Implications of Windthrown Trees on Forest Succession at the University of Notre Dame Environmental Research Center

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Monica S. Depies

Advisor: Bethany Blakely

ABSTRACT

A variety of factors influence forest succession, but in the northern hardwood forests of Wisconsin and the Upper Peninsula of Michigan, windthrow is the main disturbance regime. An unusually severe thunderstorm in July of 2016 caused vast damage to many of the forests across the University of Notre Dame Environmental Research Center, leaving its mark on forest succession for many years to come. This study is a preliminary analysis of the effects this storm had on forests across property, answering the questions of whether (1) early successional species show higher susceptibility to windthrow than later successional species, (2) windthrown trees are more likely to occupy larger size classes, and finally, (3) gaps created will be small, favoring later successional, shade tolerant saplings. These questions are especially relevant today, as human induced changes to ecosystems, be it through the direct effects of forest fragmentation or the indirect effects of climate change, continue to change the dynamics of these forests. With this study, we found evidence to support that this storm will promote mid to late successional species in second growth parts of this forest, as well as mesification and declines of later successional species in old-growth forests.

INTRODUCTION

Human induced changes to forests, be it direct or indirect, are altering forest ecosystem dynamics and composition. Direct effects, such as forest fragmentation, have been shown to elevate rates of tree mortality in fragmented forests, meaning that trees near edges are subject to higher rates of stressors such as wind, which may lead to the more frequent creation of larger gaps (Esseen 1994). Even indirect effects, such as increased storm frequency and intensity due to climate change, can impact what are considered protected forests (Pinto et al. 2012). Therefore, in order to conserve and properly manage these ecosystems, it is crucial for us to further understand how forest succession is altered due to these changes.

Windstorms are historically the main drivers of succession through the disturbance of canopy trees in the mesic forests of Northern Wisconsin and the Upper Peninsula of Michigan (Canham et al. 2001; Woods 2004; Lin et al. 2004). High winds snap or uproot trees, creating gaps in the canopy that increase light to the forest floor and stimulate the growth of understory species, driving secondary succession. However, forest succession through the creation of gaps relies not only on understory composition, but also on selective canopy mortality. Because of this, in order to predict the future forest composition of a stand, it is important to determine which species in a stand are at greatest risk for mortality by wind.

Windthrow can cause a variety of disturbance intensities, opening gaps of 10s to 1,000s of meters in size (Woods 2004). Most frequently, smaller gaps, which allow little additional light to reach the understory, occur due to windthrow. These gaps favor late successional species since they are most often filled by the lateral growth of surrounding trees, which creates an unfavorable environment for the release of early successional, shade intolerant species (Woods 2004; Lin et al. 2004). This, coupled with the findings that early successional species are more susceptible to windthrow, leads to accelerated succession (Rich et al. 2007; Arevalo et al. 2000). Therefore, windthrow acts not only to remove early successional species from the canopy, but also creates an environment more conducive for the growth of later successional species, leading to late successional forest stands (Rich et al. 2007; Arevalo et al. 2000).

Early successional species are more prone to damage by wind due to their physiological characteristics. They are generally shade intolerant, meaning that they devote fewer resources to roots and wood density and more to growing up into the canopy quickly before the light source is cut off by growth of other trees, leading to overall weaker structural strength. Conversely, late successional species are able to devote more resources to wood density and more complex and deeper root systems because they are shade tolerant, causing increased resistance to windthrow (Canham et al. 2001; Rich et al. 2007).

While small gaps are the most common form of disturbance, higher intensity windstorms, such as tornadoes and thunderstorm downbursts, can cause moderate to extreme damage to canopy trees. These can create much larger gaps, encouraging the persistence of early successional species and introducing spatial heterogeneity into stands. Increased mortality rates from large windstorm events have been linked to species with larger diameters, as they are subject to greater wind forces (Canham et al. 2001; Rich et al. 2007). These events are predicted to become more frequent as climate change alters the patterns of high intensity storms (Canham et al. 2001; Woods 2004).

The mesic forests of the University of Notre Dame Environmental Research Center (UNDERC-East) experienced a severe thunderstorm in the early hours of July 21st, 2016. This storm created vast damage, causing windthrown trees throughout the property. This research acts as a preliminary case study in order to assess damage and make predictions as to how this storm will affect the future of these forests. I hypothesize that (1) early successional species will show higher susceptibility to windthrow than later successional species, (2) windthrown trees are more likely to occupy larger size classes, and finally, (3) gaps created will be small, favoring later successional, shade tolerant saplings.

METHODS

Study Site

University of Notre Dame Environmental Research Center (UNDERC-East) is a site that straddles the border between Wisconsin and the Upper Peninsula of Michigan. In total, UNDERC includes approximately 7,500 acres of land, 6,150 of that being second-growth, Northern mesic hardwood forest with a spatially complex network of forest types. On July 21st, 2016, a thunderstorm with high winds passed through the UNDERC property, causing unusually severe damage to much of the forest. This storm created many gaps within the forest canopy, and therefore may have long-lasting effects on successional processes.

Data Collection Protocol

Using a 2007 UNDERC-East GIS layer, we selected sites based on forest composition and chose two stands to sample for each forest type. We sampled late successional maple dominated forests (*Acer* spp, M1 and M2) and old-growth eastern hemlock forest (*Tsuga canadensis*, H1 and H2), as well as early successional quaking aspen dominant forest (*Populus tremuloides*, A1 and A2). Each site consisted of mature stands, avoiding lowland topography associated with wetlands, and had a contiguous area of at least 25,000 m^2, the minimum sampling area. Each site was divided into transects, utilizing lengths that accommodated site geometry, spaced 20 m apart until we had a plot size of 25,000 m^2. If next to a road or a wetland, we moved a buffer of 10 m from the edge, and then divided each transect into 40 m increments and randomly selected where a 10 m radius quadrat would be placed in each of these increments. In total, we randomly sampled a total of 12 quadrats and 15.07% of the total area in order to characterize species composition of the overstory and sapling layers. We collected data on species, diameter at breast height (DBH) 1.4 m from the ground, and distance from road or lake edge for all trees with a DBH equal to or greater than 10 cm. This was used as a representation for the forest overstory. For saplings >2 cm DBH. and <10 cm DBH, we tallied the number of each species in a 5 m radius from the center of each quadrat in order to gain knowledge about understory trees that may eventually succeed canopy trees. Along each transect, we also collected data on windthrown trees 10 m on either side of the transect from the July 2016 storm, including species, DBH, direction of fall, distance from edge, and light availability to the understory. These trees were differentiated from previous windthrown trees by signs of minimal decomposition to the wood structure (still firm), direction of tree fall, no large shelf fungal growth, and retention of bark and small branches. We differentiated trees that fell in 2017 by looking for retention of new leaves on branches.

Statistical Analysis of Data

We performed a c^2 goodness of fit test to determine whether or not the proportion windthrown trees matches the expected proportion of based on the space each species occupied in the canopy. However, in order to get a better understanding of how this may affect succession, we also performed this analysis for the proportion of sapling species to down trees. If the expected value of windthrown trees did not exceed 5, we performed a Fisher's Exact Test.

In testing the relationship between tree successional status and gap light availability, we performed a one-way ANOVA. However, since our data was not normally distributed and could not be normalized, we utilized the non-parametric Kruskal-Wallis rank sum test.

We also determined whether or not stands off of different edge types (lake and road) had significant differences in the number of down trees through performing a one-way ANOVA.

Finally, we compared the mean DBH of windthrown trees to canopy trees. The data was not normal and could not be normalized, and therefore we performed a Kruskal-Wallis test in replacement of a two-sample t-test. All statistical analyses were performed in R.

RESULTS

Each site was analyzed for diversity using the Shannon Diversity Index (Table 1). This test utilizes species richness and evenness, and was quantified for stems greater than or equal to 10 cm DBH, as well as the sapling layer. Maple forests had by far the lowest H' values due to the overwhelming dominance of sugar maple trees, leading to stands with low diversity. However, both the Aspen and Hemlock stands had relatively high tree diversity compared to the maple stands, with H' near or exceeding 1 for both seedling and overstory.

Results of the c^2 and Fisher's Exact Test varied with both species and site. At M2, sugar maple trees were less likely to be windthrown compared to the overstory ($p=0.03853$, FET).

Alternatively, this stand also showed ash trees to have a significantly greater proportion of down trees from what was expected ($p=0.04921$, FET). We also found that both sugar maple ($p=2.474e-10$, FET) and ash ($p=0.002482$, FET) down trees are overrepresented compared to their sapling layer.

In H2, Balsam fir was overrepresented in the number of windthrown trees compared to the percent it occupies in the overstory (chi-squared $(1,50)=17.984$, $p=2.228e-05$). Sugar maple trees were also less likely to be windthrown compared to what was expected (chi-squared $(1,50)= 6.577$, $p=0.01033$). In the sapling layer, red maple had fewer down trees compared to what was expected from the sapling layer (chi-squared $(1,50)= 5.2138$, $p=0.02241$). Alternatively, hemlock showed a significant overrepresentation of windthrown trees compared to the sapling layer ($p=0.0002311$, FET).

Just as in the H2, in A2 we found a underrepresentation of red maple windthrown trees compared to the proportion of saplings ($p=0.007519$). For quaking aspen, we found a greater proportion of down trees compared to the proportion of saplings ($p=0.01238$).

Using a non-parametric Kruskal-Wallis rank sum test, we found no significance in whether or not species successional status impacts the light made available in the gaps of fallen trees ($df=2$, $p=0.5431$).

We performed a one-way ANOVA and found that stands on the eastern edge of lakes had significantly more windthrown trees than stands off of a road edge ($F(1,4)=183.4$, $MSE= 1925.3$, $p=0.000172$).

Finally, we found a significant difference between the average DBH of windthrown and live trees, with windthrown trees having a larger DBH than overstory trees ($df=1$, $p=2.342e-05$).

DISCUSSION

UNDERC hosts a mosaic of varied forest stands, wetlands, and lakes. This creates a diverse landscape that may be differentially affected by strong winds. Therefore, understanding the different successional processes these forests go through after widespread disturbance gives important insight for the future forest tree composition. Many different variables have been shown to impact species susceptibility to windthrow, such as DBH, species physical characteristics, distance from an edge, topography, as well as many others (Ruel 1995). Through our survey of the UNDERC property, we took many of these variables into consideration in order to determine how these forests were affected by an unusually intense thunderstorm in late July of 2016.

While we initially expected the strongest interaction for susceptibility to windthrow would be species successional status and DBH, we discovered that edge type (lake or road) was a much more important indicator when looking at overall stand damage. The two sites with the greatest number of down trees, M2 and H2, were both located on the eastern edge of lakes. M2 was sampled off of Roach Lake, which has an area of 45.07 ha, and H2 was sampled off of Plum Lake, with an area of 91.43 ha. These lakes act as large gaps, much larger than those created by the roads around the property. In this region, storms also move from west to east, meaning that sites located on the eastern side of a large gap would be subject to greater wind forces, causing more down trees.

Another similarity between these two sites is topography, which also has effects on wind speed. M1 has many ridges and swales that run east to west, which may have worked to funnel wind to these low lying areas as they narrowed, causing high densities of windthrown trees (Ruel 1995). H2 suffered the most damage at high topographical relief compared to the surrounding landscape, as wind turbulence and speed increases when passing over a ridge (Ruel 1995).

While location was the main driver of windthrown trees, there were also important results in relation to species. The majority of the tree species across sites showed the results we expected, with the proportion of windthrown trees predicted by the percent that species occupied within the overstory. Since we found this strong of a relationship for so many species, it made those that significantly deviated from the expected that much more interesting, giving us insight into processes of forest succession. In relation to succession, the most insight was gained at the sites hit hardest by the storm, M2 and H2, as well as the early successional A2.

In M2, our results showed that sugar maple is increasing in its dominance through its replacement of ash trees, which are more susceptible to windthrow. However, the sapling understory adds an important chapter to the story of the future of this stand. The proportion of both ash and sugar maple windthrown trees was much greater than what would have been expected based on the sapling layer. This maple forest was much different from M1, with a thick herb layer dominated by a species of nettle (family *Urticaceae*), especially where there were large gaps in the canopy created by windthrown trees. This herbaceous plant can grow up to 40 inches tall, and since it forms such a dense layer, it may prevent the release of seedlings by shading them out. However, as the gaps begin to close due to lateral ingrowth of surrounding trees, this herb layer might thin, causing the growth of shade tolerant seedlings and saplings.

Our results for H2 also gave insight into the future forest composition of this stand. Old-growth hemlock trees were found to be underrepresented in the sapling layer compared to number of windthrown trees. This could point to Hemlock slowly being replaced, as when these trees suffer mortality, be it from wind or another factor, they will most likely be replaced by a faster growing species. Another species that may be outcompeted in this stand is balsam fir. It was found to have a higher susceptibility to windthrow, and therefore could be replaced by a species that is more shade tolerant with a smaller likelihood for windthrow, as was found with sugar maple. However, in a few large gaps, there were higher densities of balsam fir saplings, meaning that while it may be replaced in areas with decreasing light availability, it may instead begin to occupy areas with greater light availability. Red maple saplings were also much more abundant than what was anticipated. They were often found in gaps or low-lying areas, which may cause them to compete with balsam fir saplings.

We also discovered expected, but still meaningful results for the succession of A2. Quaking aspen is an early successional, short-lived species, and therefore it is not surprising that these trees fell at a higher rate than what would be expected by the sapling layer. Sites dominated by this species have canopies that allow high amounts of light to reach the understory and stimulate growth. However, since quaking aspen is an early successional, shade intolerant species, it cannot compete in the thick understory layer without large-scale disturbances. From our data, we can predict that red maple, may replace aspen as the dominant species, moving this stand from consisting of early-successional species to mid-successional trees. In the future, it would be interesting to see whether or not quaking aspen can continually regenerate in an early successional forest on the eastern edge of a large gap, such as a lake, since we found these sites to experience high rates of disturbance from windthrow. Alternatively, this may lead to the prevalence of later successional trees, as they are more resistant to windthrow (Woods 2004; Lin et al. 2004).

Overall, our results both support and challenge the previous literature findings. While the mean DBH for windthrown trees was larger on average than overstory trees, it was still not as large as expected. What we predicted was that the largest DBH class species would fall the most frequently, yet what we found is that midsized trees actually fall the most regularly (Figure 1). This may be due to the fact that these are primarily second-growth forests, and therefore do not have many old growth trees to occupy larger DBH categories.

These results are important not only for the regional UNDERC property, but also for the wider range of northern mesic forests. Many of our results support those from Amatangelo *et al*. (2011), who found an overall mesification and homogenization of similar forest types. Our study has shown not only that maple is likely to remain dominant in its current habitat, but also that it is slowly creeping into both early successional aspen forests as well as succeeding old-growth hemlocks. This is presumed to occur for a variety of reasons, such as fire suppression across the landscape and deer herbivory of sensitive trees such as hemlock (Amatangelo et al. 2011). This, coupled with evidence that climate change will alter forest disturbance regimes, could cause vast changes to the future of the composition of these forests (Pinto et al. 2012). Therefore, we must continue to perform long-term studies of these forests to further grasp the implications these changes have on all other ecosystem processes.

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REFERENCES

Arevalo J. R., J. K. DeCoster, S. D. McAlister, and M. W. Palmer. 2000. Changes in two Minnesota forests during 14 years following catastrophic windthrow. *Journal of Vegetation Science*. 11(6):833-840.

Canham C. D., M. J. Papaik, and E. F. Latty. 2001. Interspecific variation in susceptibility to windthrow as a function of tree size and storm severity for northern temperate tree species. *Canadian Journal of Forest Research*. 31(1):1-10.

Esseen P. A. 1994. Tree mortality patterns after experimental fragmentation of an old-growth conifer forest. *Biological Conservation*. 68(1):19-28.

Lin Y, M. L. Hulting, and C. K. Augspurger. 2004. Causes of spatial patterns of dead trees in forest fragments in illinois. *Plant Ecology*. 170(1):15-27.

Pinto, J. P., M. K. Karremann, K. Born, P. M. Della-Marta, M. Klawa. 2012. Loss potentials associated with European windstorms under future climate conditions. *Climate Research*. 54(1): 1-20.

Rich, R. L., L. E. Frelich, and P. B. Reich. 2007. Wind-throw mortality in the southern boreal forest: Effects of species, diameter and stand age. *Journal of Ecology*. 95(6):1261-1273.

Ruel, J. C. 1995. Understanding windthrow: silvicultural implications. *The Forestry Chronicle*. 71(4): 434-445.

Woods K. D. 2004. Intermediate disturbance in a late-successional hemlock-northern hardwood forest. *Journal of Ecology*. 92(3):464-476.

FIGURES AND TABLES

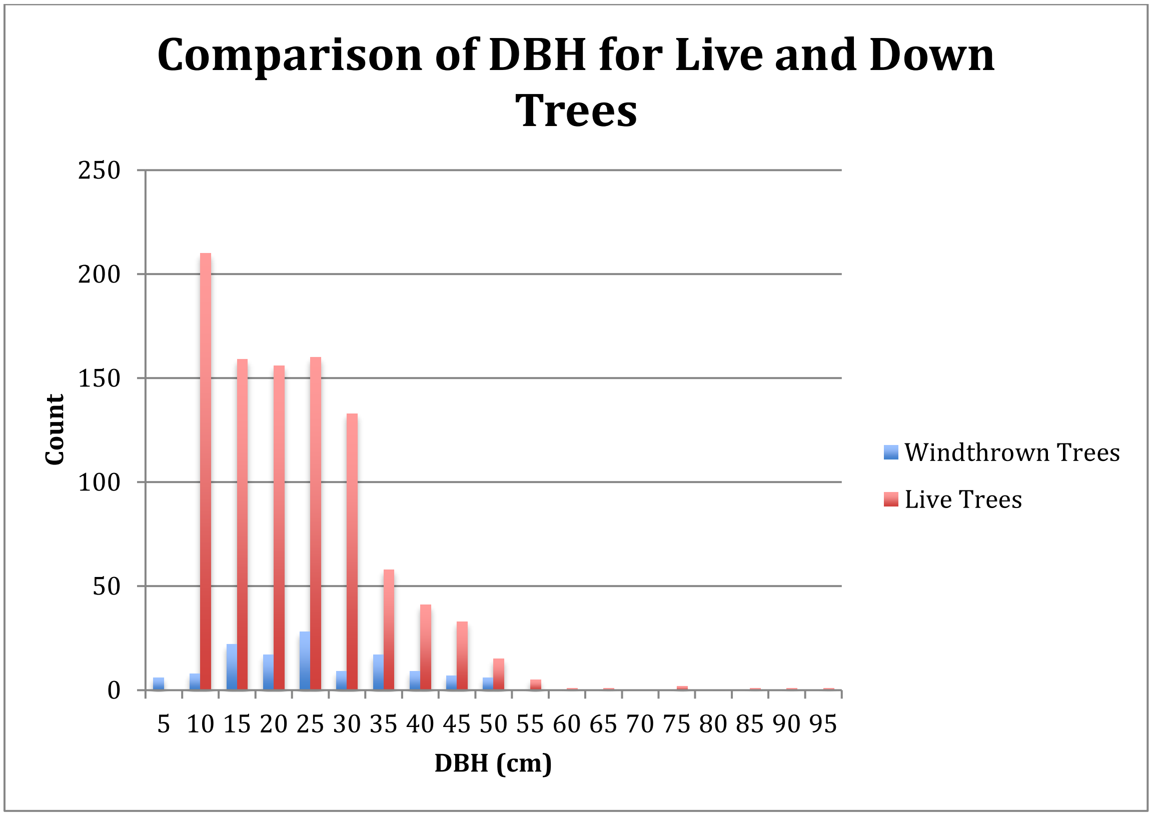

Figure 1. DBH was separated into 5 cm increments for both windthrown and live (overstory) trees in order to see if the counts between the two match. The overstory layer is not scaled to represent the entire site, just the sampled quadrats. While windthrown trees peak at the 25-30 cm DBH size class category, the most abundant group of overstory species have a DBH of 10-15 cm.

Table 1. Shannon Diversity Test to determine the diversity ranking of each site. Sites with more diverse tree species evenness and richness have a higher H' value.

	A1	A2	M1	M2	H1	H2
Overstory Layer	1.71	1.22	0.16	0.31	1.19	1.65
Sapling Layer	1.14	1.04	0.64	0.30	0.93	1.21