## Effects of an experimental ice storm on forest canopy structure

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Effects of an experimental ice storm on forest canopy structure

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Abstract: Intermediate disturbances are an important component of many forest disturbance regimes, with effects on canopy structure and related functions that are highly dependent on the nature and intensity of the perturbation. Ice storms are an important disturbance mechanism in temperate forests that result in moderate severity, diffuse canopy damage. However, separating the specific effect of ice storm intensity (as ice accretion) from pre-disturbance stand characteristics and physiographic factors has not previously been possible. In this study we utilized a novel experimental ice storm treatment to evaluate effects of variable ice accretion levels on forest canopy structure. Our results verified significant impacts of ice storm disturbance on near-term canopy structural reorganization. Canopy openness, light transmission, and complexity increased significantly relative to pre-disturbance baselines and undisturbed controls. We documented variable impacts with disturbance intensity, as significant canopy changes largely occurred with ice accretion levels of $\geq12.7$ mm. Repeated ice storm disturbance (two consecutive years) had marginal, rather than compounding, effects on forest canopy structure. Our findings are relevant to understanding how ice storms can affect near-term forest canopy structural reorganization and altered ecosystem processes, and add to a growing base of knowledge on the effects of intermediate disturbances on canopy structure.

Key words: Intermediate disturbance, canopy structure, complexity, ecosystem function.
Introduction

Moderate severity disturbances are an important driver of ecosystem functioning, structural development, and successional change in forest ecosystems (Frelich 2002; Cohen et al. 2016). Disturbances that result in damage to the existing vegetation community can strongly affect canopy structure and related patterns of light transmission/absorption, microclimate, and competitive interactions among individuals or cohorts (Hanson and Lorimer 2007; Gough et al. 2013; Fahey et al. 2016). Very high and low severity disturbances, i.e., stand-replacing events and gap-phase disturbance regimes, can result in simplification of stand structure and composition (Foster et al. 1998; Reyes et al. 2010; Halpin and Lorimer 2016). In contrast, intermediate severity disturbances frequently increase the structural and functional complexity of forests (Woods 2004; Fahey et al. 2015; Stuart-Haëntjens et al. 2015; Halpin and Lorimer 2016). Structural complexity is increased through incorporation of horizontal patchiness as well as vertical differentiation. Structural reorganization is often associated with heterogeneity in resource environments and population processes (e.g., regeneration) that can lead to increases in the diversity of species and functional group composition (Cooper-Ellis et al. 1999; Fahey et al. 2016), and also strongly affect ecosystem functioning (Amiro et al. 2010; Nave et al. 2011; Flower and Gonzalez-Meler 2015; Gough et al. 2016). For example, light transmittance and light use efficiency of the canopy can be impacted by disturbance, with implications for forest productivity (Stuart-Haëntjens et al. 2015).

The effects of intermediate disturbance on canopy structure and related functions are highly dependent on the causal agent of disturbance, the severity of disturbance, and the characteristics of the forest prior to disturbance (Peterson 2007; Reyes and Kneeshaw 2008; Reyes et al. 2010; Fahey et al. 2015; Stuart-Haëntjens et al. 2015; Gough et al. 2016).
Characteristics of the underlying disturbance mechanism—in terms of agent, intensity, and timing—can have substantial effects on forest structural outcomes. For example, fire and windstorm disturbances—for the most part—have inherently different directionality, with fire largely having bottom-up impacts and wind top-down (Stephens et al. 2009; Mitchell 2013). In addition, for most disturbance agents the intensity and timing of the disturbance also affects impacts on canopy structure. For example, high-intensity wind and fire both lead to mortality across a broader range of size classes, lessening the differences in directionality and creating more homogenous impacts on structure (Turner and Romme 1994; Peterson 2000). In addition, the composition and structure of the forest at the time of the disturbance interacts with causal agent and intensity to affect severity and structural impacts. For example, wind disturbance has less of an impact on young forests with low complexity canopies across a wide range of wind intensities (Woods 2004; Peterson 2007).

Ice storms are a common source of intermediate disturbance in forests for which a large body of research exists, much of it focused on, or motivated by, the intense ice storm event that affected southeastern Canada and the northeastern US in 1998 (Irland 2000; Gyakum and Roebber 2001). Ice storms can have variable effects on forest structure and dynamics, resulting largely from differences in storm intensity (i.e., ice thickness and duration), as the directionality of the disturbance is largely fixed (Duguay et al. 2001; Rhoads et al. 2002; Arii and Lechowicz 2007). Ice storm intensity is associated with total ice accretion as well as the interactive effects of topography, microclimate, and weather conditions (e.g., wind and temperatures) during and immediately after the storm (Irland 2000; Millward and Kraft 2004; Kraemer and Nyland 2010; Nagel et al. 2016). However, the ultimate severity and structural impact of the ice disturbance can also be affected by characteristics of the pre-disturbance trees and forest (Jones et al. 2001;
Turcotte et al. 2012; Nock et al. 2016). For example, successional stage or age of the forest has been shown to strongly affect damage from equivalent ice loading (Rhoads et al. 2002), and species composition is also likely to affect impacts (Jones et al. 2001; Kraemer and Nyland 2010). There have been many assessments of post-ice storm forest structure and canopy conditions (Duguay et al. 2001; Rhoads et al. 2002; Takahashi et al. 2007; Weeks et al. 2009), including a few studies that opportunistically collected post-ice storm data in existing plots with pre-disturbance canopy structure data (Arii and Lechowicz 2007; Beaudet et al. 2007). However, separating the specific effect of ice loading intensity from that of pre-disturbance forest composition and structure has not previously been possible (Rustad and Campbell 2012).

We evaluated the near-term impact of a novel experimental ice storm disturbance on forest canopy structure and assessed the specific effects of variable disturbance intensity and repeated disturbance on canopy structure. We addressed the following specific research questions: 1) How does ice storm damage affect canopy leaf area, density, complexity in arrangement of canopy elements, and light transmission? and 2) How do increasing ice storm disturbance intensity and repeated disturbance affect near-term reorganization of canopy structure? Our findings are relevant to understanding how ice storms can affect forest canopy structure and processes, and add to a growing base of knowledge on the effects of intermediate disturbance on forest structure and functioning.

**Methods**

**Study site and experimental design**

The study was conducted within the Hubbard Brook Ice Storm Experiment (ISE), which was initiated in 2015 at the Hubbard Brook Experimental Forest (HBEF) in New Hampshire.
The HBEF is a ~3,200-ha northern hardwood forest situated in the southern part of the White Mountain National Forest, New Hampshire, USA (43°56'N, 71°45'W). The HBEF has a cold continental climate with mean air temperatures of -9 °C in January and 18 °C in July, and mean annual precipitation of ~1400 mm yr\(^{-1}\). HBEF was impacted by the 1998 ice storm and establishment of the ISE was partially motivated by observational research documenting the ecosystem consequences and variable impacts (related to topography, environmental conditions, and stand structure and composition) of the 1998 ice storm (Rhoads et al. 2002; Houlton et al. 2003).

The ISE was established in a 70-100 year-old mixed hardwood stand dominated by American beech (\textit{Fagus grandifolia}), sugar maple (\textit{Acer saccharum}), red maple (\textit{Acer rubrum}) and yellow birch (\textit{Betula alleghaniensis}). Ten 20 x 30 m plots were established in summer 2015, and pre-treatment measurements were initiated. Two plots were randomly assigned to each of five treatments with variable ice intensity targets and frequency: 1) Control; no experimental icing applied, i.e., 0 mm; 2) Low; 6.4 mm of ice in year 1 only; 3) Mid; 12.7 mm of ice in year 1 only; 4) Midx2; 12.7 mm of ice in years 1 and 2; and, 5) High; 19.0 mm of ice in year 1 only. The targeted amounts of ice accretion were chosen to be relevant to National Weather Service Ice Storm Warnings in the Northeast US, which occur at 6.4 mm (0.25 in) in the mid-Atlantic region and 12.7 mm (0.5 in) in New York and New England.

Ice treatments were implemented during subfreezing conditions in 2016 (year 1; across five different dates: January 18, January 27-29, February 2) and 2017 (year 2; January 14). Ice addition targeted the entire 20 x 30 m plot, but biogeochemical measurements were restricted to the inner 10 x 20 m leaving a 5 m buffer (Fig. 1). Ice accretion was quantified using caliper measurements on wooden dowel ‘ornaments’ suspended in the canopy (Rustad and Campbell
Accretion levels differed significantly among treatments and were qualitatively close to those targeted (generally within 2 mm, except for high treatment which was within 5 mm; L. Rustad unpublished data); thus the treatment designations were used as an indicator of disturbance intensity. Additionally, fine woody debris mass produced by treatments was sampled using litter traps installed in each treatment plot, and used as an indicator of disturbance severity. Fine litter (woody material < 2 cm and foliar litter; hereafter FWD) was collected in plastic baskets (52L x 37W x 27H cm) that were placed in the center of each of the eight interior subplots (5 x 5 m) in both treatment and control plots (Fig. 1). Litter collections used to estimate treatment disturbance severity were made in each winter (approximately two to three weeks after icing treatments) and at the end of summer. In addition, litter was collected in early November following leaf fall and used to estimate leaf area index (see below). In instances where fallen branches lay on the litter baskets, twigs less than 2 cm were clipped around the perimeter of the basket and were included as part of the sample. After sorting and subsampling for leaf area (see below), litter was oven-dried at 60°C for 48 h (or constant weight) and weighed to estimated total mass of FWD.

**Measurement and quantification of canopy structure and light transmission**

We quantified canopy structure and light transmission in each plot before and following ISE treatments using a variety of methods and metrics. We placed particular emphasis on four response variables that describe different aspects of canopy structure: leaf area index (LAI), gap light index (GLI; Canham 1988), canopy rugosity (Rc; Hardiman et al. 2011), and the fraction of photosynthetically active radiation absorbed by the canopy (fPAR; Atkins et al. 2018b). Specific methods used to collect data and derive these metrics are detailed below. Unless indicated
otherwise, all methods included sampling during the summer/fall before the initial treatment in 2015, in the summer/fall before the second treatment in 2016, and again in summer/fall of 2017 after all treatments were completed.

Plot-level LAI was quantified based on measurements of leaf litter mass for each species in each year: 2015 (pre-treatment), 2016 and 2017 (post-treatment). Leaf litter from each litter trap was sorted by species (sugar maple, red maple, beech, yellow birch). For each species and plot, a subsample of about 30 leaves was carefully collected and stored in leaf presses. The area of each individual leaf was measured on a Licor LAI-2000 leaf area meter to ± 1 mm². The subsamples of each species and plot were dried to constant mass at 60 °C and weighed to determine the area to dry weight ratio. The plot-level area:weight ratio was multiplied by the total leaf litter mass for each species in each litter trap in each plot and divided by trap collection area to estimate leaf area index. The standard errors for LAI in Table 1 represent within plot variation among eight traps for the sum of the four species.

We used hemispherical canopy imaging to estimate canopy openness, optically-derived LAI, and modeled light transmittance. Images were collected in two locations (north and south edges of the “interior” plot; Fig. 1) in each plot at a height of 1.5 m above the ground. A north-facing, leveled Nikon D3200 outfitted with a 5.8mm 180° circular fisheye lens was used to collect images under uniform diffuse sky conditions. Images were analyzed with Gap Light Analyzer (Hardy et al. 2004) to quantify canopy openness, effective LAI between zenith angles 0 to 60° (to minimize error from nearby canopies outside plots), and percent direct and diffuse transmitted radiation (based on modeled sun path throughout the growing season). Estimated percent of total above canopy radiation transmitted through the canopy was used to derive the Gap Light Index (Canham 1988).
The fraction of above canopy photosynthetically active radiation (PAR) absorbed by the canopy (fPAR) to 1 m height was estimated using an ACCUPAR LP-80 handheld ceptometer paired with an open canopy (unobstructed by vegetation, collected also at 1m height ~ 600 m away in a road-associated opening) PAR sensor and datalogger (Decagon Devices; Pullman, WA). Below canopy PAR (bPAR) at 1 m height was recorded every 2 m along three 20 m long transects running along the edges and central axis of the interior intensive plot (Fig. 1). Transect-level means of bPAR were then calculated from the average of all values along each transect. Above-canopy PAR (aPAR) was estimated as the average of all readings logged on the open canopy PAR sensor during the time that the below canopy readings were being collected (based on timestamps on both instruments). fPAR for each transect was calculated from the difference between aPAR and bPAR, divided by aPAR. Data on fPAR were collected only in 2017 on two dates (July and September); means and standard errors in Table 1 represent treatment-level averages of all transects and both sampling dates.

We quantified canopy arrangement and complexity using a ground-based, portable canopy LiDAR (PCL) system (Parker et al. 2004; Hardiman et al. 2011). Data were collected in each year (2015-17) along 5 permanently marked 30 m transects per plot (Fig. 1). Raw PCL data were processed using the forestr package in R (Atkins et al. 2018a). In the forestr algorithm, PCL returns are binned into 1 m² bins with light saturation corrections made based on LiDAR return density. A suite of canopy structure metrics are then calculated that describe a variety of canopy structure metrics focused on the density, distribution, and variance of LiDAR returns along the horizontal and vertical axes of the 2D plane that transects the canopy (Hardiman et al. 2013; Atkins et al. 2018a). Many expressions of canopy structure can be derived from LiDAR. We utilized a set of 24 metrics that describe five different aspects of canopy structure (Atkins et
al. 2018a): 1) *height variables* such as mean leaf height that describe the vertical height distribution of vegetation within a canopy; 2) *density variables* such as vegetation area index (VAI) that summarize vegetation volume, area, and density; 3) *arrangement variables* such as clumping index (Ω) that describe internal canopy architecture; 4) *cover and openness variables* such as gap fraction (θ) that indicate the extent and distribution of canopy gaps; and 5) *variability variables* such as canopy rugosity (R<sub>C</sub>) that describe vegetation arrangement and variability. We placed special emphasis in the analysis on R<sub>C</sub> because of evidence from previous studies that this metric is indicative of variation among canopies that can be related to intermediate disturbance (Fahey et al. 2015), and represents useful functional information (Atkins et al. 2018b; Gough et al. 2019). In addition to a univariate focus on R<sub>C</sub>, we also utilized the full suite of LiDAR-derived canopy structural metrics as traits that describe multi-variate characteristics of the forest canopy (Fahey et al. 2019).

**Data analysis**

We analyzed the influence of ice storm treatments using linear mixed effects models, with model set up differing depending on the collection protocol for the data. We compared each of the primary canopy structure response variables (LAI, GLI, R<sub>C</sub>, fPAR) among treatments and in relation to treatment severity (based on FWD production). We analyzed treatment outcomes for post-treatment data (2017) for all four response variables. For this analysis we conducted mixed model ANOVA with plot and transect (for fPAR and R<sub>C</sub>) or subplot (for LAI and GLI) as random effects nested within treatments. We also assessed treatment effects for response variables with yearly data (LAI, R<sub>C</sub>, and GLI) using repeated measures mixed effects ANOVA with plot and transect (for R<sub>C</sub>) or subplot (for LAI and GLI) as random effects nested within
treatments and unstructured variance for the repeated measurements on individual
transects/subplots. All ANOVA analyses were conducted using PROC MIXED in SAS v. 9.4.

The effect of disturbance severity (as total FWD mass) on canopy structure was analyzed
using simple linear regression. Plot level means and proportional change from pre-treatment
condition for LAI, GLI, and $R_c$ in 2016 were regressed against treatment-related FWD mass
(collected in spring and summer 2016 following the initial winter 2016 treatment). Plot level
means and proportional changes from pre-treatment condition for 2017 were regressed against
overall disturbance severity (as sum of 2016 and 2017 treatment-related FWD mass) for all
response variables (but only plot mean for fPAR). All simple regression analyses were conducted
using PROC GLM in SAS v. 9.4.

To assess relationships between different aspects of canopy structure and measured light
transmittance after the treatments in 2017, we evaluated the relationship between fPAR and
different canopy structure characterizations (GLI, $R_c$ and LAI). We used multiple regression in
an information-theoretic model selection framework to identify the combination of canopy
structure variables that most strongly predicted plot-level fPAR. Models incorporating all
combinations of the three predictors were ranked based on Akaike’s Corrected Information
Criterion (AICc). Multiple regression modeling was conducted using PROC GLM in SAS v. 9.4.

Finally to evaluate the effect of treatments on overall canopy structure as measured by the
broad suite of metrics derived from the PCL using the forestr package, we utilized multivariate
analysis methods. Ordination was conducted on a matrix of all 24 PCL-derived metrics
(relativized to the maximum value for each metric to scale all metrics equivalently) using Non-
metric Multidimensional Scaling (NMS) in PC-ORD v. 5.31 (McCune and Mefford 2006) with
Sorensen’s distance measure and the “slow-and-thorough” auto-pilot setting, using 250 runs of
real data and 250 Monte Carlo randomizations to assess the robustness of the solution. We tested for differences among treatments (blocked by year) in multivariate suites of complexity metrics using permutational multivariate analysis of variance (PerMANOVA) with Sorensen’s distance measure in PC-ORD. To evaluate whether ice storm treatments had differential effects on multivariate canopy structure, plots in the ordination space were connected with transition vectors representing change in canopy structure through time and the length and direction of these vectors was compared among treatments using MANOVA (using PROC GLM in SAS v. 9.4).

Results

Fine woody debris (FWD) mass following ice application did not differ among treatments for 2016 alone (ANOVA; \( F_{4,5} = 3.50, p = 0.100 \)), but did differ for a contrast of the control vs. treatment plots (\( F_{4,5} = 7.13, p = 0.044 \)). FWD mass differed very strongly among treatments for 2016 and 2017 combined (\( F_{4,5} = 11.76, p = 0.009 \)). The level of FWD mass produced by the treatments was strongly related to ice thickness targets (in mm) for the treatments (simple linear regression: 2016 FWD and ice addition - \( R^2 = 0.68 \); total (2016 + 2017) FWD and total ice addition; \( R^2 = 0.87 \)). This finding indicates that ice treatment severity (as FWD produced) was strongly related to ice treatment intensity (as ice load applied). We therefore used FWD mass, in addition to treatment designations, as a predictor of canopy structural changes related to ice treatments.

Vertical profiles of vegetation area index (VAI) from terrestrial LiDAR illustrated shifts in vertical canopy structure in response to treatment. Cumulative VAI profiles were similar among years in the Control, but showed substantial shifts in treatment plots following the ice
storm (Fig. 2). In particular, a higher proportion of VAI was observed in the lower canopy in the ice treatments. In addition, the pattern of response to treatments differed with treatment intensity and timing. In the Low and Mid ice treatments, VAI accumulation with height was decreased relatively uniformly across the vertical canopy profile (Fig. 2b,c). The same was true of the initial (2016) ice application in the Midx2 treatment (Fig. 2d). However, in both the High intensity treatment and following the second (2017) ice application in the Midx2 treatment the accumulation rate of VAI was much greater in the lower part of the canopy (~0-5m) than in the pre-treatment condition (Fig. 2d,e).

Total litter trap estimated leaf area index (LAI) differed strongly among years ($F_{2,10} = 37.87$, $p < 0.001$) and there was a significant interaction between treatment and year ($F_{8,10} = 5.07$, $p = 0.010$). LAI differed among years in the Low, Midx2, and High treatments (Fig. 3), with pre-treatment values (2015) differing significantly from both post-treatment years (2016 and 2017) in each case. Mean LAI in 2017 declined by 27% in the Low intensity treatment, 31% in the Midx2 treatment, and 37% in the High treatment relative to pre-treatment LAI values (Table 1). Annual variation in litter trap derived LAI was also observed in the Control plots (despite apparent constancy in total VAI; Fig. 2), but differences among years were not significant (Fig. 3). Litter trap LAI was strongly correlated with hemispherical photograph-based LAI estimates following treatments in 2016 and 2017, but not in the 2015 pre-treatment analysis (Fig. S1; Supplemental Material). Total LAI and LAI change relative to pre-treatment conditions were strongly significantly related to FWD mass in 2016, but only total LAI was related to FWD mass in 2017 (Table 2).

Gap light index (GLI) differed significantly among years ($F_{2,10} = 15.57$, $p < 0.001$) and treatments ($F_{4,10} = 3.64$, $p = 0.044$), and there was also a strong interaction between treatment
and year ($F_{8,10} = 3.97$, $p = 0.023$). GLI differed among years for the Mid and High treatments (Fig. 4), with pre-treatment values differing from immediate post-treatment (2016) for the Mid treatment, and both years (2016 and 2017) for the High treatment. GLI increased by $>200\%$ in 2017 relative to pre-treatment values in the High treatment. GLI was very strongly related to FWD mass in 2016, and change in GLI relative to pre-treatment was significantly related to FWD mass in both 2016 and 2017 (vs. total treatment-related FWD; Table 2).

$R_C$ differed strongly among years ($F_{2,10} = 187.14$, $p < 0.001$) and treatments ($F_{4,10} = 10.45$, $p = 0.001$), and there was also a highly significant interaction between treatment and year ($F_{8,10} = 22.72$, $p < 0.001$). $R_C$ differed among years for each of the treatments, but not the control, with increased complexity following disturbance for each level of treatment (Fig. 5). Following the initial ice treatment, $R_C$ was $\sim100\%$ higher than pre-disturbance level in High ice accretion plots, 80% in Mid, and 30% in Low. The second ice treatment increased mean $R_C$ in the Midx2 treatment by an additional 25%, but there was not a statistically significant difference between 2016 and 2017 in this (or any other) treatment. Both 2016 $R_C$ and change in $R_C$ from 2015 to 2016 were significantly related to 2016 FWD mass, but neither relationship was significant in 2017 (Table 2).

$\text{fPAR}$ differed significantly among treatments in 2017 ($F_{4,18} = 6.40$, $p = 0.002$), with the High and Midx2 treatment exhibiting significantly greater light transmittance than the Control (Fig. 6). Light transmittance by the canopy in 2017 was strongly positively related to total FWD mass (2016 + 2017; Table 2). Multiple regression analysis illustrated that 2017 $\text{fPAR}$ was most strongly predicted by a model that included both 2017 LAI and $R_C$, which very strongly explained variance in canopy light absorption ($R^2 = 0.89$; Table 3).
Multivariate analysis of canopy structural metrics illustrated substantial shifts in overall canopy structure that varied among treatments in directionality and magnitude (Fig. 7). The NMS ordination of multivariate canopy structure for the full dataset had a two dimensional solution and explained 97.5% of the variance in the original data matrix (Fig. 7). The first axis explained the majority of the variation in the dataset (73.8%) and was strongly related to effective number of layers ($r = 0.926$), while the second axis explained 23.7% of the variance and was related to variance in mean canopy height ($r = 0.932$). In general, canopy complexity and height variance increased with treatment intensity, while vegetation density decreased. Treatments differed significantly from each other in suites of canopy structure traits based on PerMANOVA in both 2016 ($F_{4,45} = 7.48, p < 0.001$) and 2017 ($F_{4,45} = 8.44, p < 0.001$), with significant pairwise differences for all comparisons except Control vs. Low and Mid, and Low vs. Mid. There was a significant difference among treatments in the direction and magnitude of change in multivariate canopy structure in 2016 (Wilks’ Lambda - $F_{8,8} = 3.74, p = 0.04$), but not 2017 (Wilks’ Lambda - $F_{8,8} = 1.34, p = 0.34$), based on analysis of change vectors using MANOVA.

**Discussion**

Intermediate disturbance is increasingly recognized as an important factor in temperate forest dynamics and commonly used as the basis for ecological silviculture practices (Hanson and Lorimer 2007). However, the impact of intermediate disturbance on forest ecosystems is strongly related to the pattern and intensity of effects on canopy structure and processes that are mediated by the canopy (Gough et al. 2013). The ice storm disturbance analyzed here had a substantial effect on canopy structure and light interception that was largely aligned with...
expectations based on the characteristics of the disturbance and prior work on the topic (Irland 2000; Rhoads et al. 2002; Arii and Lechowicz 2007; Beaudet et al. 2007). However, the experimental results here also illustrate the substantial variation that disturbance intensity (as ice accretion) and timing (single vs. repeat disturbance) can impart on canopy structural outcomes. The alteration of canopy structure in a broad, multi-trait sense was also substantial and may represent disturbance-mediated shifts in generalized canopy structural type caused by ice storms (Fahey et al. 2019).

Ice storm disturbance directionality is generally characterized as “top-down” with shifts in vegetation area to lower-levels of the canopy (Weeks et al. 2009). Our results support such characterizations—with a relative shift in vegetation area from upper to lower levels of the canopy (Fig. 2). Our findings also indicate that the canopy vertical dislocation illustrated in prior studies is related to both immediate within-season structural changes, as well as longer-term canopy architecture and subcanopy tree response to increased resource availability (Beaudet et al. 2007; Weeks et al. 2009). This immediate shift in vertical structure is likely related to the combination of physical dislocation of tree crowns through bending and breaking (Duguay et al. 2001), the response of existing buds and leaves to increased light availability (Fotis et al. 2018), and removal of the upper canopy (leading to increased relative density in the lower canopy; Beaudet et al. 2007). The direct transfer of material among layers may be highly characteristic of (but not limited to) ice storms as a disturbance type, and places this type of disturbance somewhat outside existing disturbance impact frameworks (Roberts 2007). There was fine-scale horizontal variability in vertical canopy reorganization, which had the effect of increasing horizontal heterogeneity in canopy height and vertical layering within the canopy volume, despite decreased overall canopy height (which is often positively associated with these factors;
Increased canopy vertical layering is important to many ecosystem functions, including photosynthesis, gas exchange, and wildlife habitat value (MacArthur and Horn 1969; Reich et al. 1990; Ellsworth and Reich 1993; Parker and Brown 2000; Lesak et al. 2011).

Although vertical canopy reorganization was an important component of the near-term response of canopy structure to ice storm disturbance, there were also substantial (and linked) shifts in overall leaf area, canopy openness, and horizontal heterogeneity in canopy density. Natural ice storms have been shown to reduce overall leaf area and increase canopy openness as a result of ice damage (Duguay et al. 2001; Rhoads et al. 2002; Olthof et al. 2003; Weeks et al. 2009). The 20-30+% post-treatment LAI declines and 2-3 fold increase in canopy openness estimated in the moderate-high intensity treatment plots here generally align with findings from stands affected by intense natural ice storms. Combined shifts in vertical and horizontal canopy density and arrangement also produced an overall near-term increase in the complexity of the canopy, which is reflected in the positive response of integrative metrics, such as canopy rugosity, that describe canopy complexity. These metrics have been related to potentially important ecosystem functions such as primary productivity, light capture and use efficiency, and habitat value (Lesak et al. 2011; Ehbrecht et al. 2017; Atkins et al. 2018a; Gough et al. 2019).

Although there were shifts in canopy structure in all treatment plots (relative to both pre-disturbance conditions and control plots), there was substantial variation among treatments that appeared to be strongly related to disturbance intensity (e.g., Figs. 2 and 7). Intensity of intermediate disturbance is often an important factor in canopy structural response, especially when comparing different instances of the same type of disturbance (Reyes et al. 2010; Fahey et al. 2015; Stuart-Haëntjens et al. 2015). We utilized two different metrics (representing...
disturbance intensity and severity) as predictors, and both were strongly related to the degree of
disturbance impact on canopy structural characteristics. Direct measurements of ice accretion are
a common indicator of ice storm intensity and are used in predicting and classifying storm
impacts (L. Rustad unpublished data). Such measurements formed the basis for treatment
designations in this study (based on preliminary work and validated by field measurements;
Rustad and Campbell 2012), and the treatment differences evident here validate the relationship
between ice accretion and disturbance impacts. FWD mass as an indicator of disturbance severity
also showed a strong relationship with shifts in canopy structure (as well as predicted variation
among treatments; L. Rustad unpublished data). This finding is noteworthy, as measurement of
FWD is easier to implement than a direct measure of ice accretion and can be performed in any
location with existing litter traps (including National Ecological Observatory Network sites and
other long-term study plots). There may be some evidence for a threshold in disturbance impacts
related to intensity (Frelich and Reich 1999), as low intensity treatments generally had less
impact on response variables than moderate-high intensity treatments. However, this was not true
for all variables and the strength of differences with disturbance intensity varied among canopy
structural characteristics.

Repeated or interacting disturbances often have compounding effects on ecosystem
structure and functioning, that manifest as additive or even multiplicative impacts on structural
or functional features (Buma 2015; Cannon et al. 2017). In this study, repeated moderate
intensity ice storm disturbance exhibited additional impacts on canopy structure beyond that of a
single equivalent intensity disturbance. However, in contrast to some studies of repeated
disturbance (Buma and Wessman 2011; Lucash et al. 2018; Cannon et al. 2019), the effects of
back-to-back ice storm disturbance generally had a marginal, rather than additive or
multiplicative, effect. Canopy structural changes related to repeated disturbance were not consistently greater than moderate or high intensity single disturbance, but these plots were the only ones that showed additional changes in structure the second year. This included changes to the vertical VAI profile that resulted in a shift from a pattern more consistent with the initial Mid disturbance to a more “bottom-heavy” pattern associated with the High intensity treatment (Fig. 2). Interestingly, disturbance severity in terms of FWD mass produced was equivalent or even higher in the second application than the first, indicating that the effect on the canopy in some respects may have been exacerbated by the second disturbance. However, the overall structural changes resulting from the first disturbance were consistently greater than the subsequent one, indicating a potential saturating response or even some degree of resistance to further structural change related to the initial disturbance (Buma and Wessman 2011; Johnstone et al. 2016). These results are likely associated with the fact that two disturbances were essentially equivalent in terms of agent, directionality, and intensity; the potential for compounding effects related to repeat disturbance may be greater where the disturbances are more dissimilar (Buma 2015).

Although the near-term structural response to repeat disturbance did not consistently illustrate compounding impacts, there may be longer term effects (especially considering the FWD results). Of particular interest would be an evaluation of whether repeat disturbance lowered resilience to disturbance (e.g., in terms of LAI recovery or NPP).

Moderate severity disturbances can have significant impacts on ecosystem processes and function including light capture, productivity, nutrient and water cycling (Gough et al. 2013). While it is premature to evaluate the response of forest productivity to the experimental ice storm, the treatments did have a substantial effect on light interception/transmittance. Prior ice storm studies have also found increased heterogeneity in light availability (Beaudet et al. 2007).
Such an effect was apparent in this study (based on greater variance in fPAR), but limited to moderate and high intensity disturbance treatments. Altered post-disturbance light transmittance was most strongly related to the combined effect of leaf area and complexity in canopy arrangement (as $R_C$, based on multiple regression; Table 3), which matched prior work in undisturbed (Atkins et al. 2018a), and partially disturbed forest ecosystems (Stuart-Haëntjens et al. 2015). In other studies, the effect of increased canopy complexity was manifested not only in altered light capture, but also increased light-use-efficiency (productivity per unit light captured), which appeared to be related to changes in leaf traits and their position within the canopy volume/light environment (but could also be related to light quality/scattering within the canopy volume; Gough et al. 2016). The effects of altered light conditions on leaf area, morphology, and physiology are not likely to have been fully manifested (Fotis et al. 2018), so light environments within treated plots are unlikely to be static in coming years. There was not a recovery of LAI to pre-disturbance levels during this initial study period, which matches results from the 1998 ice storm (Rhoads et al. 2002; Weeks et al. 2009). Continued monitoring will be needed to evaluate treatment effects on light use efficiency over time as well as effects of canopy reorganization on other ecosystem functions such as nutrient and water cycling (Scheuermann et al. 2018).

Conclusion

Ice storm intensity may increase in the future within northern hardwood-dominated forests of the northeastern US/southeast Canada region as a result of global climate change (Cheng et al. 2011; Swaminathan et al. 2018). The results of this study illustrate the variable impacts that ice storms can have on forest canopy structure and suggest potential functional effects that may be associated with these shifts. The general relationships illustrated here
between ice storm intensity and severity (as ice accretion thickness and fine woody debris production) and degree of impacts on various aspects of forest canopy structure should allow for improved modeling and prediction of the effects of ice storms (and a potential increased intensity and frequency of these events) on ecosystem structure and function. Further work is needed to validate these experimental results, either through additional experimentation or monitoring of ice storm affected plots with permanently installed litter traps using FWD mass as a metric of ice storm intensity. Continued monitoring of the ISE plots will allow for assessment of ice storm effects on forest productivity and other ecosystem functions and relationships between intensity, severity, disturbance frequency and longer-term ecosystem resilience (Curtis and Gough 2018).

Acknowledgements

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References


Olthof, I., King, D.J., and Lautenschlager, R. 2003. Overstory and understory leaf area index as indicators of forest response to ice storm damage. Ecological Indicators 3(1): 49-64.


Tables

Table 1. Treatment-related fine woody debris mass (an indicator of disturbance severity) and canopy structural metric means (and standard errors) for all available treatment by year combinations including pre (2015) and post (2016 and 2017) treatment values.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Fine woody debris (g)</th>
<th>Leaf area index</th>
<th>Gap light index (%)</th>
<th>Canopy rugosity (m)</th>
<th>fPAR*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>186.2</td>
<td>207.4</td>
<td>393.6</td>
<td>5.8</td>
<td>4.6</td>
</tr>
<tr>
<td></td>
<td>(0.6)</td>
<td>(1.6)</td>
<td>(0.7)</td>
<td>(0.3)</td>
<td>(0.1)</td>
</tr>
<tr>
<td>Low</td>
<td>365.6</td>
<td>275.5</td>
<td>641.1</td>
<td>6.7</td>
<td>4.9</td>
</tr>
<tr>
<td></td>
<td>(2.0)</td>
<td>(1.9)</td>
<td>(1.4)</td>
<td>(0.1)</td>
<td>(0.1)</td>
</tr>
<tr>
<td>Mid</td>
<td>798.2</td>
<td>249.8</td>
<td>1048.0</td>
<td>4.9</td>
<td>3.7</td>
</tr>
<tr>
<td></td>
<td>(4.9)</td>
<td>(1.5)</td>
<td>(3.1)</td>
<td>(0.2)</td>
<td>(1.2)</td>
</tr>
<tr>
<td>Midx2</td>
<td>583.8</td>
<td>1087.1</td>
<td>1670.9</td>
<td>6.1</td>
<td>4.6</td>
</tr>
<tr>
<td></td>
<td>(2.5)</td>
<td>(10.4)</td>
<td>(4.6)</td>
<td>(0.1)</td>
<td>(0.1)</td>
</tr>
<tr>
<td>High</td>
<td>910.6</td>
<td>218.7</td>
<td>1129.3</td>
<td>5.5</td>
<td>3.2</td>
</tr>
<tr>
<td></td>
<td>(6.0)</td>
<td>(1.5)</td>
<td>(3.7)</td>
<td>(1.2)</td>
<td>(0.4)</td>
</tr>
</tbody>
</table>

* Fraction of above canopy photosynthetically active radiation intercepted by the canopy
Table 2. Regression results relating canopy structural characteristics to disturbance severity (as fine woody debris mass – using 2016 only in comparison with 2016 canopy structure and sum of 2016 and 2017 for comparison with 2017 structure). Bolded numbers indicate parameters/years that are statistically significant at $P \leq 0.05$.

<table>
<thead>
<tr>
<th>Variable</th>
<th>$R^2$</th>
<th>$p$</th>
<th>$R^2$</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf area index</td>
<td>0.76</td>
<td>0.001</td>
<td>0.43</td>
<td>0.040</td>
</tr>
<tr>
<td>Δ Leaf area index</td>
<td>0.48</td>
<td>0.027</td>
<td>0.36</td>
<td>0.069</td>
</tr>
<tr>
<td>Gap light index</td>
<td>0.88</td>
<td>&lt;0.001</td>
<td>0.30</td>
<td>0.104</td>
</tr>
<tr>
<td>Δ Gap light index</td>
<td>0.70</td>
<td>0.002</td>
<td>0.66</td>
<td>0.005</td>
</tr>
<tr>
<td>Canopy rugosity</td>
<td>0.44</td>
<td>0.037</td>
<td>0.39</td>
<td>0.056</td>
</tr>
<tr>
<td>Δ Canopy rugosity</td>
<td>0.64</td>
<td>0.005</td>
<td>0.33</td>
<td>0.083</td>
</tr>
<tr>
<td>fPAR*</td>
<td>--</td>
<td>--</td>
<td>0.60</td>
<td>0.009</td>
</tr>
</tbody>
</table>

* Fraction of above canopy photosynthetically active radiation intercepted by the canopy.
Table 3. Results of multiple regression model selection for predicting fraction of above canopy photosynthetically active radiation intercepted by the canopy (fPAR) in 2017 based on canopy structural characteristics.

<table>
<thead>
<tr>
<th>model</th>
<th>k</th>
<th>AICc</th>
<th>delta</th>
</tr>
</thead>
<tbody>
<tr>
<td>LAI*2017 R_C† 2017</td>
<td>4</td>
<td>-49.0</td>
<td>0.0000</td>
</tr>
<tr>
<td>LAI2017</td>
<td>3</td>
<td>-46.9</td>
<td>2.1414</td>
</tr>
<tr>
<td>GLI‡2017 R_C 2017</td>
<td>4</td>
<td>-42.2</td>
<td>6.8506</td>
</tr>
<tr>
<td>GLI2017</td>
<td>3</td>
<td>-41.9</td>
<td>7.1415</td>
</tr>
<tr>
<td>LAI2017 GLI2017</td>
<td>4</td>
<td>-41.5</td>
<td>7.5483</td>
</tr>
<tr>
<td>LAI2017 GLI2017 R_C 2017</td>
<td>5</td>
<td>-41.1</td>
<td>7.9605</td>
</tr>
<tr>
<td>R_C 2017</td>
<td>3</td>
<td>-38.8</td>
<td>10.2227</td>
</tr>
<tr>
<td>Null</td>
<td>2</td>
<td>-37.0</td>
<td>12.0142</td>
</tr>
</tbody>
</table>

* Leaf area index
† Canopy rugosity
‡ Gap Light Index
Figure 1. Map of nested plot layout indicating locations of measurements of canopy structural variables. The entire plot received the ice treatment, but intensive sampling of biogeochemical response variables was limited to the interior 10 x 20m subplots.
Figure 2. Cumulative vegetation area index (VAI) by height above ground for each treatment across the three years as measured using terrestrial LiDAR (Atkins et al. 2018a).
Figure 3. Leaf area index (LAI) as estimated from litter trap sampling across years and treatments. LAI differed among treatments and years based on ANOVA (Treatment x Year interaction - $F_{8,10} = 5.07, p = 0.010$). Letters above bars indicate significant differences among years for those treatments that illustrated a significant effect of year on LAI.
Figure 4. Gap Light Index (GLI; Canham 1988) across years and treatments calculated as percent of total above canopy radiation transmitted through the canopy as estimated from hemispherical canopy photographs. GLI differed among treatments and years based on ANOVA (Treatment x Year interaction - $F_{8,10} = 3.97, p = 0.023$). Letters above bars indicate significant differences among years for those treatments that illustrated a significant effect of year on GLI.
Figure 5. Canopy rugosity ($R_C$) sampled using terrestrial LiDAR (Atkins et al. 2018a) across years and treatments. $R_C$ differed among treatments and years based on analysis of variance (Treatment x Year interaction - $F_{8,10} = 22.72$, $p < 0.001$). Letters above bars indicate significant differences among years for those treatments that illustrated a significant effect of year on $R_C$. 
Figure 6. Post treatment (2017) fraction of photosynthetically active radiation absorbed by the canopy (fPAR) by treatment as estimated from ceptometer measurements. fPAR differed among treatments based on ANOVA results ($F_{4,18} = 6.40, p = 0.002$). Letters above bars indicate significant differences among treatments after adjustment for multiple comparisons.
Figure 7. Ordination of canopy structure metrics with plot points connected by successional vectors illustrating shifts in canopy structure through time – starting point of vectors is pre-treatment (2015) and arrowhead indicates 2017 condition. Treatments differed significantly from each other in suites of canopy structure traits based on PerMANOVA in both 2016 ($F_{4,45} = 7.48, p < 0.001$) and 2017 ($F_{4,45} = 7.48, p < 0.001$). Biplot overlay results indicate that total treatment-produced fine woody debris (FWD) was associated with the ordination solution and was especially strongly related to Axis 2.
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217x279mm (300 x 300 DPI)
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