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Causes of spatial patterns of dead trees in forest fragments in Illinois

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Abstract

Natural disturbances introduce spatial heterogeneity into forests by causing non-random mortality of trees. We examined whether wind was the primary cause of spatial patterns of dead trees at fragment- and individual tree-levels in three fragments of temperate deciduous forests in Illinois, USA. Dead trees and wind-caused types of mortality were expected to be higher at forest edges, on windward aspects, in poorly-drained soils, and adjacent to existing canopy gaps. The extent of wind-related mortality was determined by comparing spatial and temporal patterns of dead trees, as well as characteristics of trees downed by single windstorms versus all dead trees. At the fragment-level, we used randomly located quadrats of 25×25 m to sample edge and interior areas of Trelease Woods, Brownfield Woods, and Hart Woods in 1995-1996 and again in 1999-2000. We noted type of mortality (standing dead, snapped-off, or uprooted trees), and measured DBH ($\geq$ 10 cm) and direction of fall of each dead tree. The same measures were made for trees felled by two single storms in 1994. At the individual tree-level, domino effects were evaluated by comparing openness surrounding target treefalls vs. an equal sample size of living trees. The study provided limited evidence that wind caused spatial patterns of dead trees. Instead, spatial patterns of dead trees in the fragments accumulated from domino effects at the individual tree-level in two of the three fragments. Dead trees were more associated with preexisting gaps. Contrary to our predictions at the fragment-level, the frequency of dead trees was not greater at edges, on windward aspects, or in poorly drained soils. This study demonstrated the complexity of spatial patterns of dead trees in forest fragments. The significant domino effects indicated that the occurrence of dead trees was not random, but determined by previous disturbances.

Introduction

Natural disturbances introduce spatial heterogeneity into forests by causing non-random mortality of trees (Harmon et al. 1986; Everham and Brokaw 1996). Over time, the spatial patterns of dead trees that accumulated from multiple disturbances reflect to some extent the spatial heterogeneity of disturbances (Muller and Liu 1991; Rebertus et al. 1997). The linkage between spatial patterns of dead trees and disturbances should be especially strong if a forest ecosystem is dominated by a single type of disturbance (Rebertus et al. 1997). In such a forest, spatial patterns of dead trees may be caused largely by the spatial heterogeneity of the primary disturbance agent.

Windstorms may be the main cause of spatial patterns of dead trees in deciduous forests in the U.S.A., where small-scale disturbances, caused by the death of a single or multiple trees, are dominant (Runkle 1985; Runkle 1990; Oliver and Larson 1996). Windstorms, disease, lightning, and senescence have been attributed as disturbance agents in these forests (Runkle 1985; McCune et al. 1988). The role of windstorms may be particularly important in forest fragments of deciduous forests. Fragmentation induces complex wind profiles near forest edges and increases turbulence and wind speed (McNaughton 1989; Kruijt et al. 1995). As a result, wind may cause a relatively high proportion of tree mortality in a forest fragment, thus determining its spatial patterns of dead trees.

Identifying spatial patterns of wind mortality is difficult, because such mortality results from complex interactions between wind characteristics and various biotic and abiotic factors (Everham and Brokaw 1996; Ruel 2000; Kramer et al. 2001). Furthermore, windstorms operate at multiple spatial and temporal scales (Attiwill 1994; Ulanova 2000). As a result, spatial patterns of tree mortality caused by wind are difficult to characterize and predict without taking into consideration multiple factors and scales.

Studies of episodic storms provide a direct link between wind and tree death. Their contribution to overall spatial patterns of dead trees can be evaluated by comparing tree mortality caused by independent windstorms versus overall patterns (Rebertus et al. 1997). If windstorms are primarily responsible for spatial patterns, the overall patterns represent an accumulation from multiple episodic storms. Similar patterns are expected from single storms and overall, especially if winds come from a prevailing direction.

Spatial patterns of dead trees cannot be divorced from temporal patterns of tree mortality, which are also complex. Multiple censuses in permanent plots document overall rates of tree mortality (Sheil and May 1996; Laurance et al. 1998), but they do not evaluate the relative importance of episodic disturbances, unless annual censuses occur over a long time. The influence of episodic storms can be estimated by comparing the magnitude of tree mortality caused by single windstorms versus annual mortality rates arising from multiple causes.

Given this spatial and temporal complexity of wind damage, studies must simultaneously appraise tree mortality at multiple levels of space and time (Ruel 2000). In this study of forest fragments, we took an integrated approach to determine whether wind causes spatial patterns of dead trees at both fragment- and individual tree-levels. We also compared mortality overall vs. from episodic windstorms.

Spatial patterns of wind-caused mortality at the fragment-level may arise because complex wind patterns are generated as wind interacts with topography, trees in different soil types, and forest fragment edges. For example, wind damage is greater on windward slopes (Everham and Brokaw 1996; Kramer et al. 2001) and in moist soils where root support is weaker (Brokaw 1985; Mayer 1989). The evidence for greater wind damage at forest fragment edges is mixed. Some studies show greater mortality (Bierregaard et al. 1992; Laurance et al. 1998) and density of dead trees (Williams-Linera 1990) at forest edges. Other studies document that tree fall density (Laurance 1997) and canopy cover (Turton and Freiburger 1997) are not greater near edges. Confounding factors, such as topography (Laurance 1997) and history of the fragments (Murcia 1995), may be responsible for these inconsistent findings.

Spatial patterns of wind-caused mortality at the individual tree-level may be generated because wind interacts with existing gaps. The combination of increased wind turbulence in existing gaps and the greater exposure of trees to wind may result in a higher mortality rate of border trees, thus generating ‘domino’ effects (Spurgel 1976; Foster and Reiners 1986). They cause non-random patterns of tree death, and are influenced by the distribution of existing gaps (Hubbell and Foster 1986; Tanaka and Nakashizuka 1997). Ultimately, they may be a consequence of the forest’s disturbance history (Everham and Brokaw 1996).

The study’s objective was to determine whether wind is the primary cause of spatial patterns of dead trees in three fragments of temperate deciduous forest. Spatial patterns of dead trees and their type of mortality were expected to reflect wind heterogeneity generated as wind interacts with forest edge and aspect, soil drainage, and existing canopy gaps. The spatial patterns of dead trees were examined separately at fragment- and individual tree-levels.

Fragment-level predictions were: 1) More dead trees and wind-related damage (snapped-off and uprooted trees) occur at forest edges, especially on windward aspects, because trees have greater exposure to strong winds at edges than in the forest interior (Bierregaard et al. 1992; Laurance et al. 1998), and 2) More uprooted trees occur in poorly-drained soils because trees with weak root support are more vulnerable to wind (Brokaw 1985; Mayer 1989).

The individual tree-level prediction was that domino effects occur, i.e., trees are more likely to fall adjacent to existing gaps than is a random tree in a forest. This phenomenon results in a more open area surrounding a recent dead tree than a living tree. Domino effects occur because asymmetric crowns of trees adjacent to gaps and their greater exposure to complex winds make them vulnerable to windthrow

Table 1. Description of forest type, stand characteristics, fragment size, soil types, topography, and land-use history of the three study sites.

	Trelease Woods	Brownfield Woods	Hart Woods
Forest type[a]	Mesic upland forest	Mesic upland forest	Dry-mesic upland forest
Fragment size	24 ha	24 ha	14 ha
Three most dominant species[b]	Sugar maple (55.7)[e] Hackberry (22.3) Slippery elm (19.3)	Sugar maple (100.0) [f] Red oak (21.6) Ohio buckeye (14.1)	White oak (98.1) [h] Black oak (57.4) Slippery elm (11.9)
Basal area (m^2 / ha)	28.1[e]	33.7 [f]	N/A
Density (stems / ha)	579 [e]	422 [f]	N/A
Canopy Height [c] (m)	25–30	25–30	20-25
Major soil types [d]	Drummer silt clay loam (M) Flanagan silt loam (M)	Xenia silt loam (AL) Russell silt loam (AL)	Martinsville silt loam (AL) Ambraw silty clay loam (M)
Drainage classes[d]	Poorly drained Somewhat poorly drained Moderately well drained	Poorly drained Somewhat poorly drained Moderately well drained Well drained	Poorly drained Somewhat poorly drained Moderately well drained Well drained
Maximum topographic relief (m)	6	9	9
Land-use history	Never clear-cut, little grazing or public use[c]	Selective logging, minor road, grazing, public use until 1935 [f, g]	Heavily logged between 1867-1876 [i]

[a] Iverson et al. 1989; [b] Number in parentheses = importance value based on relative density and relative dominance; [c] S. Buck, personal communication; [d] All soil data are from Mount (1982)(AL: Alfisol, M: Mollisol); [e] Pelz and Rolfe (1977), DBH $\geq$ 6.6 cm; [f] Edgington 1991, DBH $\geq$ 6.4 cm; [g] Leffler 1991; [h] Root et al. 1971; [i] County maps in 1867 and 1876.

(Foster and Reiners 1986; Young and Hubbell 1991; Young and Perkocha 1994). These individual tree-level deaths may obscure or reinforce patterns at the fragment-level. Therefore, we also determined whether trees involved in domino effects demonstrated spatial patterns associated with edge, aspect, or soil drainage.

Finally, the extent of wind-related mortality was determined by comparing 1) spatial patterns and characteristics (type of mortality, DBH, and directionality) of trees downed by single windstorms versus all dead trees, and 2) temporal patterns of annual mortality versus mortality from single windstorms.

Methods

Study sites and study species

This study was conducted in three forest fragments in Champaign County, Illinois, USA. (40°09' N, 88°10' W)(Table 1). Trelease Woods and Brownfield Woods are old-growth remnants of a large presettlement forest known as "The Big Grove", and are located 5 km northeast of Urbana. Hart Woods is a remnant of a separate presettlement forest along the Sangamon River, and is 15 km northwest of the other two fragments. Soils of the fragments are either Mollisols or Alfisols (Table 1). The major canopy species in Trelease Woods and Brownfield Woods is *Acer saccharum* Marsh. (sugar maple) (Pelz and Rolfe 1977; Edgington 1991). Hart Woods is dominated by *Quercus alba* L. (white oak) and *Quercus velutina* Lam. (black oak) (Root et al. 1971). Nomenclature is based upon Mohlenbrock (1986).

The average annual temperature (1961-1990) is 10.9 °C at the Champaign weather station (Illinois Water Survey data). January is the coldest month (-4.6 °C) and July is the hottest month (23.9 °C). Average annual precipitation is 101 cm with a maximum monthly mean in July and a minimum in January. Average daily wind speed was 2.7 m/s during this study (1994-2000). Daily maximum wind gusts ranged from 0.3 to 24.5 m/s from 1994-2000. The minimum wind gusts that can damage individual or small groups of trees is estimated between 22-25 m/s (Savill 1983; Webb 1989). Of the three records exceeding 22 m/s, severe damage occurred only from the storm of November 21, 1994 in Trelease Woods.

The fragments differ in their land-use history (Table 1). Trelease Woods and Brownfield Woods are old-growth forests and have had no major human disturbances. Large, old oaks, common in Trelease Woods and Brownfield Woods, are lacking in Hart Woods. It is considered a secondary forest, judging from the even size distribution of oak trees in the fragment.

Fragmentation of these three forests occurred in the late 19th century. The current size and shape of the forest fragments were established by 1918. All fragments have well-defined edges maintained by mowing. Trelease Woods and Brownfield Woods are quadrangles with sides oriented to E, N, S, W, and are surrounded by roads, agricultural fields, and human residencies. Hart Woods is surrounded by roads and human structures on the east and north sides and is adjacent to a flood plain forest and a river on the south and west sides, respectively.

Dutch elm disease in the 1950s killed many American elms (*Ulmus americana* L.) and slippery elms (*Ulmus rubra* Muhl.), two important components of all study sites at the time (Boggess 1964; Root et al. 1971; Pelz and Rolfe 1977; Edgington 1991). Abundant dead American elm trees were noted in Trelease Woods in a survey in the 1960s (Boggess 1964). The dead trees created by this epidemic had disappeared by 2000 (Y. Lin, personal observation). Most American elm occurred in the flood plain in Hart Woods, (Root et al. 1971), an area not included in this study.

Fragment-level: edge, aspect, and soil effects

Dead trees were first sampled in Trelease Woods in 1995 and in Brownfield Woods and Hart Woods in 1996. We resampled in December 1999 – January 2000 for new trees dying after the first survey. Each fragment was divided into interior and edge (within 100 m of edges) areas. Twenty quadrats (25×25 m) were randomly established in each of these two areas in Trelease Woods and Brownfield Woods. Ten quadrats were randomly established in both interior and edge areas in the upland portion (above 210 m) of Hart Woods. Edge quadrats in Hart Woods were located within 100 m of the north and east sides; interior quadrats were greater than 100 m from the north and east edges, and at least 50 m interior to the transition zone and slope leading to the flood plain forest.

In limiting the edge area to 100 m, the narrower E-W dimension of 400 m in each fragment was taken into consideration. Prior studies have shown that wind damage can be elevated up to 100 m (Laurance et al. 1998) or $>$ 100 m (Chen et al. 1992) from the edge. We delineated all edges as 100 m, resulting in 200 m as the E-W width and 400 m as the N-S length of the interior area for Trelease Woods and Brownfield Woods. The validity of the 100 m decision was tested by determining whether frequency of dead trees differed among the four 25 m intervals (0-25, 25-50, 50-75, 75-100 m) of each 100 m edge. The frequency of dead trees did not differ among those four distances in edge areas in any fragment, when analyzed either for all trees (Trelease Woods: $x^2 = 0.43$, df = 3, $P = 0.93$; Brownfield Woods: $x^2 = 7.57$, df = 3, $P = 0.06$; Hart Woods: $x^2 = 5.38$, df = 2, $P = 0.07$) or only canopy trees (Trelease Woods: $x^2 = 2.91$, df = 3, $P = 0.41$; Brownfield Woods: $x^2 = 0.36$, df = 3, $P = 0.95$; Hart Woods: $x^2 = 3.5$, df = 2, $P = 0.17$). The sampling effort (number of quadrats) did not differ significantly among the four distances in the edge area (Trelease Woods: $x^2 = 2.0$, df = 3, $P = 0.57$; Brownfield Woods: $x^2 = 2.8$, df = 3, $P = 0.42$; Hart Woods: $x^2 = 4.4$, df = 3, $P = 0.22$). Basal area of living trees per 50×50 m quadrat did not differ significantly between edge vs. interior areas in Trelease Woods or Brownfield Woods (Trelease Woods: $t = 1.46$, df = 92, $P = 0.15$; Brownfield Woods: $t = 1.29$, df = 93, $P = 0.20$), but edge plots had a higher density of living trees in both fragments (Trelease Woods: $t = 3.93$, df = 92, $P = 0.02$; Brownfield Woods: $t = 4.38$, df = 93, $P < 0.0001$) (J. Edgington, unpublished data). Comparable data for Hart Woods were not available.

Topographic relief was so limited in all three fragments that slope was not a relevant variable in this study. Each edge quadrat was categorized into one of four aspects (N, E, S, W) based on the nearest aspect of a given quadrat. The sampling effort (number of quadrats) did not differ among aspects in any fragment (Trelease Woods: $x^2 = 0.4$, df = 3, $P = 0.94$; Brownfield Woods: $x^2 = 1.2$, df = 3, $P = 0.75$; Hart Woods: $x^2 < 0.01$, df = 1, $P > 0.99$).

Soil drainage classification was obtained from soil surveys made by the USDA (Mount 1982), which recognizes seven soil drainage classes. The study fragments included 3-4 of the seven classes (Table 1). The fragments do not contain extreme classes of drainage.

Mortality patterns of dead trees

All dead trees with diameter at breast height (DBH) $\geq$ 10 cm and rooted inside quadrats were sampled and mapped. These trees accumulated over an unknown time period. Type of mortality, DBH, direction of fallen bole, and cause of fall (primary trees felled independently or secondary trees felled by a falling adjacent tree) were determined for each dead tree. We measured DBH at 1.4 m from the ground;

for snapped-off trees, 1.4 m was either in the remaining stump or the snapped-off portion, depending on the height of the snap. The minimum size for canopy trees was set at 33 cm DBH for two reasons. First, the comparative dataset that we used for living tree (see below) set $\geq$ 33 cm as the size of canopy trees (J. Edgington, unpublished data). Second, field observations confirmed that trees of this size created canopy gaps when they fell (Y. Lin, personal observation). Trees with fully collapsed boles were not included in the study. Species of most dead trees was unidentifiable because most dead trees were highly decomposed.

Three types of mortality were recognized: uprooted, standing dead, and snapped-off. Uprooted trees have the root ball pulled up and exposed during their fall. Standing dead trees (snags) have upright boles with progressive loss of branches. Snapped-off trees have a break in their bole usually < 10 m above ground, and all woody parts above the break fall to the ground. Some standing dead trees during the first survey had uprooted or snapped-off by the second survey. Their type in the first survey was used.

Individual tree-level: domino effect

We evaluated domino effects by examining the association between a newly fallen tree and its proximity to a gap. The quadrat data could not be used because dates of treefalls and the preexisting status of trees surrounding a treefall were unknown. Instead, we used an existing dataset from the Treefall Monitoring Program (TMP) that included treefalls occurring from 1994-2000 in all fragments (S. Buck, unpublished data). Each treefall was mapped, tagged, and identified to species in each forest fragment. No standing dead trees were included in this dataset. We selected treefalls from the TMP dataset that had DBH $\geq$ 33 cm and fell independently (not knocked down by another falling tree). This subset of the TMP dataset was designated as "target trees".

Domino effects were evaluated by characterizing the area surrounding each target tree in February – March 2000. An area of 20 m radius surrounding each target tree was divided into six pie-shaped zones (per 60 degrees in compass reading). The use of 20 m as the boundary of this area around a target tree was based upon the 90th percentile (19.6 m) of the distribution of distances between 152 pairs of randomly chosen canopy trees in the three fragments. Mean distance between trees did not differ significantly among the three fragments ($F = 1.81$, df = 2,149, $P = 0.17$). Six zones were used based on the following geometric argument. We assumed equal distances between the target tree and each surrounding tree and equal radii of crowns of all canopy trees. The target tree would form an equilateral triangle with the center of each pair of surrounding trees. Given the triangle's 60° angles, six triangles (and hence six trees) fit in the 360° surrounding the central tree.

The status of the closest canopy tree in each of the six zones was placed into one of the following three mutually exclusive categories: 1) alive, 2) none, 3) died. A zone with no living canopy tree, i.e., categories 2-3, was defined as an "open zone".

For comparison, the same methodology was applied to an equal sample size of living canopy trees. These trees were chosen based on the wandering quarter method with a minimum distance of 25 m between trees (Catana 1963). Random starting points were chosen at two north and two south edges in each fragment. Thus, the area sampled for living trees and target trees was approximately the same.

Characteristics and spatial patterns of storm trees

We examined characteristics (mortality type, DBH, and directionality) and spatial patterns of trees downed by single storms. Trees felled by two isolated windstorms were included in the TMP dataset and were designated as "storm trees". A storm on November 21, 1994 in Trelease Woods felled 31 trees. The maximum wind gust on November 21, 1994 was 22.8 m/s; it ranked as the second highest wind gust during 1994-2000. Also, a storm on an unknown date in August, 1994 felled 25 trees in the upland portion in Hart Woods. The same variables were measured for storm trees as for dead trees in the quadrats. The storm trees were analyzed separately from the quadrat analyses. Almost all storm trees were not in the quadrats.

Temporal patterns of tree mortality: annual-level versus single storm events

From the resampling of the original quadrats in each fragment in December 1999 – January 2000, annual mortality rate, λ, was calculated as follows (Sheil et al. 1995):

$\lambda = (\log_e N_0 - \log_e N_1) / t$

N_0 = mean number of living trees per hectare in 1995 (trees / ha)

N_1 = mean number of living trees per hectare in 1999 or 2000 (trees / ha)

N_1 = [N_0 – mean number of trees per hectare that died between two surveys (trees / ha)]

t = interval between two surveys (yr)

λ values are estimates because the number of living trees for each quadrat was derived from a complete census in 1995 (trees ≥ 17.8 cm DBH) in Trelease Woods and Brownfield Woods (J. Edgington, unpublished data), rather than specific counts in each quadrat. In addition, number of tree deaths caused by the above single storm in Trelease Woods as a percentage of number of living trees was calculated. No data on living trees were available for Hart Woods.

Data analysis

We tested whether number of dead trees per quadrat was predicted by fragment, location (edge versus interior), soil drainage, and mean DBH of dead trees in a quadrat. Square root transformation of number of dead trees per quadrat was necessary to meet the assumptions of random and normal residuals of linear models. A general linear model was run by Proc GLM in SAS (SAS 1993). None of the variables or interactions between variable was significant in the full model. Therefore, effects of individual variables were examined separately by tests of goodness-of-fit and two-way contingency tables.

We examined separately whether more dead trees were associated with edges, windward aspects, or poorly drained soils. Tests of goodness-of-fit were used to compare total frequency of all dead trees (≥ 10 cm DBH) and canopy trees only (≥ 33 cm DBH) between edge versus interior areas, and among aspects, and soil drainage classes. Only edge quadrats were included in the aspect analysis. In the soil analysis, expected values of dead trees in each drainage class were based upon their proportional area in the sampling quadrats in each fragment. Dead trees located in somewhat poorly drained and poorly drained soils in Hart Woods were combined because of small sample size. The same analyses were done for target trees and storm trees to evaluate their fragment-level spatial patterns.

We analyzed whether wind-related types of mortality were more important at edges, on windward aspects, or in poorly drained soils. Two-way contingency tables were used to compare the relative importance of mortality types between edge versus interior areas, among aspects, and among soil drainage classes. The significance level was adjusted to $P = 0.002$ based upon Bonferroni adjustment for all goodness-of-fit and contingency tests (SAS 1993).

We compared characteristics (mortality type, DBH, and directionality) of storm trees versus all dead trees in quadrats. We extracted al dead trees with DBH ≥ 25.4 cm from the quadrat data for the DBH comparison, because 25.4 cm DBH was the minimal size used in the TMP dataset. The relative mortality type and DBH were compared by two-way contingency test and t-test, respectively. The randomness of treefall direction was tested by the Rayleigh test (Batschelet 1981); only trees felled independently were included in analyses of directionality. The Rayleigh test generates a circular statistic that is used to determine if a group of observed directions differs significantly from randomness.

Results

Fragment-level: edge, aspect, and soil effects

Forest fragments differed in density of dead trees. The total number of dead trees in the two surveys was 213 in Trelease Woods, 207 in Brownfield Woods, and 127 in Hart Woods (Table 2). Density of dead trees was 85, 83, and 102 trees / ha, respectively.

Most trees in this study were uprooted, fell independently of other trees, and fell in random directions. Overall, uprooting was more common than the other two types of mortality in all fragments (57% combined for all fragments). Eighty-five percent of all snapped-off and uprooted trees fell independently. The direction of trees felled independently of other trees was not significantly different from random in any fragment (Table 3).

No spatial patterns were associated with edge, aspect, or soil drainage in any fragment. The frequency of dead trees, when analyzed either for all trees (DBH ≥ 10 cm) or only canopy trees (DBH ≥ 33 cm), was not significantly different either between edge versus interior quadrats or among quadrats on different aspects in any fragment (Table 2, Table 3). The relative frequency of mortality types also did not differ significantly between edge versus interior quadrats or among aspects in any fragment (Table 3). The frequency of all dead trees and canopy trees was evenly distributed among soil drainage classes in each fragment (Table 3). When the analysis was restricted to uprooted trees, the frequency of dead trees also did

Table 2. The number of dead trees and their relative frequency of mortality types in edge versus interior quadrats and among aspects in the three fragments (aspect data are from edge quadrats only).

Site	Location	Sample size		Mortality type		
		n	n_q	Standing dead (%)	Snapped-off (%)	Uprooted (%)
Trelease	Interior	116	20	22	31	47
	Edge	97	20	20	28	52
	North	28	5	14	21	64
	East	30	6	20	23	57
	South	17	4	18	47	35
	West	22	5	32	27	41
	Total	213	40	21	30	49
Brownfield	Interior	90	20	10	27	63
	Edge	117	20	18	24	58
	North	20	4	20	30	50
	East	31	5	26	26	48
	South	17	4	12	29	59
	West	49	7	14	19	67
	Total	207	40	15	25	60
Hart	Interior	65	10	11	17	72
	Edge	62	10	28	19	53
	North	34	5	32	15	53
	East	28	5	21	25	54
	Total	127	20	19	18	63

n = sample size of dead trees; n_q= number of quadrats.

Table 3. Summary of test statistics for individual variables related to spatial patterns of dead trees in the three fragments.

Factor	Dependent Variable	Test Statistic	df	Trelease	Brownfield	Hart
Direction	Randomness[a,b]	r	Varies	0.17 (132)	0.07 (154)	0.09 (95)
Edge vs. Int.	Frequency[c]	X^2	1	1.69	3.52	0.07
	Frequency of canopy trees[c]	X^2	1	7.84	0.32	0.29
	Mortality type[d]	X^2	2	0.39	2.60	6.59
Aspect	Frequency[c]	X^2	3	1.11	3.93	0.58
	Frequency of canopy trees[c]	X^2	3	2.25	2.11	1.14
	Mortality type[d]	X^2	6	7.20	4.49	1.50
Soil drainage	Frequency[c]	X^2	2, 3[e]	1.07	4.62	0.20
	Frequency of canopy trees[c]	X^2	2, 3[e]	4.02	4.38	0.14
	Frequency of uprooted trees[c]	X^2	2, 3[e]	1.26	0.99	0.35

[a]Rayleigh test; (Batschelet 1981); [b]Computed test statistic; number in parentheses = sample size (n); [c]Goodness-of-fit test; [d]Two-way contingency Table; [e]df is 2 for Trelease Woods and Hart Woods, but 3 for Brownfield Woods. No tests were significant after Bonferroni adjustment (the adjusted $\alpha = 0.002$).

not differ significantly among soil drainage classes in any fragment (Table 3).

Individual tree-level: domino effects

Domino effects occurred in two of the three fragments. A dead tree was more likely to occur adjacent to an existing gap than was a random living tree in Trelease Woods and Brownfield Woods. The frequency distributions of number of open zones with no living canopy trees surrounding target treefalls versus living canopy trees differed significantly in Trelease Woods and Brownfield Woods, but not in Hart Woods (Kolmogorov-Smirnov test. Trelease Woods: x^2= 10.91, df = 2, P = 0.009; Brownfield Woods: x^2= 13.07, df = 2, P = 0.003; Hart Woods: x^2= 5.79, df = 2, P = 0.11). The distributions were shifted toward a greater number of open zones surrounding treefalls compared to the area surrounding living trees in Trelease Woods and Brownfield Woods

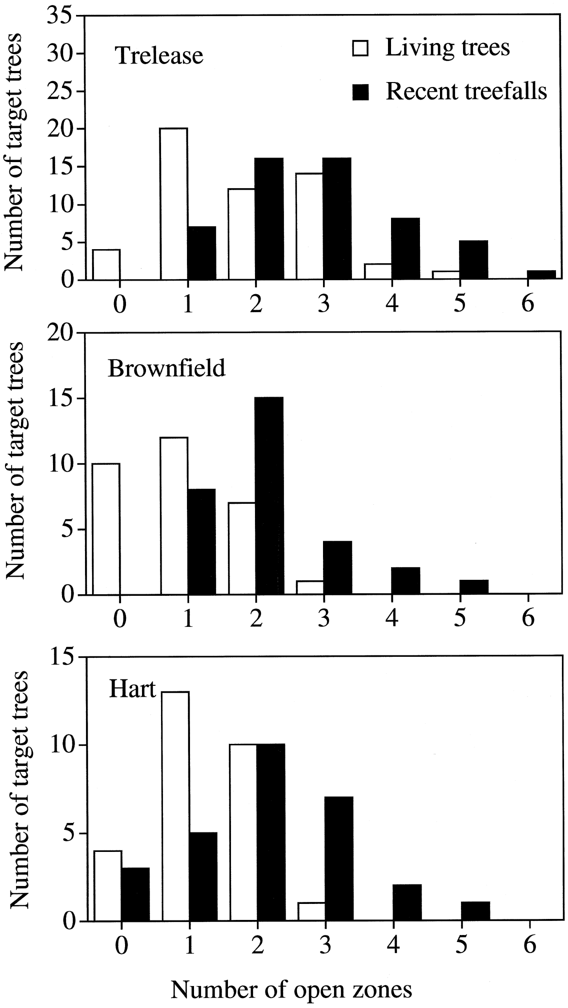

Figure 1. Frequency distributions of number of open zones surrounding target treefalls (1994-2000) versus surrounding an equal number of living canopy trees in Trelease Woods (n = 53), Brownfield Woods (n = 30), and Hart Woods (n = 28). An open zone was defined as a zone without a living canopy tree (see methods).

(Figure 1). The average number of open zones surrounding target vs. living trees was 2.83 vs. 1.87 in Trelease Woods, 2.10 vs. 0.97 in Brownfield Woods, and 2.11 vs. 1.29 in Hart Woods. Most open zones (categories 2-3) were occupied by no canopy tree or a dead tree that died prior to the fall of target trees (87% in Trelease Woods, 97% Brownfield Woods, and 71% in Hart Woods). These open zones rarely contained dead trees that fell at the same time as or after the fall of the target trees.

The target trees did not reinforce expected fragment-level patterns as they showed no spatial patterns related to edge, aspect, or soil drainage. The above target trees were evenly distributed between edge versus interior areas (Trelease Woods: $x^2 = 1.59$, df $= 1$, $P = 0.21$; Brownfield Woods: $x^2 = 1.35$, df $= 1$, $P = 0.25$; Hart Woods: $x^2 = 2.64$, df $= 1$, $P = 0.10$), among aspects (Trelease Woods: $x^2 = 3.19$, df $= 3$, $P = 0.36$; Brownfield Woods: $x^2 = 2.57$, df $= 3$, $P = 0.46$; Hart Woods: $x^2 = 3.56$, df $= 1$, $P = 0.06$), and among soil drainage classes (Trelease Woods: $x^2 = 0.44$, df $= 2$, $P = 0.80$; Brownfield Woods: $x^2 = 2.85$, df $= 3$, $P = 0.41$; Hart Woods: $x^2 = 5.54$, df $= 2$, $P = 0.06$).

Characteristics of these target trees presumably downed by domino effects were similar to the quadrat dead trees in Trelease Woods and Brownfield Woods. The relative frequency of mortality types did not differ significantly between target trees and quadrat trees in Trelease Woods ($X^2 = 0.54$, df $= 1$, $P = 0.46$), but significantly more snapped-off trees than expected occurred in Brownfield Woods ($X^2 = 5.21$, df $= 1$, $P = 0.02$). Target trees fell in random directions in both Trelease Woods and Brownfield Woods (Trelease Woods: $r = 0.19$, n = 48, $P > 0.05$; Brownfield Woods: $r = 0.05$, n = 30, $P > 0.05$).

Characteristics and spatial patterns of storm trees

Storm trees differed from quadrat dead trees in mortality types, being larger, and having directionality. Significantly more snapped-off trees occurred for the storm trees than other dead trees in Hart Woods ($X^2 = 15.9$, df $= 1$, $P < 0.0001$; Figure 2). The relative frequency of mortality type did not differ in Trelease Woods between storm trees and quadrat dead trees ($X^2 = 1.74$, df $= 1$, $P = 0.19$; Figure 2). The mean DBH of storm trees was significantly greater than the mean DBH of all quadrat trees in both fragments (Trelease Woods: $t = -2.6$, df $= 155$, $P = 0.01$; Hart Woods: $t = -4.2$, df $= 66$, $P < 0.0001$; log transformation). The mean DBH of storm trees was 61.4 cm and 60.4 cm in Trelease Woods and Hart Woods, respectively. In contrast, the mean DBH of all quadrat dead trees was 47.4 cm in Trelease Woods and 44.9 cm in Hart Woods. A strong directionality of treefall was shown for the storm trees in both fragments in contrast to the random direction of quadrat trees (Trelease Woods: $r = 0.83$, n = 16, $P < 0.001$; Hart Woods: $r = 0.77$, n = 25, $P < 0.001$) (Figure 3). Most storm trees fell toward the N-NE in Trelease Woods and the S-SE in Hart Woods.

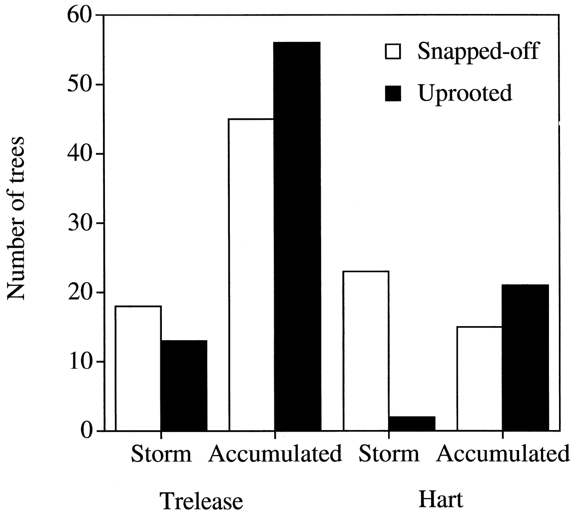

Figure 2. Comparison of number of snapped-off versus uprooted trees between all dead trees versus trees that fell in the November 21, 1994 storm in Trelease Woods and the August, 1994 storm in Hart Woods. The area used for storm trees in the analysis is 24 ha in Trelease Woods and 6.8 ha in Hart Woods. The area used for all dead trees is 2.5 ha (40 quadrats) in Trelease Woods and 1.25 ha (20 quadrats) in Hart Woods.

Storm trees were not associated with edges or poorly-drained soils in either fragment, but were more frequent on the windward aspect in Trelease Woods. Storm tree frequency did not differ between edge versus interior areas (Trelease Woods: $x^2 = 0.79$, df $= 1$, $P = 0.37$; Hart Woods: $x^2 = 3.51$, df $= 1$, $P = 0.06$) or among soil drainage classes in either fragment (Trelease Woods: $x^2 = 4.24$, df $= 2$, $P = 0.12$; Hart Woods: $x^2 = 2.69$, df $= 3$, $P = 0.26$). The total frequency of storm trees was significantly different among aspects in Trelease Woods ($X^2 = 7.78$, df $= 3$, $P = 0.05$), but not in Hart Woods ($X^2 = 0.60$, df $= 1$, $P = 0.44$). Storm trees were more frequent on the windward aspect (W) in Trelease Woods.

Temporal patterns of tree mortality: annual-level versus single storm events

The isolated storm in Trelease Woods contributed significantly to its annual tree mortality. It caused 0.8% mortality of living canopy trees, a level about one-half of the estimated annual mortality during 1995-2000. Annual mortality was higher in Hart Woods (5.2 trees/ha/yr), considered a fragment of secondary forest, than in the fragments of the two old-growth forests, Trelease Woods (3.3 trees/ha/yr) and Brownfield Woods (2.4 trees/ha/yr). Mortality rates (λ) were equivalent to 1.7% and 0.9 % of living canopy trees dying per year in Trelease Woods and Brownfield Woods, respectively. The turnover of canopy trees in Trelease Woods and Brownfield Woods was estimated at 59 and 111 years, respectively.

Discussion

The study provided limited evidence that wind caused spatial patterns of dead trees in these three fragments. Wind was apparently not the primary disturbance agent. Instead, spatial patterns of dead trees in the fragments accumulated from domino effects at the individual tree-level in two of the three fragments. Dead trees were more associated with preexisting gaps. Contrary to our predictions at the fragment-level, the frequency of dead trees was not greater at edges, on windward aspects, or in poorly drained soils.

Both direct and indirect evidence allows evaluation of whether wind caused tree mortality, thus generating spatial patterns of dead trees. First, direct evidence of wind-caused mortality arose from the large number of trees felled by the two isolated windstorms. They contributed about one half of the annual mortality in one fragment. The importance of windstorms as a disturbance agent depends also upon their frequency. The frequency of such windstorms may be too low to generate patterns and/or to swamp patterns generated by other causes. Storms with gusts strong enough to fell trees ($>$ 22-25 m/sec; Savill 1983; Webb 1989) have occurred on only five days in the past 12 years (Illinois Water Survey data).

Indirect evidence that windstorms may not predominate comes from the finding that quadrat dead trees were significantly different from the storm trees. Specifically, quadrat dead trees showed a random direction of fall, unlike the directional fall of storm trees. The inference is that many trees were felled by multiple causes, and not predominately by wind. In the study region, 77% of the prevailing wind systems are from the WNW-WSW (Changnon 1981). If such winds were to cause much tree mortality, the direction of fall overall should correspond to this prevailing wind direction (Rebertus et al. 1997). Some storms originate from other directions, diluting the prevailing direction, but they are unlikely to come from so many directions as to generate a random distribution of directions. Therefore, it is likely that

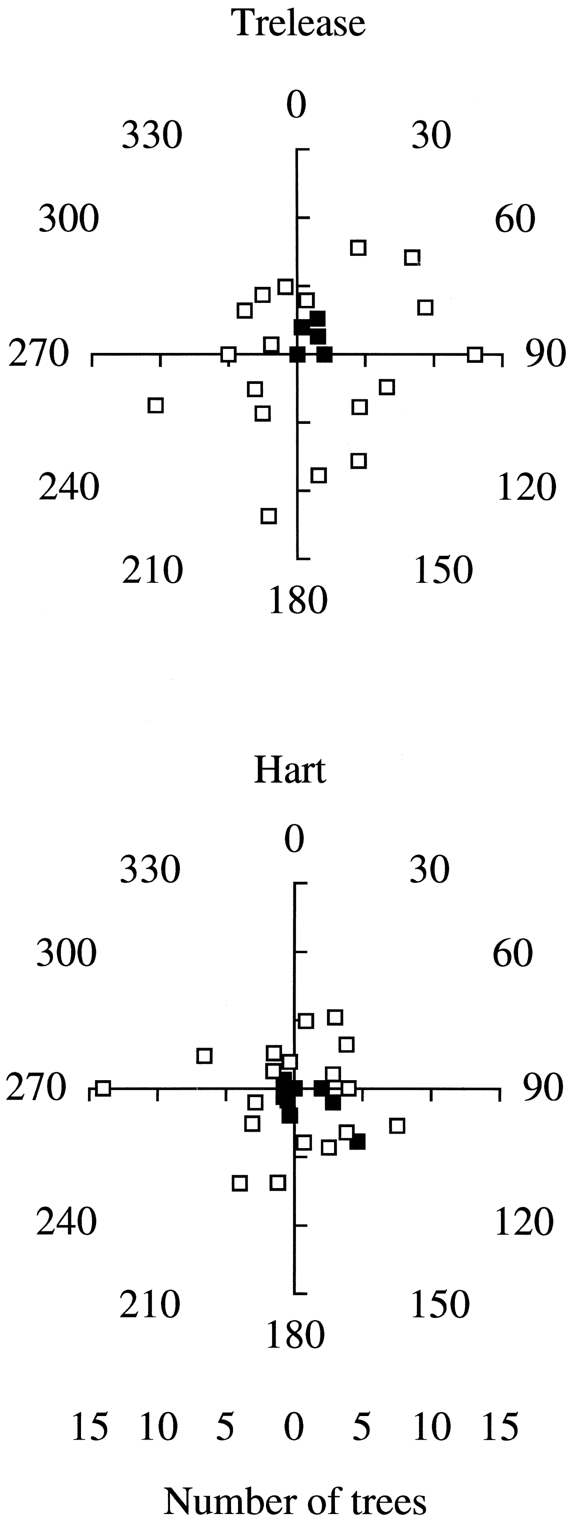

Figure 3. Circular histograms of the directionality for all dead trees (open square) versus storm trees (closed square) that fell in the November 21, 1994 storm in Trelease Woods and the August, 1994 storm in Hart Woods. Each value on the circular graph represents the midpoint of a 20° angle class (360° is divided into 18 classes). The radius of each value represents the number of dead trees in a given angle class.

many deaths arose from non-wind-related causes, such as disease and senescence. Many oak trees in Trelease Woods and Brownfield Woods are old and dying (Leffler 1991). These causes have been documented in other deciduous forests (McCune et al. 1988; Runkle 1985).

Spatial patterns of dead trees in Trelease Woods and Brownfield Woods accumulated mainly from trees falling adjacent to canopy gaps. Thus, the occurrence of dead trees was not random, but determined by previous disturbances. The occurrence of these domino effects in Trelease Woods and Brownfield Woods may be ultimately a consequence of their history of large numbers of relatively synchronous deaths by Dutch elm disease in the 1950s. The lack of domino effects in Hart Woods may arise from its lower density of American elm trees in our upland study area (Root et al. 1971).

The extent to which wind caused the domino effects in the two study fragments is not clear. Wind has been attributed as a cause of domino effects (Foster and Reiners 1986), but our study did not provide strong evidence for wind damage. Undoubtedly, some deaths were cause by wind based upon the frequency of snapped-off trees, especially in Brownfield Woods. The random direction of the fallen target trees, however, indicated other causes were also operating. Alternative explanations for domino effects include even-aged clusters of trees dying at nearly the same interval, and a tree's instability due to an asymmetrical crown arising from extension of lateral branches into existing gaps (Young and Perkocha 1994).

Domino effects have been reported in temperate deciduous forests (Tanaka and Nakashizuka 1997), spruce-fir forests (Spurgel 1976; Foster and Reiners 1986), and a tropical forest (Hubbell and Foster 1986). Kubo et al. (1996) modeled spatial patterns of gaps in a forest and concluded that their model could be improved by taking domino effects into consideration. The extent of this phenomenon is in question, however, due to inconsistent results. Mortality rates of trees adjacent to canopy gaps were not greater in some deciduous (Runkle and Yetter 1987; Runkle 1990) and tropical forests (Van Der Meer and Bongers 1996).

The fragment-level patterns expected to be generated by wind were not evident. Multiple reasons may explain this lack of patterns. First, wind was apparently not the primary disturbance agent, as discussed above. Second, any pattern generated at the fragment-level may have been diluted by deaths caused by domino effects at the individual tree-level. Target trees demonstrated domino effects, but did not show any fragment-level spatial patterns. Third, the lack of fragment-level patterns may be because the three fragments lack extremes in poor soil drainage and have almost no topographic relief. This homogeneity in physical factors would lessen any possibility for wind-generated spatial patterns.

The long history of fragmentation of the study sites is not a likely explanation for the lack of fragment-level patterns. Theoretically, trees at these old forest edges might have made morphological adjustments to wind that made them less vulnerable to windthrow. Trees exposed to wind generally have a more compact growth form with shorter branches (Telewski 1995) and higher wood density (Nadkarni et al. 2000). This explanation is unlikely in the study fragments, because edge trees have asymmetrical crowns, their trunks lean away from the forest interior, and they have more branches lower on the edge side (C. Augspurger, unpublished data). These adjustments are more likely a response to strong light rather than wind.

The lack of edge and aspect effects does not eliminate wind as a factor in causing some tree deaths. The lack of difference in mortality between edge and interior areas may be because of two non-mutually exclusive reasons. First, the small width of the fragments may result in strong penetration of prevailing winds into interior as well as edge areas. Turbulence can be elevated up to ten tree heights from a forest edge (McNaughton 1989; Kruijt et al. 1995). Given canopy heights of 25-30, the 400 m width from W to E of these fragments may be too small to produce significant edge effects. The spatial patterns of tree death caused by the 1994 storm in Trelease Woods are consistent with this estimated penetration distance. Second, the lack of edge effects on tree mortality may be explained by downbursts, rapid downdrafts of wind from single cell thunderstorms (Fujita 1981, Roberts and Wilson 1989). The localized strong wind produced by downbursts would cause severe damage at the below-fragment scale and would not be localized at edges.

Comparable data on spatial patterns of dead trees in eastern deciduous forests of U.S.A., especially in the Midwest, are limited. Tree mortality of dead trees has been estimated on a whole fragment basis (Parker et al. 1985; Runkle 1990). Spatial heterogeneity of tree mortality in relation to edge, aspect, and soil drainage has rarely been examined. Most research on forest fragments in this region has focused on edge effects on species composition (Ranney et al. 1981; Whitney and Runkle 1981; Brandeis 1988; Brothers 1993) and microclimate (Matlack 1993; Gehlhausen et al. 2000).

Temporal patterns found in our study are similar to other studies in the overall mortality rate. The range of annual mortality rates (0.9%-1.7%) and turnover times (59-111 years) in this study are within the range found in studies of other temperate deciduous forests, as determined by a variety of methodologies (Abrell and Jackson 1977; Runkle 1985; Volk and Fahey 1994; McCune et al. 1988; Nakashizuka et al. 1992; McCune and Henckel 1993; Nakashizuka and Iida 1995; Ward et al. 1996). Based on 14 stands of eastern deciduous forests in U.S.A., Runkle (1982) found that mortality rate was 0.5-2% per year; turnover time averaged 100 years. Our current estimate for mortality rate in Brownfield Woods of 0.9% per year (DBH $\geq$ 17.8 cm) is also similar to the 1.4% per year estimate from 1939-1951 in Brownfield Woods (DBH $\geq$ 7.6 cm) (Cortright 1952).

This study demonstrates the complexity of spatial and temporal patterns of dead trees in forest fragments. Spatial patterns are generated by multiple causes and from multiple spatial and temporal patterns. Treating biological processes in forest fragments as a function of distance to a forest edge (Murcia 1995) or fragment size (Esseen 1994) has proven to be too simplistic. We emphasize two approaches to further understand the mechanisms generating the complexity of spatial patterns of dead tree in forest fragments. First, our data show that an approach using more than one scale can identify causes operating at different spatial scales. Second, a retrospective approach provides one way to evaluate effects of past disturbances on present-day dynamics of forest fragments. The prevalence of domino effects suggests the importance of previous disturbances on current spatial patterns of dead trees. In the future, a multiple-scale and retrospective approach will contribute to our understanding of the complexity of tree mortality in forest fragments.

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