

forest ecology

Nitrogen Availability Decreases the Severity of Snow Storm Damage in a Temperate Forest

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Storms are among the greatest natural disturbances in temperate forests, and increased nitrogen (N) availability is thought to increase storm damage. However, the extent to which N availability increases damage from snowfall is less clear. To test how N availability might affect the susceptibility of trees to snow damage in a temperate forest, we took advantage of an opportunistic storm and surveyed damage in fertilized and unfertilized stands, and across a native N availability gradient. In response to a severe, early season snow storm—a consequence of Superstorm Sandy—the percentages of both basal area and stems damaged were lower in a fertilized watershed than in an unfertilized watershed. Across the native N availability gradient, the percentage of basal area damaged by snow decreased with higher soil N. The effects of N availability on damage were also affected by tree species. Our results suggest that N availability decreases damage from snow storms, contrary to our hypotheses drawn from broader studies. Understanding the relation between storm damage and N availability is important, considering the global increase in N deposition, and since severe storms are likely to become more prevalent with climate change.

Keywords: hurricanes, Superstorm Sandy, fertilization, snow, N deposition, disturbance

Storm damage is the most significant natural disturbance in the forests of eastern North America (Fischer et al. 2013) and can disrupt forest ecosystems in a variety of ways and at a diversity of spatial scales. The effect of storm damage on individual trees is often positively associated with tree diameter (Zimmerman 1994, Platt et al. 2000, Van Bloem et al. 2006), suggesting that larger trees are the most susceptible. However, smaller understory trees may also be damaged (bent or broken) when overstory trees fall. The damage to overstory and understory vegetation can alter the forest environment in several ways that may, in turn, alter species composition and diversity. For example, at the stand level, tree damage can increase maximum canopy gap sizes by more than 30 percent (Xi et al. 2008) and increase canopy gap light levels by more than 45 percent (Sherman et al. 2001). At the forest scale, storm-created canopy disturbance has caused lasting changes in

tree recruitment (Pascarella 1997, Baldwin et al. 2001, Batista and Platt 2003), diversity (Uriarte et al. 2004), and species composition (Merrens and Peart 1992).

How storms interact with nitrogen (N) additions to alter forest structure and function is less understood. However, understanding the interaction of these two global change factors is increasingly important, since anthropogenic N fixation has more than doubled the ambient rate of N inputs to land (Galloway et al. 2004), and the frequency of intense storms is expected to increase in a warmer world (Grinstead et al. 2013). Elevated soil N can lead to ecosystem changes that may leave forests more susceptible to damage by intense storms (Foster et al. 1997). Trees growing in areas with high N availability typically allocate less carbon to structural tissues (Chapin 1980, Bloom et al. 1985, Pitre et al. 2007) yet are often taller and have greater stem and leaf biomass (Miller 1981, Grier

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et al. 1984). Increased nutrient availability can also reduce the specific length and mass of roots, and alter three-dimensional root architecture (Ostonen et al. 2007, Kobe et al. 2010, Domenicano et al. 2011). Thus, increased N availability could produce trees that are more susceptible to storm damage because they are taller, have fewer structural tissues and roots, and have a greater mass of leaves. At the stand and forest level, increased N can change tree seedling composition in ways that alter adult tree composition in forest regrowth trajectories (Lu et al. 2010, Siddique et al. 2010). Thus, if tree species differ in damage response to storms, then N availability could indirectly influence the extent of storm damage by altering tree species composition.

Evidence for increased N availability altering the susceptibility of forest stands to storm disturbance is sparse because it requires either long-term damage surveys over gradients (Mayer et al. 2005) or the chance occurrence of a storm passing through a fertilization experiment. In both cases, most information comes from tropical forests, because larger storms are more likely to strike in equatorial latitudes. In studies across nutrient gradients in tropical forests, areas with higher soil N were damaged more by hurricanes and cyclones than in nutrient-scarce areas (Beard et al. 2005, Gleason et al. 2008). In an experimental fertilization study in an N-limited mangrove forest in Florida, Feller et al. (2015) found that defoliation from Hurricanes Frances and Jeanne led to more than three times more leaf area loss in N fertilized areas than in unfertilized areas. In a phosphorus (P)-limited forest in Hawaii, Herbert et al. (1999) measured damage from Hurricane Iniki and discovered that the hurricane caused more stem damage and leaf area loss in the P-fertilized plots than in the unfertilized plots. These results suggest that the addition of limiting nutrients (adding N in N-limited areas and P in P-limited areas) likely increases forest storm damage.

Even though the evidence of the interactive effects of fertilization and storm damage from tropical forests is compelling, it may not be directly applicable to the temperate deciduous forests of N. America. Tropical forests are mainly affected by one aspect of storms, wind, and rarely experience the effects of heavy snowfall. Furthermore, tropical regions are typically more limited by P and have experienced less chronic N deposition, relative to temperate forests (Galloway et al. 2004). Therefore, knowledge about how storms interact with N fertilization in temperate forests may be critical, as the frequency of high-intensity, Atlantic origin storms is increasing with climate change (Emanuel 2005, Bender et al. 2010, Grinstead et al. 2012, 2013). The occurrence of Superstorm Sandy in a temperate experimental forest provided an opportunistic test of whether stand damage from a severe snow storm depended on N availability. The objective of this study was to measure the effect of snow damage from Superstorm Sandy in stands that differed in age, tree size, and N availability. We measured damage from the storm in two areas—a watershed scale N fertilization experiment, and across a native N availability gradient. Based on previous work in tropical forests, we hypothesized that temperate forests with greater N availability would be more susceptible to damage from a severe snow storm.

Materials and Methods

Study Site and Research Areas

The Fernow Experimental Forest (FEF) is a 1,902-hectare research forest located in the Allegheny Mountain physiographic

province of north central West Virginia. The forest type at FEF is mixed mesophytic, the soils are predominately a loamy-skeletal, mixed, active, mesic Typic Dystrachrept, and the average annual temperature and rainfall are 8.9° C and 145.8 cm, respectively (Kochenderfer 2006). FEF maintains many long-term silvicultural and ecological treatments. Overall, a variety of areas in FEF were used in this study to test whether stand damage from a severe snow storm increased in areas with higher N availability: (1) we used reference areas with a relatively old stand age to test for differences in snow damage across a native N availability gradient, and (2) we compared differences in snow damage between a fertilized and unfertilized watershed—each with stand ages younger than the uncut reference areas (Table 1 and Figure 1).

The reference areas used to test snow damage across an N availability gradient were Watershed 4 (39 hectares), Watershed 10 (15 hectares), Watershed 13 (14 hectares), and a stand of mature trees known as the Biological Control Area (31 hectares). They were last cut ca 1910, have not undergone any experimental treatments since cutting, and have not been fertilized. The watersheds are each first-order drainages that are weired at their junction with other stream branches. As such, they vary in their geographic size. The Biological Control Area is a portion of a large, separate watershed with the same stand age as watersheds 4, 10, and 13. Collectively, these areas are hereafter referred to as the “uncut reference areas,” and they were used to represent snow damage across a native N availability gradient.

The N-fertilized watershed used to test the effect of N fertilization on snow damage was Watershed 3 (34 hectares), hereafter referred to as the “fertilized watershed.” The fertilized watershed was last cut between 1969 and 1972, and is currently fertilized as a part of a whole watershed acidification experiment. Since 1989, 35 kg N/ha/year as ammonium sulphate has been applied to the watershed by aircraft. We used Watershed 7 (24 hectares), hereafter referred to as the “unfertilized watershed,” as a reference to the fertilized watershed (often called a “control” treatment in nonsilvicultural studies). It was cut in two phases between 1963 and 1967, and was maintained barren with herbicide until 1969. Both the fertilized and unfertilized watersheds are first-order watersheds and have similar stand ages, so they are often paired together as a treatment and reference. We acknowledge that using an unreplicated watershed-scale experiment is a case of pseudoreplication—a tradeoff necessitated by the cost and practical constraints associated with long-term and large-scale experimental manipulations of entire watersheds.

Management and Policy Implications

This manuscript investigates the interaction between two major factors affecting forests—nitrogen availability and storm disturbance. Anthropogenic nitrogen fixation has more than doubled the ambient rate of nitrogen inputs to land, and the frequency of large-magnitude storms is expected to increase with climate change. This research represents a rare, real-world opportunity to study the interaction of these two global change factors. We discovered that stands with an increased presence of nitrogen availability resulted in less tree damage during a severe snow storm. If our results are indicative of other forests, we expect that, in areas receiving higher rates of anthropogenic nitrogen deposition, the increased snow storm intensity that is predicted from rising air and sea surface temperatures will lead to less tree damage.

Table 1. Description of stand age, extent of basal area damage, and tree community in each of the areas surveyed for damage after a Superstorm at Fernow Experimental Forest.

Area	Treatment	Approximate stand age (years)	Number of trees surveyed	Number of survey plots	Basal area damaged (percent)	Percentage of total basal area of the most common species								
						<i>Acer rubrum</i>	<i>Acer saccharum</i>	<i>Betula lenta</i>	<i>Fagus grandifolia</i>	<i>Liriodendron tulipifera</i>	<i>Prunus serotina</i>	<i>Quercus prinus</i>	<i>Quercus rubra</i>	<i>Sassafras albidum</i>
WS7	Cut and unfertilized	45	814	18	25.9	4.2	36.2	13.8	0.3	11.0	18.9	1.2	2.9	3.3
WS3	Cut and fertilized	45	930	18	19.2	9.9	1.9	6.6	2.7	6.0	52.4	3.7	5.8	1.3
BCA; WS4; WS10; WS13	Uncut reference	115	3,512	27	43.5	9.9	12.3	2.1	2.0	11.4	7.5	10.2	27.7	0.1

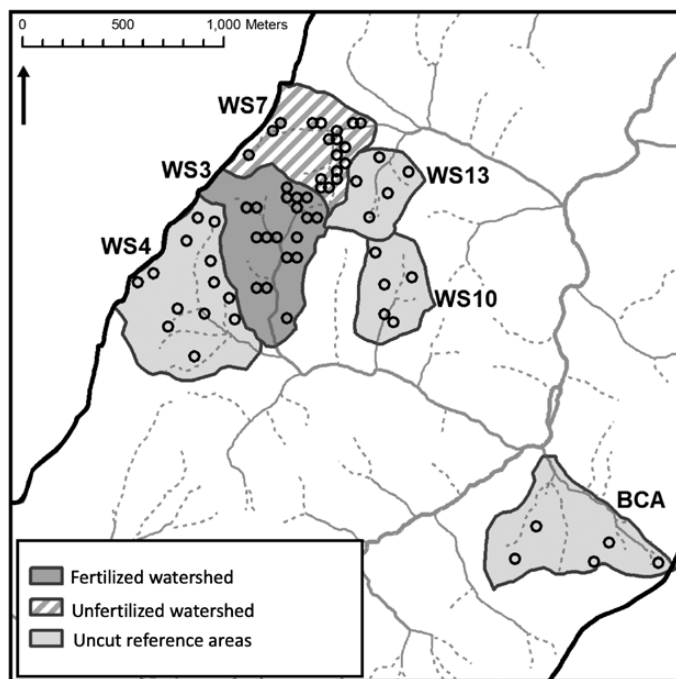


Figure 1. Spatial arrangement of the uncut reference areas that formed the native nitrogen availability gradient, and the fertilized and unfertilized watersheds within the Fernow Experimental Forest. Open circles represent the location of the plots where damage surveys were carried out.

Snow Storm

To test whether trees experiencing various levels of soil N availability at this location were differentially susceptible to storm damage, we took advantage of an opportunistic, severe snow storm caused by Superstorm Sandy in late October of 2012. Prior to being downgraded to a superstorm, Sandy was the largest-diameter Atlantic hurricane ever recorded. Even though the center of the storm made landfall ca 550 km east and 160 km north of the FEF, its effects were observed across a large portion of the eastern United States. Upon reaching the FEF on October 30, 2012 it was downgraded to a superstorm, and there was only a moderate increase in wind speed. Thus, the majority of damage to trees at the FEF (some still retaining leaves; [Figure S1](#) in Supplementary Material) was caused by snow, with an accumulation estimated to have been as high as 1 m during the first 24 hours (C. Cassidy, pers. commun., US Forest Service, Northern Research Station). To test the effect of N availability on storm damage to trees caused by a severe snow storm, we measured the damage across a native

N availability gradient in the uncut reference areas of FEF, and in both the fertilized and unfertilized watersheds.

Damage Measurement

Damage from the 2012 snow storm was measured from June to August of 2013, using an ordinal classification system based on the following seven classes: (1) no damage; (2) <50 percent crown damage; (3) bent; (4) leaning; (5) >50 percent crown damage; (6) stem snapped below crown; or (7) uprooted. The classification system was based on a common damage assessment system used to measure forest disturbance ([Meeker et al. 2005](#)). If a damaged tree happened to fall within two classes, the tree was classified using the greater number. Across the four uncut reference areas, damage was measured in twenty-seven 25-m radius circular plots. Within each plot, every tree was measured for dbh and identified to species, and the damage of each tree was classified. Within both fertilized and unfertilized watersheds, eighteen 10-m radius circular plots were surveyed. Inside each plot, each tree was identified by species, measured for dbh, and assigned a damage classification. Plots between uncut reference areas and the fertilized and unfertilized watersheds differed in size because the plots were selected from a network of existing, long-term monitoring plots that were established at different time periods, and to address separate research questions. Generally, the plots were distributed throughout each study area to be representative of the watersheds and BCA, capturing variance in slope, aspect, and elevation. We selected all available plots in each watershed and in the BCA.

Nitrogen Availability Gradient

To characterize N availability across the uncut reference areas (i.e., the N availability gradient), potential net mineralization rates were measured using a lab-based soil incubation. Within each plot, eight soil cores (2.2-cm diameter) of the mineral soil were taken to a depth of 5 cm and composited to create a single sample per plot. The soils were then sieved through a 2-mm mesh, and approximately 10 g (wet weight) of the soil was placed into individual plastic cups—one preincubation cup and one postincubation cup per plot. The soils were allowed to acclimate in the dark at room temperature (21–24° C) for 5 days. Nitrate and ammonium were extracted from the soils in the preincubation cups by shaking the soil in 100 mL of 1 M KCl for 15 minutes. The extractant was filtered through a 0.45 µm filter and frozen until analyzed. Soils in the postincubation cups were incubated for 30 days before being extracted, and the extracts were immediately frozen until analysis. Extracts were

analyzed using Lachat QuickChem 8500 Series 2 Autoanalyzer, method 12-107-04-1-B for nitrate and method 12-107-06-2-A for ammonium with 1 M KCl as a carrier (Hofer 2003, Knepel 2003). Net N mineralization rates were calculated by dividing the change in inorganic N (nitrate + ammonium) per gram of soil that occurred during the incubation by the number of incubation days.

Statistical Analysis

To test for differences in damage between the fertilized and unfertilized watershed at the tree level, a contingency table analysis and Fisher's exact test were used among damage classes. This tree level analysis allows for ease of interpretation—using the sums of stems in a table as output—but does have the drawback of ignoring plot effects. To include random plot effects, and to test tree damage between the fertilized and unfertilized watershed at the plot level, we aggregated the tree-level data. The basal area of undamaged (class 1) and damaged (classes 2–7) trees was summed to the plot level by species and converted into a continuous variable by calculating the percentage basal area damaged in each plot by species. A mixed effects model was used to test our hypothesis that storm damage would be different between the fertilized and unfertilized watersheds, and that species and tree size would be important variables influencing damage. The model contained the following effects: plot (random effect), watershed, species, average basal area per tree, and watershed \times species. Watershed is a fixed effect in this model because N fertilization only occurs in one watershed, so the watershed effect is the same as the N fertilization effect. Multiple comparisons between species and watersheds were made using Tukey's HSD test, and we excluded from the analysis species that were not present in at least three plots in each watershed.

We used a similar approach to test for differences in damage across the N availability gradient. Since net N mineralization rate was measured at the plot level, we analyzed damage from the 2012 snow storm across the N availability gradient at the plot level. We aggregated the tree-level data to the plot level using the percentage of basal area damaged (percent of total basal area in damage classes 2–7) by species as the independent variable in a multiple linear regression model. Given that previous studies have found relations between storm damage and both tree species and size, we expected they would be important factors to test with N availability. The model effects were: N mineralization rate; species; mean tree basal area per plot; N mineralization \times species; and N mineralization \times mean tree basal area per plot. Since N mineralization occurred as a gradient, its values were not unique to each plot, and as such, plot was not included as a random effect. Because the regression spanned a range of N mineralization rates (a continuous variable), we wanted to ensure that a broad range of N mineralization values were represented. Therefore, since we were interested in examining variation across the N mineralization gradient, species that were not present in at least four plots were not included in the analysis. To determine whether the mean of slopes produced by the N mineralization \times species interaction was different from zero, we used a Wilcoxon Signed-Rank test, since the distribution of slopes was determined to be nonparametric. All data were analyzed in SAS JMP version 14.

Results

Damage Overview

In total, 5,256 stems were measured across all study areas: 3,512 in the uncut reference areas, 930 in the fertilized watershed, and 814 in the unfertilized watershed. The damage from the 2012 snow storm was extensive (see Figure S2 in Supplementary Material for a photo). On average, 53.2 percent of the stems that were measured across all areas were damaged by the storm (damage classes 2–7). Across all areas, the majority of damage was in the <50 percent crown damage class, followed by stem bending (Figure S3 in Supplementary Material). However, stem snaps, as well as leaning and uprooted trees were also observed. The percentage of basal area damage was greater in the uncut reference areas (43.5 percent) than in the fertilized (19.2 percent) and unfertilized (25.9 percent) watersheds with younger stand ages (Table 1).

Damage across the N-Availability Gradient

Across the native N-availability gradient, we found that N availability was associated with the amount of damage sustained at the plot level, but the effect was dependent on species (Table T1 in Supplementary Material). This was determined by N mineralization \times species interaction in the regression model ($F = 1.55$, $P = .0640$). The relation between N mineralization and damage varied widely across species (Table T2 in Supplementary Material), but the mean effect was a significant decrease in damage with increasing N mineralization rates (Figure 2). This was determined using the Wilcoxon signed-rank test, which asked whether the average slope of damage across the N availability for all species was less than zero (signed-rank = -150, $P = .0390$). Specifically, when averaged across all species, each unit increase in N mineralization ($\mu\text{g N/g dry soil/day}$) resulted in a 3.5 percent decrease in the basal area damaged. There was also marginal evidence for an interaction between N mineralization and mean basal area per plot ($F = 2.79$, $P = .0959$), and a significant singular effect of species ($F = 3.34$, $P < .0001$).

Damage between the Fertilized and Unfertilized Watershed

The fertilized watershed was damaged less by the 2012 snow storm than the unfertilized watershed. At the tree level, 56.3 percent

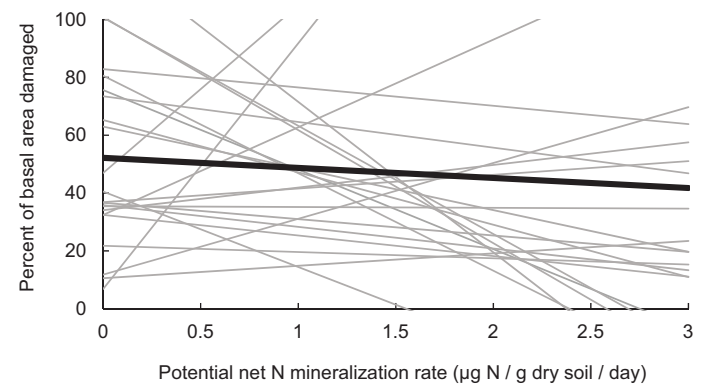


Figure 2. Slopes of the percentage of basal area damaged for each species (gray lines) in the 2012 snow storm across a native N-availability gradient as measured by potential net N-mineralization rate. The mean of all slopes is represented by the black line. Trends for individual species are given in Table T3 in Supplementary Material.

of all stems in the fertilized watershed were damaged (classes 2–7), compared to 59.5 percent in the unfertilized watershed. Across all damage categories, there was a difference in the relative proportion of stem damage between watersheds, determined by Fisher’s exact test ($P = 0.0386$; Figure 3a). The fertilized watershed had a greater percentage of stems with <50 percent crown damage and >50 percent crown damage. The unfertilized watershed was damaged more by bending, leaning, and trees with stem snaps (Table T3 in Supplementary Material).

At the plot scale, the percentage of basal area damaged differed between fertilized and unfertilized watersheds, but the watershed effect depended on tree species (i.e., watershed \times species interaction; $F = 2.842$, $P = .0061$). When averaged across all species, the mean percentage of the total basal area damaged in the fertilized watershed was 19.2 percent, and 25.9 percent in the unfertilized watershed. However, multiple comparison tests found marginal evidence for only one species experiencing a significantly different amount of damage between watersheds, with the percentage of total basal area damaged in *A. saccharum* being 33.1 percent lower in the fertilized watershed than in the unfertilized watershed ($t = 3.3$, $P = .0960$). The discrepancy between a significant watershed \times species interaction in the regression model and marginal evidence for a difference

in only one species between watersheds in the post-hoc test is likely the result of the conservative nature of Tukey’s HSD test, particularly when making comparisons between species/watershed groups with unequal sample sizes (see Table T4 in Supplementary Material for a complete list of comparisons).

Discussion

After a severe snow storm at FEF, we found evidence that increased N availability lowered the percentage of both the total basal area and the total number of stems that were damaged. We observed a pattern of decreasing damage with increasing N across a native N-availability gradient and in response to experimental N fertilization. Our results did not support our hypothesis that increased N availability would lead to greater snow storm damage in broadleaf temperate forests—a hypothesis that drew largely on results from wind storm damage in tropical forests N-fertilization studies.

Although opportunistic studies such as this provide valuable insights under realistic conditions, their inherent lack of replication and control can often present challenges to understanding the exact causes of the results that are observed. In the case of this study, the

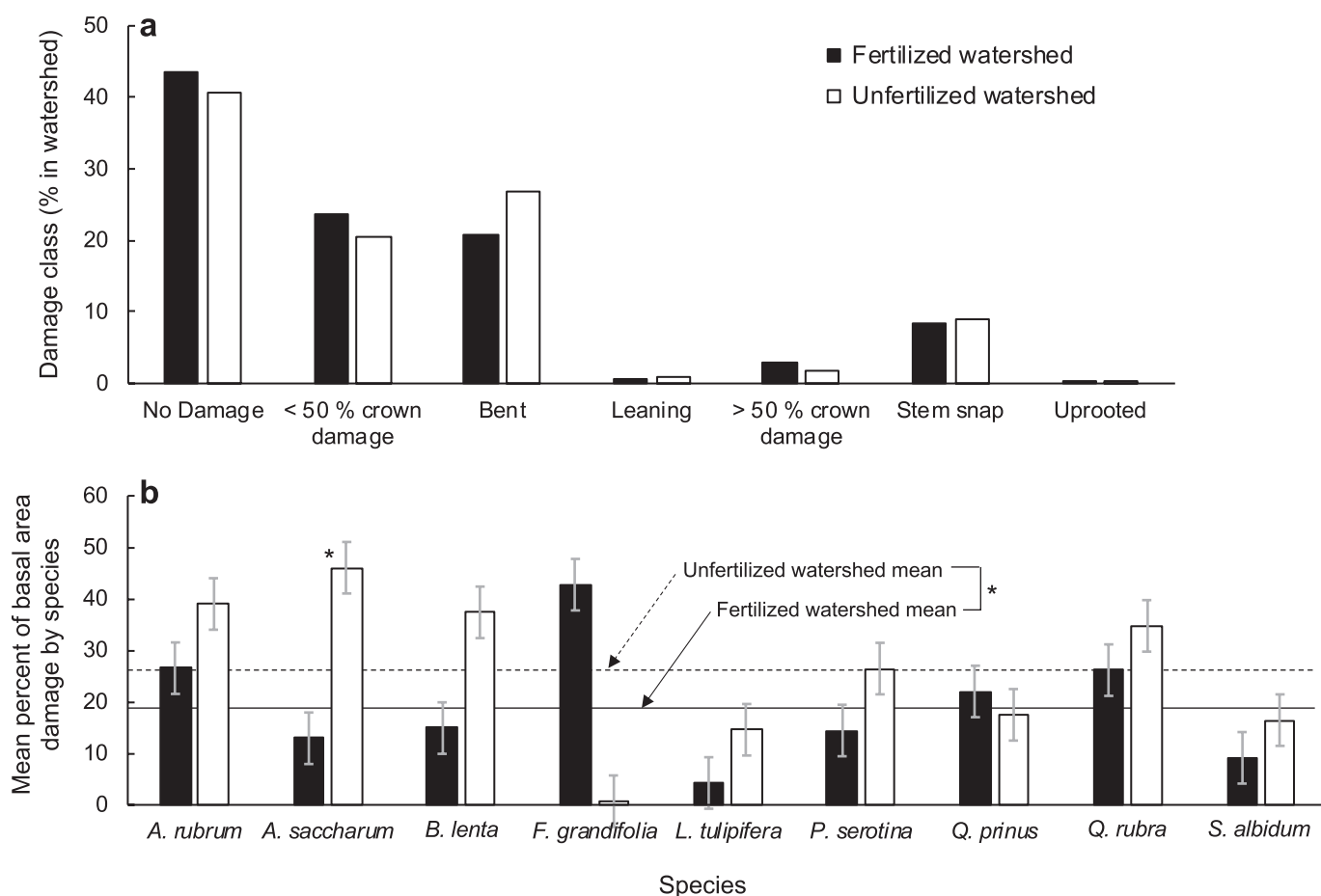


Figure 3. Damage to trees in the watershed-scale fertilization experiment by Superstorm Sandy in 2012. (a) Percentage of all stems damaged by damage class and watershed (tree-scale analysis) and (b) mean percentage and standard error of basal area damaged across all damage classes, by species and watershed (plot-scale analysis). The solid line represents the mean percentage basal area damage in the fertilized watershed, and the dashed line represents the mean percentage basal area damage in the unfertilized watershed. Significant differences between treatments and species: $**P < .05$; $*P < .1$.

underlying causes for the relations observed between storm damage and N availability cannot be determined. However, in general it is reasonable to expect that N availability can influence a forest's susceptibility to storm damage in several ways, including: (1) a change in the abundance of species that differ in their inherent susceptibility; (2) a change in structural features (e.g., canopy height, rooting depth, stand density, etc.) and/or phenological events (e.g., the time of leaf fall); or (3) a combination of both of these indirect and direct factors.

Greater N availability reduced the susceptibility of forest stands to damage by the vertical force of heavy snow. We speculate that the reduced susceptibility of N enriched forest stands to damage by a heavy snow event in late October may be attributable to differences in both structural features and phenological events, including an altered crown allometry and earlier leaf fall. In the predominately light-limited forests of FEF, additional N appears to stimulate trees to grow taller, have more vertically oriented crowns that may shed snow quickly, or be more structurally capable of supporting heavy snow loads (Ibáñez et al. 2016). Indeed, terrestrial lidar data collected in our study watersheds during the summer of 2011, just prior to Superstorm Sandy, show that the fertilized watershed is more vertically stratified and is on average 2.5 m taller than the unfertilized watershed (Parker 2011; Figure S4 in Supplementary Material). In addition, because leaf longevity is often inversely related to leaf N (Wright et al. 2004), it is also possible that N fertilization and higher N availability have led to earlier leaf abscission. Earlier leaf fall from high N trees could explain the decrease in tree damage we observed in response to a medial force such as heavy snowfall—especially since the snowfall from Superstorm Sandy occurred when many species of trees had yet to drop all of their leaves (Figure S1 in Supplementary Material).

Upon examining the effects of the snow storm in more detail, it appears that differences in the composition of tree species may have also contributed to the differential effect of N availability on damage to forest stands. Although the extent to which differences in species composition were caused by differences in N availability is unknown, we found that the lower percentage of damaged trees in the fertilized watershed resulted from an apparent differential effect of N fertilization on the damage experienced by various species (Figure 3b). And a similar overall pattern was observed for older forest stands across a native N availability gradient, where the relation between the percentage of damaged trees and N availability varied widely for different species; however, the overall effect was a decline in damage with increasing N availability (Figure 2). Furthermore, the differential amount of damage experienced by particular species may help to explain the overall differences in damage between high and low N areas. For example, there was a greater abundance of *Prunus serotina* in the fertilized watershed, and this species appears to have been less damaged by heavy snowfall when growing in the fertilized watershed (Figure 3b). Likewise, the abundance of *Acer saccharum* was greater in the unfertilized watershed, where it experienced a greater amount of damage than the fertilized watershed. However, the differential amount of damage by a heavy snowfall to a particular tree species in the fertilized and unfertilized watersheds did not always show the same response across the native N availability gradient. For example, in the fertilized and unfertilized watersheds, the percentage of basal area damaged was lower in the fertilized watershed for both *P. serotina* and *A. saccharum*

(Figure 3b). In contrast, damage to the same species was positively associated with greater levels of N availability in the more mature forested stands (Table T2 in Supplementary Materials), suggesting that stand age may also influence susceptibility of some species to damage by a severe snow storm in late October.

Not surprisingly, previous studies have reported that storm damage affects species differently (Foster 1988, Everham and Brokaw 1996, Rebertus et al. 1997). However, even for a given species, the nature of the damage may depend on the type of storm causing the damage. For example, Bruederle and Stearns (1985) found that *P. serotina* was more susceptible than other species to damage by ice storms, whereas our study suggests that, if anything, *P. serotina* was less damaged, on average, than several other species by heavy snowfall (e.g., *A. rubrum*; Figure 3b). The reasons for inter- and intra-species differences in susceptibility to storm damage are undoubtedly numerous and complex. However, for *P. serotina* growing in younger stands at the FEF, we speculate that the inherent low density of branches, relatively thin canopy, and early leaf drop, relative to other species such as *Quercus rubra* (C. A. Walter, unpublished), prevented significant retention of snow by the canopy during an early autumn snow event.

Whatever the causes that led to differential damage in response to increased N availability among tree species, storm damage can have drastic and lasting effects on tree composition, favoring the recruitment and regeneration of certain species over others (Fajvan et al. 2006). Disturbances that change tree composition and canopy cover could also lead to changes in composition and competition for light among plants in the forest herbaceous layer (Whitney and Foster 1988). Beyond plant community shifts, N-induced changes that affect damage to trees by severe storms have the potential to also affect forest carbon biogeochemistry. For example, Hurricane Katrina was responsible for severe damage to ca 320 million trees, resulting in a 105 Tg C shift from live to dead biomass (Chambers et al. 2007). Such drastic additions of coarse woody debris can cause long-lasting increases in soil respiration (Chambers et al. 2004) and have the potential to be a net carbon source (Fisk et al. 2013)—creating a positive climate-change feedback if storms become more severe in a warmer world.

Although severe, early autumn snowfalls are currently exceptional events, it seems likely that such events will occur more frequently as Earth's climate continues to change (Emanuel 2005, Bender et al. 2010, Grinstead et al. 2013). Thus, if our results are generally applicable, then forests that have experienced high levels of N input in the past (such as temperate forests in the eastern United States) may be less susceptible to damage by snow storms than those less impacted by N deposition. This research underscores the importance of long-term ecological research sites that allow for opportunistic, and realistic, assessments of factors that may influence the consequences of unique weather-related events in the future. However, many of the tree- and stand-level factors known to impact storm damage—tree height, crown allometry, wood density, and leaf area index, among others—are not regularly (or ever) measured in many forest-research areas. Thus, if we hope to gage more accurately the interaction between N availability and storm damage in these long-term sites in the future, we must begin regularly collecting these types of data and plan better for opportunistic storms.

Supplementary Materials

Supplementary data are available at *Forest Science* online.

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