with ≥ 2.5 cm DBH), as calculated by the logistic mortality model. **b.** Mortality probability as a function of damage type. **c.** Damage probability as a function of diameter for seven species, as calculated by the logistic damage model. These probabilities are only to be considered within the diameter range of each species.

ACRU = *Acer rubrum* BEPA = *Betula papyrifera*
 FRNI = *Fraxinus nigra* PIST = *Pinus strobus*
 POGR = *Populus grandidentata* PRSE = *Prunus serotina*
 QUEL = *Quercus ellipsoidalis* MISC = all species not specified in the model.

was not (Wald $\chi^2 = 1.565$, $p = 0.2109$).

The two forests differed in their initial response to disturbance, and their recovery following disturbance. The basal area of the oak forest was reduced to 42% of the pre-storm level, and in 14 years recovered at 81% of the pre-disturbance level. The pine forest was more greatly impacted. Its basal area was reduced to 29% of the pre-storm level and recovered only to 43% (Fig. 2a). Tree density in the oak forest quickly increased to well

Table 3. Logistic regression for mortality. Species are entered as dummy variables and are compared to all unspecified species. Positive values for parameter estimates indicate increased susceptibility with increases in that parameter, whereas negative values indicate decreased susceptibility.

Variable	Parameter estimate	Wald χ^2	p-value
Intercept	-0.9427	10.15	0.0014
Diameter	0.0617	4.18	0.0408
<i>Acer rubrum</i>	-1.3265	1.01	0.3142
<i>Acer rubrum</i> \times diameter	-0.1084	0.13	0.7140
<i>Betula papyrifera</i>	1.5348	10.64	0.0011
<i>Betula papyrifera</i> \times diameter	-0.0603	2.34	0.1257
<i>Fraxinus nigra</i>	-3.5145	8.10	0.0044
<i>Fraxinus nigra</i> \times diameter	0.3833	4.50	0.0340
<i>Pinus strobus</i>	2.0854	28.70	0.0001
<i>Pinus strobus</i> \times diameter	-0.0746	5.32	0.0211
<i>Populus grandidentata</i>	1.3200	4.30	0.0382
<i>Populus grandidentata</i> \times diameter	0.0045	0.01	0.9495
<i>Prunus serotina</i>	0.6260	0.98	0.3234
<i>Prunus serotina</i> \times diameter	-0.0820	0.25	0.6186
<i>Quercus ellipsoidalis</i>	0.5439	1.31	0.2513
<i>Quercus ellipsoidalis</i> \times diameter	-0.0882	5.45	0.0195

above the initial values, but experienced a decline from 1993 to 1997. In contrast, in the pine forest, tree density returned to near pre-storm levels in 1997 (Fig. 2b).

The size distribution of stems over the 14 yr of the study (Fig. 3) clarifies the forest dynamics of these two sites. In both forests, all size classes showed decreases in stem number immediately following the storm due to mortality. In the pine forest, three of the size classes greater than 15 cm showed recovery approximating their pre-storm densities, while three were substantially smaller. Size classes 15 cm and smaller had densities that exceeded the pre-storm levels. In the oak forest, however, the larger size classes demonstrated recovery approximating their pre-storm densities. The smaller size classes also showed a large increase in stems that exceeded pre-storm densities, but the two smallest size classes showed declines between 1993 and 1997.

Prior to the storm, *Quercus ellipsoidalis* was the dominant species of the oak forest and it remained so

Table 4. Logistic regression for mortality. Positive values for parameter estimates indicate increased susceptibility with increases in that parameter, whereas negative values indicate decreased susceptibility. Damage types are entered as dummy variables and are compared to undamaged trees. $N = 593$ trees.

Variable	Parameter estimate	Wald χ^2	p-value
Intercept	-1.5552	61.28	0.0001
Diameter	-0.0036	0.12	0.7242
Snapped	3.5736	112.38	0.0001
Uprooted	4.9767	64.05	0.0001
Light damage	1.0891	19.88	0.0001

Table 5. Logistic regression for damage. Positive values for parameter estimates indicate increased susceptibility with increases in that parameter, whereas negative values indicate decreased susceptibility. All forms of tree damage are considered. Species are entered as dummy variables and are compared to all unspecified species. $N = 593$ trees.

Variable	Parameter estimate	Wald χ^2	p -value
Intercept	-0.1073	0.24	0.6233
Diameter	0.0225	4.47	0.0345
<i>Acer rubrum</i>	-0.7337	2.36	0.1241
<i>Betula papyrifera</i>	0.7585	4.99	0.0256
<i>Fraxinus nigra</i>	-0.2214	0.39	0.5310
<i>Pinus strobus</i>	1.7147	31.27	0.0001
<i>Populus grandidentata</i>	1.1242	5.49	0.0191
<i>Prunus serotina</i>	0.3527	1.15	0.2839
<i>Quercus ellipsoidalis</i>	-0.3704	1.23	0.2681

throughout the 14 years of the study. The basal area of *Q. ellipsoidalis* was reduced to 79% of the pre-storm level, but by 1997 it exceeded the pre-storm level (Table 1). *Betula papyrifera*, *Populus grandidentata*, *Pinus banksiana* and *P. strobus* suffered large reductions in basal area, which they did not recover after 14 yr. *Acer rubrum* and *Fraxinus nigra* were originally minor components of the forest, but by 1997 had increased in basal area 17-fold and 9-fold, respectively.

In the pine forest *Pinus strobus* was the dominant species in terms of basal area and remained dominant throughout the study. *P. strobus* was reduced to 28% of its pre-storm basal area, but after 14 yr its basal area had recovered only to 35% of its pre-storm level (Table 2). *Betula papyrifera* also showed a large reduction in basal area, and did not recover to its pre-storm level. In contrast, a number of species showed large increases in basal area throughout the study, including

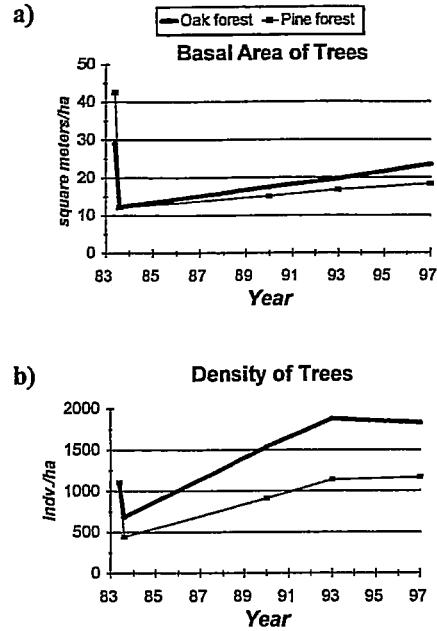


Fig. 2. Tree basal area (a) and tree density (b) as a function of time since the windstorm. The initial decline in 1983 represents the direct effects of the storm.

Acer negundo, *Acer rubrum*, *Fraxinus nigra*, *Prunus pensylvanica*, *Prunus serotina*, *Quercus alba*, *Quercus ellipsoidalis*, *Ulmus americana* and *Zanthoxylum americanum*.

Changes are not restricted to changes in abundance; there were also new appearances and disappearances. In the oak forest (Table 1), *Pinus banksiana*, *Pinus resinosa* and *Ulmus americana* were removed during the storm and did not re-establish. *Vitis riparia* and *Ilex verticillata* eventually became established. *Cornus alternifolia* and *Corylus americana* became established during the course of the study, but had disappeared by 1997. There were no

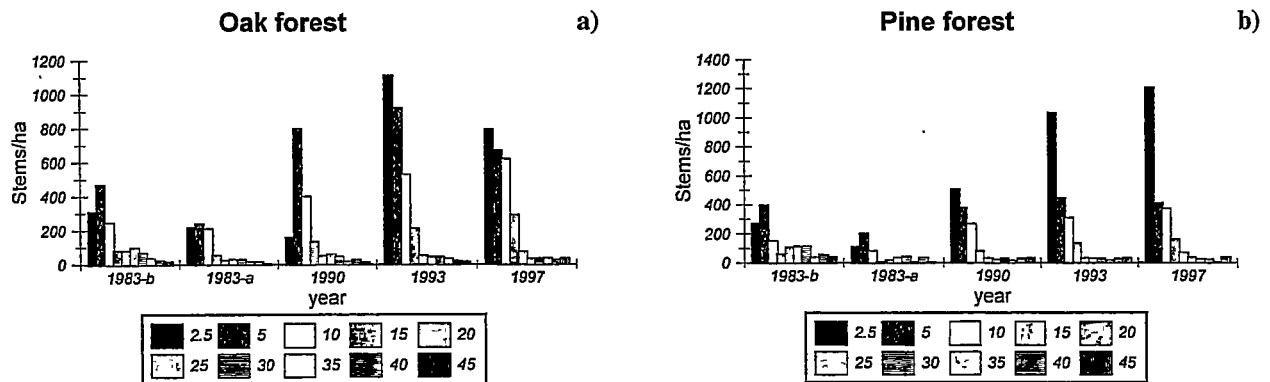


Fig. 3. Size distribution of all stems as a function of sampling period. 1983b refers to before the storm, and 1983a represents after the storm. Stems are divided into 5-cm DBH size classes, with the exception of trees under 5 cm which are divided into the classes 1 - 2.5 cm and 2.6 - 5 cm. Size classes are identified by their upper limit.

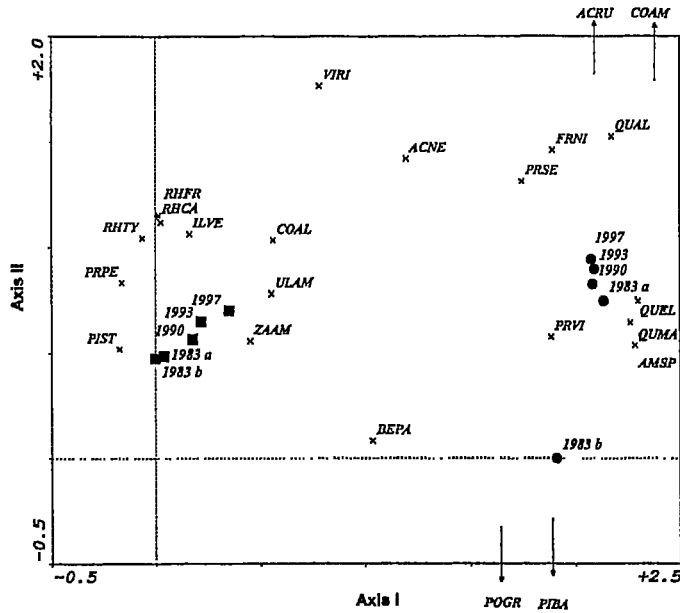


Fig. 4. Species and site scores for the first and second axis of the DCA based on basal area of trees (eigenvalues were 0.731 and 0.053 respectively and the variance explained by the first two axes was 82.7%). ● = oak forest and ■ = pine forest (labels indicating the sampling year and 'b' for before the storm and 'a' for after). The third axis (not shown; eigenvalue = 0.009) did not reveal interpretable patterns for species or sites.

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 = *Pinus strobus*
 PRPE = *Prunus pensylvanica* PRSE = *Prunus serotina*
 PRVI = *Prunus virginiana* POGR = *Populus grandidentata*
 QUAL = *Quercus alba* QUEL = *Quercus ellipsoidalis*
 QUMA = *Quercus macrocarpa* RHCA = *Rhamnus cathartica*
 RHFR = *Rhamnus frangula* RHTY = *Rhus typhina*
 ULAM = *Ulmus americana* VIRI = *Vitis riparia*
 ZAAM = *Zanthoxylum americanum*.

disappearances in the pine forest, but there were five new species: *Amelanchier spec.*, *Rhamnus cathartica*, *Rhamnus frangula*, *Rhus typhina* and *Vitis riparia* (Table 2). It is possible that some of the appearances and disappearances do not reflect true introductions and extinctions, but rather recruitment from, and dieback to, smaller size classes.

Differences in the composition and dynamics of the two forests are seen in an ordination based on basal area (Fig. 4). The first ordination axis shows a strong site effect, with species typical of the pine forest on the left and species typical of the oak forest on the right (Fig. 4). The second axis appears to be a temporal effect, with species that increased through time at the top, and those which decreased at the bottom. Third axis explained a low proportion of variability and did not reveal any interpretable pattern for species or sites. 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 suggests that the species that best survived the storm tended to exhibit rapid growth following the storm. A convergence process is confirmed by the ordination. Pine forest follows a path in ordination space towards oak forest plots. Disturbance could have accelerated the succession of the pine forest.

Discussion

The oak and pine forests of this study demonstrated different dynamics in the 14 years following the wind-storm. The storm acted upon the two forests of differing

composition by inflicting differential damage and causing differential mortality with respect to species and tree size. In the 14 years following the storm, differential establishment and growth of species determined the successional trajectory of the two forests. Both sites are relatively close to one another (< 1 km) and have similar soil characteristics and flat topography.

The greater damage severity on the pine site could be the result of the dominant, *Pinus strobus*, being highly susceptible to wind, but we cannot discount the possibility that higher wind speeds or greater exposure may have also contributed to the greater damage on this site.

While mortality generally increased with tree size, two species showed the reverse trend (*Pinus strobus* and *Quercus ellipsoidalis*). Mortality has generally been found to increase with tree size (Dittus 1985; Webb 1989; Baldwin et al. 1995), but a few studies have found small tree sizes to sustain high mortality (Whigham et al. 1991; Milton et al. 1994) likely a result of larger trees or branches falling on saplings (Aide 1987; Webb 1989; Clark & Clark 1991). However we did not test directly this possibility in our data.

Not surprisingly, trees receiving severe damage (snapping and uprooting) were most likely to be killed. Several hardwood species, including *Acer rubrum*, *Prunus serotina* and *Fraxinus nigra*, experienced low mortality despite being damaged, apparently due to their ability to sprout (DeCoster 1996).

Large individuals of early successional species, *P. strobus*, *Populus grandidentata* and *Betula papyrifera* had high damage rates. Many studies confirm this trend for large trees (e.g. Webb 1989; Runkle 1990; Peterson & Pickett 1991; Walker 1991) and soft-wooded, early-

successional species (Putz et al. 1983; Webb 1989; Foster & Boose 1992) being the most susceptible to wind damage. Some studies found the greatest damage to occur in mid-size trees (see Everham & Brokaw 1996), but we did not find such a pattern. Factors other than species and diameter are undoubtedly important in contributing to a tree's susceptibility to damage, including crown size (DeCoster 1996), root architecture (Mergen 1954; Fraser & Gardiner 1967) and presence of rot in the trunk (Webb 1989; DeCoster 1996).

In the oak forest, early successional species were removed by the storm. The basal areas of *P. strobus*, *P. grandidentata* and *B. papyrifera* were severely decreased by the storm, and their recovery was minor in terms of relative species dominance. Other early successional species, *P. banksiana* and *P. resinosa* were completely removed by the storm and did not recover. The dominant, *Quercus ellipsoidalis*, however, showed relatively little damage, thus maintaining its dominance throughout forest recovery. Several later successional hardwood species, including *Fraxinus nigra* and *A. rubrum*, increased their dominance following the storm. The storm appears to have accelerated succession, by removing the early successional species, thus allowing for the growth of the dominant *Q. ellipsoidalis* and other late-successional hardwoods. Recovery from the disturbance has proceeded relatively rapidly as evidenced by the regrowth of basal areas, the closure of canopy (pers. obs.) and the death of many saplings in the final census.

The windstorm caused much greater changes in the composition and structure of the pine forest. As with the oak forest, the early successional species sustained high damage and mortality, allowing for the rapid growth of understory hardwoods. The canopy dominant, *P. strobus*, was highly susceptible to damage, and thus the forest as a whole was severely impacted. The result of the high damage in the pine forest was an even greater acceleration of succession than in the oak forest, in the sense that hardwoods replaced pines.

However, there were trends in the pine forest that suggest an 'accelerated succession' model might be too simplistic. A number of the increasing species are typical of early succession (e.g. *Prunus serotina*, *P. pensylvanica*, and *Rhus typhina*). These apparently found regeneration opportunities with the increase of light and exposed soils in the tip-up mounds (Hutnik 1952; Webb 1988; Schaetzl et al. 1989; Peterson & Pickett 1990). There were also severely damaged areas in the pine forest with little tree regeneration (pers. obs.). In these areas, the lush growth of understory plants (including *Rubus* spp. and *Polygonum cilinode*; see Palmer et al. 2000, this issue), may have hindered tree establishment (Graves 1995). While accelerated succession seems to be occurring, the forest may actually be a mosaic of patches experiencing different dynamics. However, we did not

test for such a mosaic model.

The ordination illustrates the occurrence of accelerated succession in both forests. Each forest follows a path in ordination space towards more shade-tolerant, later successional species. The initial effects of the disturbance on species composition were qualitatively similar to succession following disturbance. Thus the 'acceleration' is both an immediate and a subsequent effect of disturbance.

The ordination reveals a strong gradient related with the site (axis I) and a temporal effect (axis II). The trajectory of the pine forest in ordination space points diagonally towards the oak forest trajectory, which suggests that it is becoming more similar in composition to the oak forest. Compositional convergence would be likely if the rate of change is greater in the pine forest than the oak forest. It is difficult to make definitive statements about convergence, however, as studies of successional convergence are greatly affected by temporal and spatial scales as well as the sampling design (Lepš & Rejmánek 1991).

This study illustrates the impacts of a windstorm on the dynamics of two forests that differ in composition. The storm acted to differentially damage and kill early-successional pines and hardwoods, allowing for the rapid growth of understory hardwoods. In the pine forest, where the susceptible trees were dominant, damage was severe and changes in species composition were dramatic. In the oak forest, where the susceptible trees were a relatively minor component, damage was less severe. Changes in this forest's composition were relatively minor, and forest recovery appeared to proceed rapidly. In both forests, however, the disturbance acted to accelerate succession, increasing the rate of compositional change from early successional pines and hardwoods to late-successional hardwoods. However, the 'accelerated succession' model in the pine forest may be somewhat simplistic; successional change in this forest appeared to possess elements of a mosaic model. There was some evidence of compositional convergence between the two sites.

Acknowledgements. We would like to thank the staff of CCNHA for the use of their facilities, and for partial waiver of the station fees. We also thank Dai Jun Zhang, Roxy Johnston, Jake Mykrantz, Holly Ewing, Richard Inouye, Nancy Huntly, David Tilman and the 1983 LTER field crew for logistical support and help in data collection. Finally, we thank Sylvie Gauthier and two reviewers for their constructive comments.

References

- Anon. 1990. *SAS/STAT User's Guide*. SAS Institute, Cary NC.
- Abrams, M.D. & Scott, M.L. 1989. Disturbance-mediated accelerated succession in two Michigan forest types. *For. Sci.* 35: 42-29.
- Aide, T.M. 1987. Limbfalls: a major cause of sapling mortality for tropical forest plants. *Biotropica* 19: 284-285.
- Arévalo, J.R., Fernández-Palacios, J.M. & Palmer, M.W. 1999. Tree regeneration and future dynamics of the laurel forest on Tenerife, Canary Islands. *J. Veg. Sci.* 10: 861-868.
- Baldwin, A.H., Platt, W.J., Gathen, K.L., Lessman, J.M. & Rauch, T.J. 1995. Hurricane damage and regeneration in fringe mangrove forests of Southeast Florida, USA. *J. Coastal Res.* 21: 169-183.
- Clark, D.B. & Clark, D.A. 1991. The impact of physical damage on canopy tree regeneration in tropical rain forest. *J. Ecol.* 79: 447-457.
- Clements, F.E. 1916. *Plant succession and indicators*. Wilson, New York, NY.
- DeCoster, J.K. 1996. *Impacts of tornadoes and hurricanes on the community structure and dynamics of North and South Carolina forests*. Ph. D. Dissertation, University of North Carolina, Chapel Hill, NC.
- Dittus, W.P.J. 1985. The influence of cyclones on the dry evergreen forest of Sri Lanka. *Biotropica* 17: 1-14.
- Everham III, E.M. & Brokaw, N.V.L. 1996. Forest damage and recovery from a catastrophic wind. *Bot. Rev.* 62: 113-185.
- Foster, D.R. & Boose, E.R. 1992. Patterns of forest damage resulting from catastrophic wind in central New England, USA. *J. Ecol.* 80: 79-98.
- Franklin, S.B., Robertson, P.A., Fralish, J.S. & Kettler, S.M. 1993. Overstory vegetation and successional trends of Land Between The Lakes, USA. *J. Veg. Sci.* 4: 509-520.
- Fraser, A.I. & Gardiner, J.B.H. 1967. Rooting and stability in Sitka spruce. *Forestry Comm. Bull.* 40: 1-28.
- Frelich, L.E. & Lorimer, C.G. 1991. Natural disturbance regimes in hemlock-hardwood forest of the Upper Great Lakes region. *Ecol. Monogr.* 61: 145-164.
- Gauch, H.G. Jr. 1982. *Multivariate analysis in community ecology*. Cambridge University Press, Cambridge.
- Graves, J.H. 1995. *Resource availability and the importance of herbs in forest dynamics*. Ph.D. Diss., University of North Carolina, Chapel Hill, NC.
- Hill, M.O. & Gauch, H.G. Jr. 1980. Detrended Correspondence Analysis: an improved ordination technique. *Vegetatio* 42: 47-58.
- Hosmer, D.W. & Lemeshow, S. 1989. *Applied logistic regression*. John Wiley and Sons, New York, NY.
- Hutnik, R.J. 1952. Reproduction on windfalls: a northern hardwood stand. *J. For.* 50: 693-694.
- Kartesz, J.T. 1994. *A synonymized checklist of the vascular flora of the United States, Canada, and Greenland*. Timber Press, Portland, OR.
- Lepš, J. & Rejmánek, M. 1991. Convergence or divergence: what should we expect from vegetation succession. *Oikos* 62: 261-262.
- Lorimer, C.G. 1980. Age structure and disturbance history of a Southern Appalachian virgin forest. *Ecology* 61: 1169-1184.
- Mergen, F. 1954. Mechanical aspects of wind-breakage and windfirmness. *J. For.* 52: 119-125.
- Milton, K., Laca, E.A. & Demment, M.W. 1994. Successional patterns of mortality and growth of large trees in a Panamanian lowland forest. *J. Ecol.* 82: 79-87.
- Overpeck, J.T., Rind, D. & Goldberg, R. 1990. Climate-induced changes in forest disturbances and vegetation. *Nature* 343: 51-53.
- Palmer, M.W., McAlister, S.D., Arévalo, J.R. & DeCoster, J.K. 2000. Changes in the understory during 14 years following catastrophic windthrow in two Minnesota forests. *J. Veg. Sci.* 11: xxx-yyy (this issue).
- Perry, D.A. 1994. *Forest ecosystems*. The Johns Hopkins University Press, London.
- Peterson, C.J. & Pickett, S.T.A. 1990. Microsite and elevational influences on early forest generation after catastrophic windthrow. *J. Veg. Sci.* 1: 657-662.
- Peterson, C.J. & Pickett, S.T.A. 1991. Treefall and resprouting following catastrophic windthrow in an old-growth hemlock-hardwood forest. *For. Ecol. Manage.* 76: 763-774.
- Pickett, S.T.A. & White, P.S. (eds.) 1985. *The ecology of natural disturbance and patch dynamics*. Academic Press, New York, NY.
- Putz, F.E., Coley, P.D., Lu, K., Montalvo, A. & Aiello, A. 1983. Uprooting and snapping of trees: structural determinants and ecological consequences. *Can. J. For. Res.* 13: 1011-1020.
- Runkle, J.R. 1990. Gap dynamics in an Ohio *Acer-Fagus* forest and speculations on the geography of disturbance. *Can. J. For. Res.* 20: 632-641.
- Schaetzl, R.J., Burns, S.F., Johnson, D.L. & Small, T.W. 1989. Tree uprooting: review on impacts on forest ecology. *Vegetatio* 79: 165-176.
- Swain, P.C. 1972. *An analysis of morphological differences among oaks in selected Minnesota stands of Quercus borealis*. M. Sc. Thesis, University of Minnesota.
- ter Braak, C.J.F. 1998 & Šmilauer, P. *CANOCO reference manual and user's guide to CANOCO for windows: software for canonical community ordination (Version 4)*. Microcomputer Power, Ithaca, NY.
- Tilman, D. 1988. *Plant strategies and the dynamics and structure of plant communities*. Princeton University Press, Princeton, NJ.
- Walker, L.R. 1991. Tree damage and recovery from Hurricane Hugo in Luquillo Experimental Forest, Puerto Rico. *Biotropica* 23: 379-385.
- Webb, S.L. 1988. Windstorm damage and microsite colonization in two Minnesota forests. *Can. J. For. Res.* 18: 1186-1195.
- Webb, S.L. 1989. Contrasting windstorm consequences in two forests, Itasca State Park, Minnesota. *Ecology* 70: 1167-1180.
- Whigham, D.F., Olmsted, I., Cano, E.C. & Harmon, M.E. 1991. The impact of Hurricane Gilbert on trees, litterfall, and woody debris in a dry tropical forest in the northeastern Yucatan Peninsula. *Biotropica* 23: 434-441.

Received 2 December 1998;

Revision received 15 September 1999;

Accepted 13 January 2000.

Coordinating Editor: O. Engelmark.