NRC
Researc h Pre ss

ARTICLE

Effects of an experimental ice storm on forest canopy structure

Robert T. Fahey, Jeff W. Atkins, John L. Campbe ll, Lindsey E. Rustad, Meghan Duffy, Charles T. Driscoll, Timothy J. Fahey, an d Paul G. Schabe rg

Abstract: Intermediate disturbances are an important component of many forest disturbance regimes, withe1fects 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 often result in moderate-severity,diffuse canopydamage.However, it has not previously been possible to distinguish the specific etfect of ice storm intensity (as ice accretion) from predisturbance stand characteristics and physiographic factors. In this study,we utilized a novelexperimental ice storm treatment to evaluate the etfects of variable ice accretion levels on forest canopy stru cture. 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 predisturbancebaselines and undisturbed controls.We documented variable impacts with disturbance intensity, as significant canopy changes largely occurred with iceaccretion levels of.:::12.7 mm. Repeated ice storm disturbance (twoconsecutive years) had marginal, rather thancompounding, etfects on forest canopy structure. Our findings are relevantto understanding how ice storms can atfect near-term forest canopy structural reorganizationand ecosystem processes and add to a growing base of knowledge on the etfects of intermediate disturbances on canopy structure.

Keywords: intermediate disturbance, canopy structure, complexity, ecosystem function.

Resume : Les perturbations intermediairessontune composante importante deplusieurs regimes de perturbationdesfor tsqui ont desetfets sur la structure du couvert forestier et les fonctions qui y sont reliees lesquels dependent fortement de la nature et de l'intensite de la perturbation. Les tem tes de verglas qui causent des dommages diffus et moderement severes dans le couvert forestier constituent un mecanisme important de perturbation dans les for ts temperees. Cependant, ii n'a pas precedemment ete possible de distinguer l'etfet speciflque de l'in tensite d'une tem te deverglas (sous forme d'accumulationde glace) des facteurs physiographiqueset des caracteristiques du peuplement avant d' tre perturb<'. Dans cette etude, nousavons utilise un nouveau traitement experimental qui reproduit une temp te deverglas pour <'valuer les etfets de ditferents niveaux d'accurnulationdeverglas sur la structure du couvert forestier. Nos resul tats ont permis de constater les impacts importants de la perturbation due a une temp te deverglas sur la reorganisation structurale a court terme du couvert forestier. L ouve rcure, la transmission de la lumiere et la complexite du couvert forestier ont significativement augment<' par rapport a la situation anterieure a la perturbation et aux temoins non perturbes. Nous avons observe des impacts variables selon l'intensite de la perturbation alors que des changements importants dans le couvert forestier sont surtout survenus avec des niveaux d'accurnulationdeverglas .:::12,7 mm. Des perturbations repetees (deux annees consecutives) dues a une tem tedeverglas ont eu des etfetsmarginaux plut0tque conjugues sur la structure du couvert forestier. Nos resultats sont pertinents pour comprendre de quelle far;on les tem tes deverglas peuvent avoir un impact a court terme sur la reorganisation structurale du couvert forestier et alterer les processus de l'ecosysteme. Ils contribuent au developpement de Ia base de connaissances sur la structure du couvert forestier. [Traduit par la Redaction)

Mots-des : perturbation intermediaire, structure du couvert forestier, complexite, fonction de l'ecosysteme.

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 and absorption, microclimate, and competitive inte ractions among individuals or cohorts (Hanso n 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 dis-

Received 16August 2019. Accepted 11November 2019.

R.T. Fahey. Department of Natural Resources and the Environment, University of Connecticut, Storrs, CT06269-4087, USA; Center for Environmental Science and Engineering, University of Connecticut, Storrs, CT06269-4210, USA.
J.W. Atkins. Department of Biology, Virginia Commonwealth University, Richmond, VA 23284-2012, USA.
J.L. Campbe ll and L.E. Rustad. USDA Forest Service, Northern Research Station, Durham, NH 03824, USA.
M. Duffy. Colgate University, Hamilton, NY13346, USA.
C.T. Driscoll. DepartmentofCivil and Environmental Engineering, Syracuse University, Syracuse, NY13244, USA.
T.J. Fah ey.• Department of Natural Resources, Cornell University, Ithaca, NY14853, USA.
P.G. **Schaberg.** USDA Forest SelVice, Northern Research Station, Burlington, VT05403, USA.
Corresponding author:Robert T. Fahey (email: robert.fah ey@uconn.edu).

"Timothy J. Fahey previously served as an Editor-in-Chief and currently serves as an Associate Editor; peer review and editorial decisions regarding this manuscript were handled byJoseph Antos.

turbances frequently increase tlle strnctural and functional complexity of forests (Woods 2004; Fahey et al. 2015; Stuart-Haentjens et al. 2015; Halpin and Lorimer 2016). Stmctural complexity is increased through incorporation of horizontal patchiness and vertical differentiation. Stmctural reorganization is often associated with heterogeneity in resource environments and population processes(e.g., regeneration) tllat canlead to increases in tl1e diversity of species and functional group composition (Cooper-Ellis et al 1999; Fahey et al. 2016) and also strongly affect ecosystem fu nctioning (Amiro et al 2010; Nave et al 2011; Flower and Gonzalez-Meler 2015; Gough et al 2016). For example, light transmittanceand light-useefficiency oftllecanopy can beimpactedby disturbance, witl1 implications for forest productivity (Stuart-Haentjens et al. 2015).

The effects of intermediate disturbance on canopy structure and related functions are highly dependent on tllecausal agent of disturbance, tlle severity of disturbance, and tl1e characteristicsof tl1e forest p1ior to disturbance (Peterson 2007; Reyes and Kneeshaw 2008; Reyes et al. 2010; Fahey et al 2015; Stuart-Haentjens et al. 2015; Gough et al 2016). Characteristics of the under lying disturbance mechanism - in termsofagent, intensity, and timing- can have substantial effects on forest structural outcomes. For example , fire and windstorm disturbances have, for the most part, inherently different directionality, witll fire largely having bottom-up impacts and wind having top-down in1pacts (Stephens et al. 2009; Mitchell 2013).In addition, for most disturbance agents, tlle intensity and timing oftl1edisturbance also affects in1pacts on canopy strncture. For example, high-intensity wind and fire botl1 lead to mortality across a broader range of size classes, lessening the differences in directionality and creating more homogenous impacts on strncture (Turner and Romme 1994; Peterson 2000). In addition, the composition and strncture of tlle forest at the tin1e of the disturbance interacts witl1 causal agent and intensity to affect severity and strnctural impacts. For exan1ple, wind disturbance has less of an impact on young forestswith low-complexity canopies across a wide range of wind intensities (Woods 2004; Peterson 2007).

lee storms are a common source of intermediate disturbance in forests for which a large body of research exists, with much of it focused on (or motivated by) the intense ice storm event tllat affected soutlleastern Canada and tlle northeastern United States (USA) in 1998 (Irland 2000; Gyakum and Roebber 2001). lee storms can have variable effects on forest structure and dynamics, resulting largely from differences in storm intensity (i.e., ice thickness and duration), as tl1e directionality of the disturbance is largely fixed (Duguayet al. 2001; Rhoads et al 2002; Arii and Lechowicz 2007). lce storm intensity is associated witll total ice accretion and tlle interactive effects of topography, microclimate, and weatl1er conditions (e.g., wind and temperatures) during and immediately after tlle storm (Irland 2000; Millward and Kraft 2004; Kraemer and Nyland 2010; Nagel et al. 2016). However, tlle ultimate severity and structural impact of the ice disturbance can also be affected by characteristics of tlle predistw·bance trees and forest Oones 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 speciescomposition is also likely to affect impacts Oones et al 2001; Kraemer and Nyland 2010). There have been many assessments of forest strncture and canopy conditions after ice storms (Duguay et al 2001; Rhoads et al. 2002; Takahashi et al. 2007; Weeks et al 2009), including a few studies that opportunistically colJected data after ice storms from existing plots witll predisturbance canopy stmcture data (Arii and Lechowicz 2007; Beaudet et al. 2007). However, it has not previously been possible to separate the specific effect of ice loading intensity from tllatof predisturbance forest composition and stn1cture (Rustad and Campbell 2012).

We evaluated the near-term in1pact of a novelexperimental ice storm disturbance on forest canopy stlucture and assessed tlle specific effects ofvariable disturbance intensity and repeated disturbance on canopy strncture . We addressed the folJowing specific research questions.

(i) How does ice storn1dan1age affect canopy leafarea, density, complexity in arrangement of canopy elements, and light transmission?

(ii) 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 baseof knowledge on the effects of intennediate disturbance on forest structure andfunctimling.

Methods

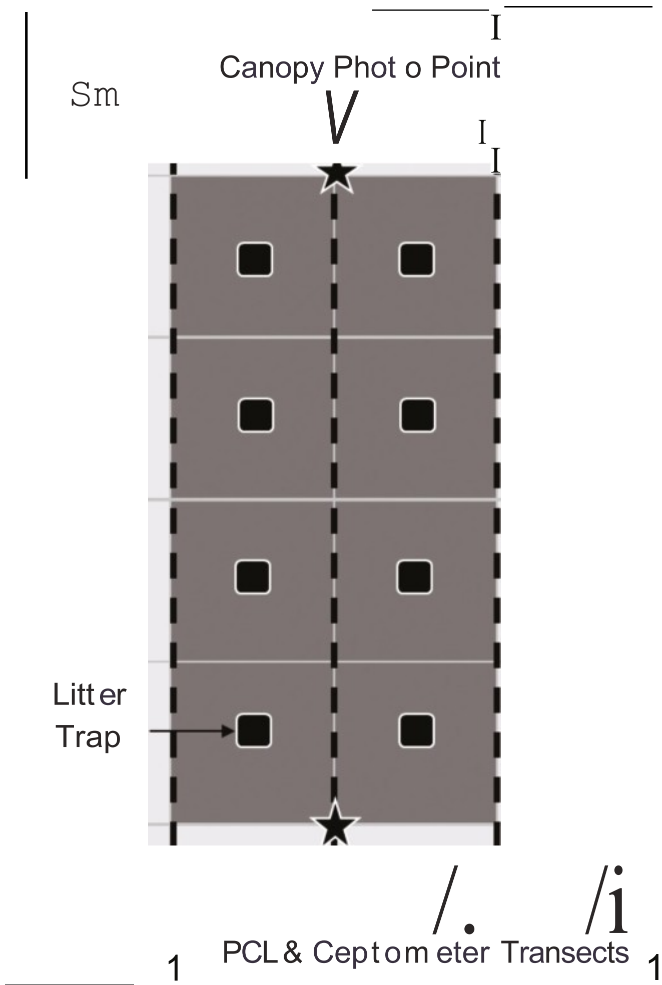
Study site andexperimental design

The study was conducted witllin the Hubbard Brook lee Storm Experiment (!SE), which was initiated in 2015 at tlle Hubbard Brook Experimental Forest (HBEF) in New Hampshire, USA. The HBEF is a ~ 3200 ha northern hardwood forest situated in the soutllern pa1t of the White Mountain National Forest (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. The HBEF was impacted by tlle 1998 ice storm, and establishment of tl1e ISE was partially motivated by observational research documenting tlle ecosystem consequences and variable impacts (related to topography, environmental conditions, and stand structure and composition) of tlle1998ice storm (Rhoads et al. 2002 ; Houlton et al. 2003).

The ISEwas established in a mixed-hardwood stand aged 70-100 years dominated by American beech *(Fagus grandifolia* Ehrh.). sugar maple (Acer *saccharum* Marsh.), red maple (Acer rubrum L.), and yellow birch *(Betula alleghaniensis* Britton) . Ten 20 m x 30 111 plots were established in sununer 2015, and pretreatment measurements were initiated. Two plots were randomly assigned to each of five treatments with vaiiable ice intensity tai·gets ai1d frequency: (i) Control, no experimental icing applied (i.e., 0 mm) ; (ii) Low, 6.4 mm of ice in year1 only;(iii) Mid, 12.7 mm of ice in year1 only; (iv) Midx2,12.7 mm ofice in years1 and 2; and (v)High, 19.0 mm of ice in year 1 only. The targeted amounts of ice accretion were chosen to be relevant to the National Weatller Service lee Storm Warnings in northeastern USA, which occur at 6.4 mm (0.25inches)in tlle mid-Atlantic region and 12.7 mm (0.5 inches) in New York and New England.

Ice treatments were implemented during subfreezing conditions in 2016 (year 1; across five different dates: 18 Januaiy, 27-29 January, and 2 Februaiy) and 2017 (year 2; on 14 Januaiy). lee addition targeted tlle entire 20m x30m plot, but biogeochemical measurements were restricted to the inner 10 m x 20 m, leaving a 5 m buffer (Fig. 1). Ice accretion was quantified using caliper measurements on wooden dowel "ornan1ents" suspended in tlle canopy (Rustad and Campbell 2012). Accretion levels differed significantly among treatments and were qualitativelyclose to tl1ose tai·geted (generally within 2 mm, except for tl1e High treatment, which was within 5 nun; L. Rustad, unpublished data); thus, the treatment designations were used as an indicator of disturbai1ce intensity. Additionally, fine woody debris (FWD) mass produced by treatments was sampled using litter traps installed in each treatlnent plot and used as an indicator of disturbance severity. Fine litter (woody material < 2 cm and foliar litter; hereafter referred to as FWD) was collected in plastic baskets (52 cm length x 37cm widtll x 27cm height)tllat were placed in tlle center of each of tlle eight interior subplots (5 m x 5 111) in botl1 treatment and control plots (Fig.1). Litter collections used to estimate treatment

Fig. 1. Map of nested plot layout indicating locations of measurements of canopystructural variables.Theentire plot received theicetreatment, but intensivesampling ofbiogeochemical response variables was limited to the interior10 m x 20 mofsubplots. PCl., portable canopy light detection and ranging (LIDAR).



disturbance severity were made in each winter (approximately 2-3 weeks after icing t reatments) and at the end of summer. In addition, litterwascollected in early November following leaf fall and used to estimate leaf area index (see the following section). In in stan ces where fallen branches lay on the litter baskets, twigs< 2cmwere clipped around the perimeter of the basketand included as part of the sample.After sorting and subsampling for leaf area (see the following section), litterwasoven-dried at 60 °C for 48 h (or until constant mass) and weighed to estimated total massof FWD.

Measure me nt and quan tification of canopy structure and light transmissio n

Wequantified 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 vaiiables that describe different aspects of cai10py structure: leaf area index (IAI), gap light index (GIJ; Canham 1988), canopy rngosity (Re; Hardiman et al. 2011),and the fraction of photosynthetically active radiation (PAR) absorbed by the canopy (fPAR; Atkins et al. 2018b).Specific methods used to collect data and derive these metrics are detailed in thissection. Unless indicated otherwise, all methods included sainpling during summer or fall before the initial treatment in 2015, during sununer or fall before the second treatment in 2016, and again during sununer or fall of 2017 after all treatments were completed.

Plot-level IAI was quantified based on measurements of leaf litter mass for each species in each yeai·: 2015 (pretreatment) and 2016 and 2017(postt reatment). Leaf litter from each litter trap was sorted by species (American beech, sugar maple, red maple, and 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 to ±1111111² on an IAI-2000 leaf area meter (LI-CORBiosciences, Linco ln, Nebr., USA). The subsan1ples of each species and plot were dried to constant mass at 60 °c and weighed to determine the ratio of area to dry mass. The ratio of plot-level area to mass 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 IA!. The standard er- rors for IAI in Table1 represent within-plot variation amongeight traps for the sun1of the four species.

We used hemispherical canopy in1aging to estimate canopy openness, opticallyderived IAI, and modeled light transmittance. Imageswere collected in two locations in each plot (northern and southern edges of the "interior" plot; Fig.1) at a height of 1.5 111 above the ground. A north-facing, leveled Nikon D3200 can1era (Nikon , Tokyo, Japan) outfitted with a 5.8 mm 180° circular fisheye lens was used to collect in1ages under uniform, diffuse sky conditions. Images were analyzed with Gap Light Analyzer (Hardy et al. 2004) to quantify canopy openness, effective IAI between zenith angles 0°-60° (to minimize error from neai·by canopies outside plots), and percent direct and diffuse transmitted radiation(basedon modeled stm path throughout the growing season). The estimated percentage of total above-canopy radiation transmitted through the canopy was used to derive the GLI (ca nham 1988).

fPAR to a hei ght ofl m was estimated using an AccuPAR LP-80 handheld ceptometer paired with an open-canopy (unobstructed byvegetation, also collected at a height ofl m - 600 m away in a road-associated opening) PAR sensor and data logger (Decagon Devices, Pullman, Wash., USA). Below-canopy PAR (bPAR) at a height of 1 111 was recorded every 2 m along three 20 m long transects runningalong the edges and central axis of the interior intensive plot (Fig. 1). Transect-level means of bPAR were then calculated from the mean of all valuesalong each transect.Above-canopy PAR (aPAR) was estimated as the mean of all readings logged on the open-canopy PAR sensor during the time that the below-canopy readings were being collected (based on time stamps on both instrun1ents). fPAR for each transect was calculated by dividing the difference between aPAR and bPAR byaPAR. Data on fPAR were collected only in 2017 on two dates Ouly and September); means and standard errors in Table 1 represent treat ment-level averages of all transects and both sampling dates.

We quantified canopy arrangement and complexity using a ground-based, portable canopy light detection and ranging (LiDAR) system (Parker et al. 2004; Hardiman et al. 2011). Data were collected in each year (2015-2017) along five pennanently marked 30 111 tr ansects per plot (Fig. 1). Raw portable canopy LiDAR (PCL) data were processed using the forestr package in R (Atkin s et al. 2018a). In the forestr algorithm, PCL returns are binned into1 111² bins, with light saturation corrections made based on LiDAR returndensity.Asuiteofcanopy structure metrics is thencalculated thatdescribes avariety of canopystructure met.J.ics focused on the density, distribution, and variance of LiDAR returns along the horizontal and vertical axes of the two-dimensional plane that transects the canopy (Hardiman et al. 2013; Atkins et al. 2018a). Many expressions of canopy structure can bederived from LiDAR. We utilized a set of24 met.J.ics that describe five different aspects ofcanopy structure (Atkins et al. 2018a): (i) heightvariablessuchas mean leaf height that describe the vertical height distribution of vegetation within a canopy; (ii) density variables such as vegetation area index (VAI) that sununarize vegetation vohlDle, ai·ea,

Table l. Treatment-related fine woody debris (FWD) mass (an indicator of disturbance severity) and canopy structural metrics for all available combinations of treatments and year, including pretreatment (2015) and posttreatment (2016 and 2017) values.

	FWD(g)			W			GU (%)			Rc(m)			fPAR
Treatment	2016	2017	Total	2015	2016	2017	2015	2016	2017	2015	2016	2017	2017
Control	186.2(0.6)	207.4(1.6)	393.6(0.7)	5.8 (0.3)	4.6 (0.1)	5.1(0.1)	3.8(0.7)	3.4(0.6)	3.1(0.3)	8.6 (1.1)	9.5 (0.6)	8.7(0.6)	0.963(0.004)
I.ow	365.6 (2.0)	275.5 (1.9)	641.1(1.4)	6.7 (0.1)	4.9 (0.1)	4.9(0.5)	3.7 (0.5)	4.3(0.4)	3.9(0.8)	9.6(1.1)	12.5(0.8)	12.8(0.6)	0.957(0.008)
Mid	798.2(4.9)	249.8 (1.5)	1048.0 (3.1)	4.9(0.2)	3.7(1.2)	4.2(1.1)	4.5 (0.9)	11.6(4.2)	8.4(3.0)	7.1(0.6)	13.0(1.5)	13.4(1.6)	0.940(0.013)
Micbc2	583.8(2.5)	1087.1(10.4)	1670.9 (4.6)	6.1 (0.1)	4.6 (0.1)	4.2(0.1)	2.7 (0.6)	5.9(0.5)	6.7 (0.9)	10.3(1.8)	14.9(1.0)	17.3(1.5)	0.917(0.009)
High	910.6(6.0)	218.7 (1.5)	1129.3 (3.7)	5.5(1.2)	3.2(0.4)	3.4(0.5)	4.3(0.6)	12.9 (2.1)	13.4(2.5)	10.1(0.5)	20.5(1.5)	19.4(2.1)	0 .899 (0.011)

Note: Values are means, with standards errors in parentheses. LAI, leaf area index; GU, gap light index; Re, canopy rugosity; fl>AR, fraction of above-canopy photosynthetically active radiation intercepted by the canopy.

and density; (iii) an-angement variables such as clumping index (!l) that describe internal canopy architecture; (iv) cover and openness variables sud1 as gap fraction (O) that indicate the extent and distribution of canopy gaps; and (v) variability variables such as Re that describe vegetation arrangement and variability. In the analysis, we placed special emphasis on Re because of evidence from previous studies that this metric is indicative of vatiation among canopies that can be related to intem1ediate 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 Re, we also utilized the full suite of LiDAR-derived canopy structural metrics as traits that describe multivariate 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 models setup differently depending on the collection protocol for the data. We compared each of the primary canopy structure response variables (LAI, GU, Re, and fPAR) among treatments and in relation to treatment severity (based on FWD product ion). We analyzed treatment outcomes for posttreatment data (2017) for all four response variables. For this analysis, we conducted mixed-model analysis of valiance (ANOVA) with plot and transect (for fPAR and Re) or subplot (for LAI and GLI) as random effects nested within treatments. We also assessed treatment effects for response variables with yearly data (LAI, Re, and GLI) using repeated measures mixed-effects ANOVA with plot and transect (for Re) or subplot (for LAI and GLI) as random effects nested within treatments and unstructured variance for the repeated measurements on individual transects or subplots. All ANOVA analyses were conducted using PROC MIXED in SAS version 9.4 (SAS Institute, Cary, N.C., USA).

The effect of disturbance severity (as total FWD mass) on canopy structure was analyzed using simple linear regression. Plot-level means and proportional changes from pretreatment condition for LAI, GLI, and Re in 2016 were regressed against treatment-related FWD mass (collected in spring and summer 2016 following the initial winter 2016 trea tme nt). Plo t-level means and proportional changes from pretreatment condition for 2017 were regressed against overall disturbance severity (as the sum of 2016 and 2017 tr eatment-re lated FWD mass) for all response valiables (but only plot mean for fPAR). ALI sin1p le regression analyses were conducted using PROC GLM in SAS version 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, Re, and LAI). We used multiple regression in an information-theoretic model selection fran1ework to identify the combination of canopy strncture variables that most strongly predicted plot-level fPAR. Models incorporating all combinations of the three predictors were ranked based on Akaike's information criterion corrected for small sample size (AICJ . Multip le regression modeling was conducted using PROCGLM.

Finally, to eval uate 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 nonmetric multidimensional scaling (NMS) in PC-ORD version 5.31 (McCune and Mefford 2006) with Sorensen's distance measure and the "slow and thorough" autopilot setting, using 250 runs of real data and 250 Monte Carlo randomizations to assess the robustness of tl1e 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 stonn treatments had differential effects on multivariate canopy structure, we connected plots in the ordination space with transition vectors representing d1ange in canopy structure through time and compared the lengt11 and direction of these vectors among treatments using multivariate analysis of variance (MANOVA; using PROC GLM).

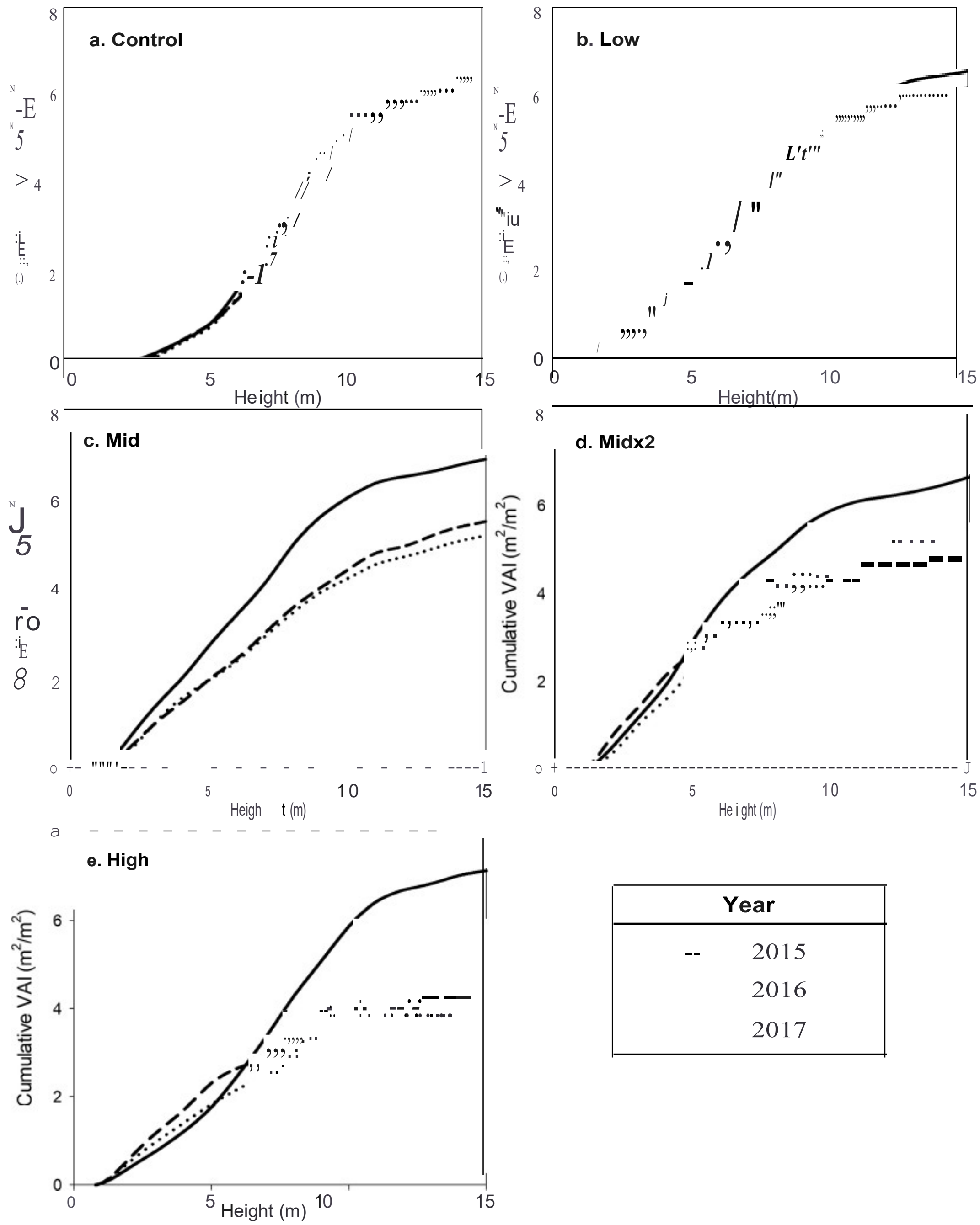
Res ult s

FWD mass following ice application did not differ among treatments for 2016 alone (ANOVA, $F_{4,5,1}$ = 3.50, p = 0.100) but did differ for a contrast of the control vs. tt-eattnent plots ($F_{4,5,1}$ = 7.13, p = 0.044). FWD mass differed very strongly among treattnents for 2016 and 2017 combined ($F_{4,51}$ = 11.76, p = 0.009). The level of FWD mass produced by the treattnents was strongly related to ice thickness targets (in millimetr-es) for the treattnents (simple linear regression: 2016 FWD and ice addition, R^2 = 0.68; total (2016 and 2017) FWD and total ice addition, R^2 = 0.87). This finding indicates that ice treattnent 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 VAl from terrestrial LiDAR illustrated shifts in vertical canopy structure in response to treattnent. Cumulative VAi profiles wer-e sin1ilar ainong years in the Control but showed substantial shifts in treattnent 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, t11e pattern of response to tt·eatments differed with treatment intensity and timing. In the Low and Mid ice treattnents, VAl accumulation with height decreased in a relatively uniform manner across the vertical canopy profile (Figs. 2b and 2c). The same was trne of the initial (2016) ice application in t11e Midx2 treatment (Fig. 2d). However, in both tl1e High treattnent 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 (-0-5 m) compared with that of the pretreattnent condition (Figs. 2d and 2e).

LAI estimated by litter traps differed strongly among years ($F_{2,101}$ = 37.87, p < 0.001), and there was a significant interaction between treatment and year ($F_{8,101}$ = 5.07, p = 0.010). LAI differed among years in the Low, Midx2, and High treattnents (Fig. 3), with

Fig. 2. Cumulative vegetation area index (VAi) by height above the ground for each treatment across the 3 years as measured using terrestrial LIDAR (Atkinset al. 2018a).



pretreatment values (2015) differing significantly from both post-treatment values (2016 and 2017) in each case. Mean LAI in 2017 declined by 27% in the Lowtreatment, 31% in the Midx2treat ment, and 37°/4 in the High treatment relative to pretreatment LAI values (Table 1). Annual variation in litter trap LAI was also observed in the Control (despite apparent constancy in total VAI; Fig. 2), but differences an10ng years were not significant (Fig.3). Litter trap IAI was strongly correlated with hemisphericalphotograph-based lAI estimates following treatments in 2016 and 2017 but not in the 2015 pretreatment analysis (see Supplementa1y data, Supplementary Fig. S1[1]). Total LAI and LAI change relative to pretreatment conditions were stro ngly significantly related to FWD mass in 2016, but onlytotal IAIwas related to FWD massin 2017(Table 2).

GLI differed significantly among years ($F_{12,101}$ = 15.57, $p < 0.001$) and treatments ($F_{4,101}$ = 3.64, $p = 0.044$), and tl1erewas alsoa strong interaction between treatment and year (F_{18-101} = 3.97, $p = 0.023$). GLI differed an1ongyears for the Mid and High treatments (Fig.4), witl1 pretreatment values differing from immediate posttreatment values(2016) for the Mid treatment and both posttreatment values (2016 and 2017) for the High treatment. GU increased

[1] Supplementary data are available with the artide through the journal Website at http:J/nrc resear ch press.co mJdoifsupp J/10.1139/cjfr-2019-0276 .

Fig. 3. Leaf area index (lAI) as estimated from liner trap sampling across years and treatments. LAI differed among treatments and years based on analysis of variance (ANOVA) (treatme nt x year interaction: $F_{18\,101}$ = 5.07. p = 0.010). Leners above bars indicate significant differences among years for those treatments that illustrated a significant effect of year on LAI.

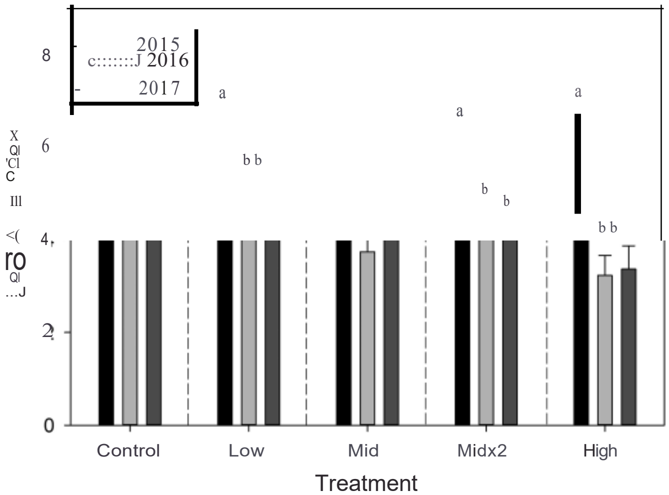


Table 2. Regression results relating canopy structural characteristics to disturbance severity (as fine woody debris (FWD) mass).

	2016		2017	
Variable	R2	p	RZ	p
LAI	0.76	**0.001**	**0.43**	0.040
6.LAI	**0.48**	0.027	0.36	0.069
GLI	**0.88**	<0 .0 01	0.30	0.104
6.GLI	0.70	0.002	**0.66**	0.005
Re	**0.44**	0.037	0.39	0.056
6.Rc	**0.64**	**0.005**	0.33	0.083
fPAR			0.60	0.009

Note: Only 2016datawere used for comparison with 2016 canopy structure. The sum of 2016 and 2017 data was used for comparison with 2017 canopy structure. Boldface type indicates parameters or years thatarestatistically significantat p S 0.05.IA!, leaf area index; Gl.l, gap light index; Re, canopy rugosity; !PAR, fraction of above-canopy pnotosyntheticanyactive radiation intercepted by the canopy.

by >200% in 2017 relative to pretreatment values in the High treatment. GLIwas verystrongly related to FWD mass in 2016, and change in GLI relative to pretreatment was significantly related to FWD mass in both 2016 and 2017 (vs. total treatment-related FWD; Table 2).

Re differed strongly among years ($F_{12\,101}$ = 187 .14 , p < 0.001) and treatments ($F_{4\,101}$ = 10.45, p = 0.001), and there wasalso a highly significant interaction between treatment and year ($F_{18\,101}$ = 22.72, p < 0.001). Re differed among years for each of the treatments except Control, with increased complexity following disturbance for each level of treatment (Fig. 5). Following the initial ice treatment, Re was - 100%, 80%, and 30% higher than predisturbance level in High ice accretion plots, Mid plots , and Low plots, respectively.The second ice treatment in Midx2 increased mean Re by an additional 25%, but there wasnot a statistically significant difference between 2016 and 2017 in this(or anyother) treatment. Both 2016 Re and change in Re from 2015 to 2016 were significantly related to 2016 FWD mass, but neither relationship was significant in 2017 (Table 2).

fPAR differed significantly among treatments in 2017 ($F_{14\,181}$ = 6.40, p = 0.002), with the High and Midx2 treatments exhibiting significantly greater light transmittance than tl1e Control (Fig.6).

Fig. 4. Gaplight index (GLI; Canham1988) across years and treatments calculated as percentage of total above<anopy radiation transmined through the canopy as estinlated from hemispherical canopy photographs. GLI differed among treatments and yearsbased on ANOVA (treatment x year interaction: $F_{8\,101}$ = 3.97, p = 0.023). Leners above bars indicate significant differences amongyears for those treatments that illustrated a significant effect ofyearon GLI.

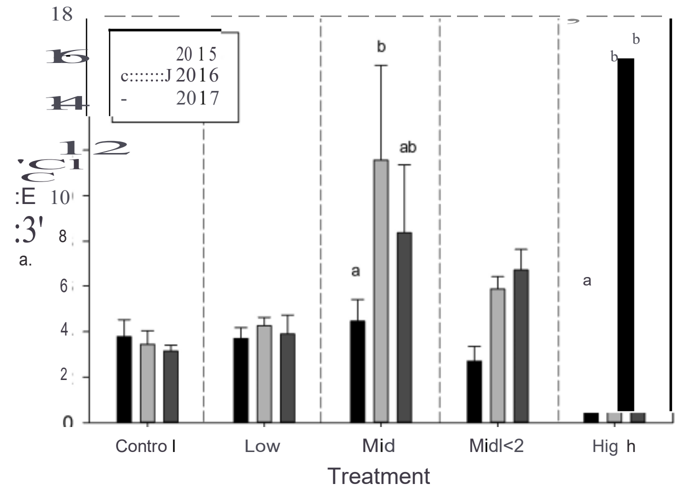
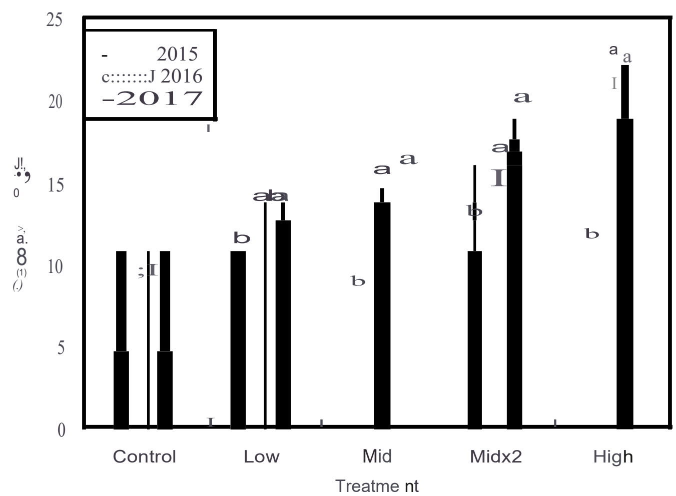


Fig. 5. Canopy rugosity (Re) sam pled using terrestrial LiDAR (Atkins et al.2018a) aaossyearsand treatments. Re differedamong treannents andyears based on ANOVA (treannent x year interaction: $F_{8\,101}$ = 22.72, p < 0.001). Leners above bars indicate significant differences among years for those treatments that illustrated a significant effect of year on Re.



Light transmittance bythe canopy in 2017 was strongly positively related to total FWD mass (2016 and 2017; Table 2). Multiple regression analysis illustrated that 2017 fPAR was most strongly predicted by a model that included both 2017 LAI and 2017 Re, 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 ordinationof multivariate canopy structure for the full data set had a two-dimensionalsolution and explained 97.5%oftl1evariance in the original data matrix (Fig. 7). The first axis explained t11e majority of the variation in the data set (73.8%) and was strongly related to effective number of layers (r = 0.926), whereas the second axis explained 23.7'/4 of the variance and was related to

Fig. 6. Posttreatment (2017) fraction of photosynthetically active radiation (PAR) absorbed by the canopy (fPAR) by treatment as estimated from ceptometer measurements. fPAR differed among treatments based on ANOVA results ($F_{4,15}$ = 6.40, p = 0.002). Leners above bars indicate significant differences among treatments after adjustment for multiple comparisons.

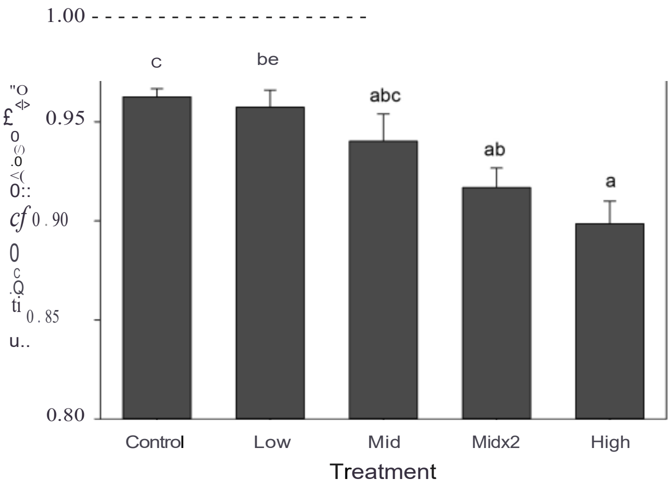


Table 3. Results of multiple regression model selection for predicting fraction of above-canopy photosynthetically active radiation intercepted by the canopy (fPAR) in 2017 based on canopy structural characteristics.

Model	*k*	AICc	
W2017 Rc2017	4	-49.0	0.0000
W2017	3	-46.9	2.1414
Gl12017 Rc2017	4	-42.2	6.8506
Gl12017	3	-41.9	7.1415
W2017 GIJ2017	4	-41.5	7.5483
W2017 GIJ2017 Rc2017	5	-41.1	7.9605
Rc2017	3	-38.8	10.2227
Null	2	-37.0	12.0142

Note: IAL leaf area index; Re, canopy rugosity; GU, gap light index; AIC„, Akaike's information criterion corrected for small sample size; *k*, numlJe:r of parameters in tne model.

vaiiance in mean canopy height (r = 0.932). In general, canopy complexity and height variance increased with treatment intensity, whereas vegetation density decreased with treatment intensity. Treatments differed significantly from each other in suites of canopy structure traits based on PERMANOVA in both 2016 ($F_{14,45}$ = 7.48, p < 0.001) and 2017 ($F_{14,45}$ = 8.44, p < 0.001), with significant pairwise differences for all comparisons except Control vs. Low, Control vs. 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: $F_{8,81}$ = 3.74, p = 0.04), but not in 2017 (Wilks' lambda: $F_{8,81}$ = 1.34, p = 0.34), based on analysis of change vectors using MANOVA.

Discussion

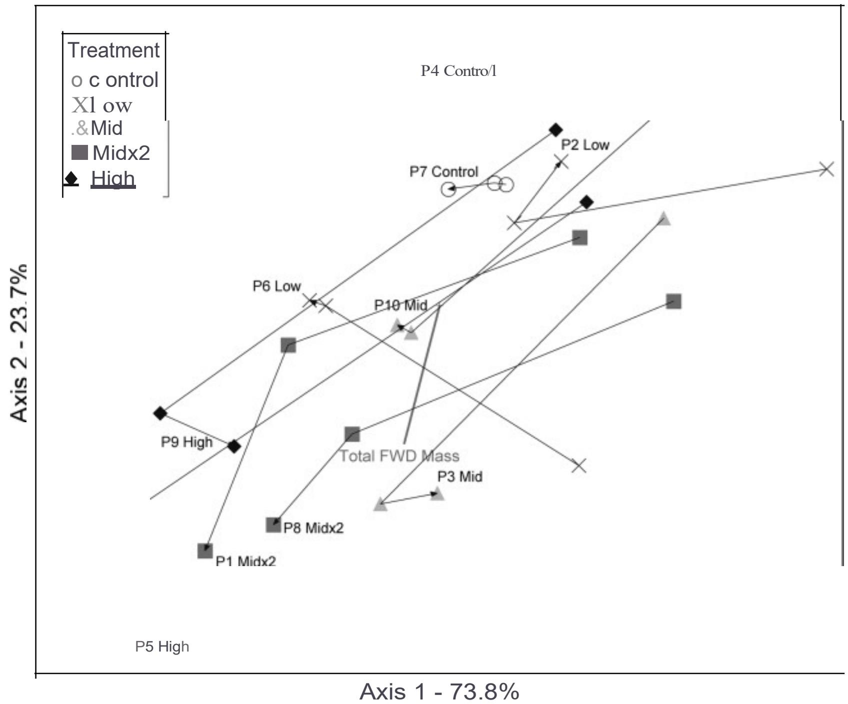
Intermediate disturbance is increasingly recognized as an important factor in temperate forest dynamics and is commonly used as the basis for ecological silviculture practices (Hanson and Lorimer 2007); however, the impact of intermediate disturbance on forest ecosystems is strongly related to the panern 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; Atiiand Lechowicz 2007; Beaudet et al. 2007). However, our expetimental results 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, mtLltitrait 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 tl1e canopy (Fig. 2). Our findings also indicate tl1at the canopy vertical dislocation illustrated in prior studies is related to both inunediate, within-season structural changes and long-term canopy architecture and subcanopy tree response to increased resource availability (Beaudet et al. 2007; Weeks et al. 2009). This inuuediate 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 the 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 frameworks of disturbance impact (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 (Ehbrecht et al. 2016; Atkins et al. 2018b). 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 stonns have been shown to reduce overall leaf area and increase canopy openness as a result of ice da.Illage (Duguay et al. 2001; Rhoads et al. 2002; Olthof et al. 2003; Weeks et al. 2009). The 20%–30% (or greater) posttreatment declines in IA! and two- to threefold increase in canopy openness estimated in our moderate- to high-intensity treanuent plots 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, including Re, that desnibe canopy complexity. These metrics have been related to potentially important ecosystem functions such as primary productivity, light capture and light-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 predisturbance 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 cai10py structural response, especially when comparing different instances of the same type of disturbance (Reyes et al. 2010; Fahey et al. 2015; Stuart-Haentjens et al. 2015). We utilized two different menics (representing disturbance intensity and severity) as predictors, and both were strongly related to the degree of disturbance in1pact on canopy structural characteristics. Direct measurements of ice accretion are a common indicator of ice storm intensity and are used in predicting and

Fig. 7. Ordination of canopy structure metrics, with plot points connected by successional vectors illustrating shifts in canopy structure through time. The starting points of the vectors indicate pretreatment conditions (2015), and the arrowheads indicate condition in 2017. Treatments di1fered significantly from each other in suites of canopy structure traits based on permutational multivariate analysis of variance (PERMANOVA) in both 2016 ($F_{4,51}$ = 7.48, p < 0.001) and 2017 ($F_{4,45}$ = 8.44, p < 0.001). Biplot overlay results indicate that total treatment-produced fine woody debris (FWD) was associated with the ordination solution and was strongly related to axis 2. P, plot.



classifying stonn impacts (L. Rustad, unpublished data). Such measurements fonned the basis for treatment designations in thisstudy (basedon preliminary work and validated by field measurements; Rustad and Campbell 2012), and the treatment differencesevident herevalidate 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 (and predicted variation among treatments; L Rustad, w1published 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-tern1 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- to high-intensity treannents; however, this was not nue for all variables, and the sn-ength of differences with disturbance intensity varied among canopy structural characteristics.

Repeated or interacting disturbances often have compounding effects on ecosystem snucture and functioning that manifest as additive, or even multiplicative, impacts on structural or functional features (Bwna 2015 ; Cannon et al. 2017). In this study, repeated moderate-intensity ice storm disturbance exhibited additional in1pacts on canopy structure beyond that ofa single disturbance of equivalent intensity. However, in contrast to some studies of repeated disturbance (Buma and Wessman 2011; Lucash et al. 2018; Cannon et al. 2019), the effectsof consecutive 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 those related to single moderate- or high-intensitydisturbance, but these plots were the only ones that showed additional structural changes in the second year. This included changes to the vertical VAi profile that resulted in a shiftfrom a pattern more consistent with the initial Mid disturbance to a more"bottom-heavy" pattern associated with the High treannent (Fig. 2). Interestingly, disturbance severity in terms of FWD mass produced was equivalent or even higher in the second application than the infirst application, indicating that the effect on the canopy may have, in some respects, been exacerbated by the second disturbance. However, the overall structural changes resulting from the first disturbance were consistently greater than those from the subsequent disturbance, 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 resultsare likely associated with the fact that the two disturbances were essentially equivalent in terms of agent, directionality, and intensity; the potential for compounding effects related to repeat disturbance may be greater when the disturbancesare lesssimilar (Buma 2015). Although the near-term structural response to repeat disturbance did not consistently illustrate compounding impacts, there may be long-term effects (especially considering the FWD results). An evaluation of whether repeat disturbance lowered resilience to disturbance (e.g., in termsofIAI recovery or net primary production (NPP)) would be of particular interest.

Moderate-severitydisturbances can have significant in1pacts on ecosystem processes and function , including light capture, productivity, and nutrient and water cycling (Gough et al. 2013). Although it is premature to evaluate the response of forest productivity to the experimental ice storm, the n·eatments did havea substantial effect on light interception and transmittance. Priorice storm studies havealso found increased heterogeneity in light availability (Beaudet et al. 2007). Such an effect was apparent in our study (based on greater variance in fPAR) but was limited to moderate- and high-intensity disturbance treatments. Altered postdisturbance light transmittance was most strongly related to the combined effect of leaf a1-ea and complexity in canopy arrangement (as Re, based on multiple regression; Table 3), which matched prior work in undisturbed (Atkins et al. 2018a) and partially disturbed forest ecosystems (Stuart -Haentjens 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 canopyvolume or light environment (but could also be related to light quality or 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 (Fotiset al. 2018), so light environments within treated plotsare unlikely to be static in coming years. A recovery of LAI to predisturbance levels was not observed dming 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 and 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 th e future within northern hardwood-dominatedforests of northeastern USA and southeastern Canada 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 FWD production) and the degreeofin1pacts on various aspectsof forest canopy structure should allow for improved modeling and prediction of th e effects of ice storms (and potential increased intensity and frequency of these events) on ecosystem structure and function. Fmtlier work is needed to validate these experin1ental results, either through additional experimentation or monitoring of plots affected by ice storms using permanently installed litter traps with 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 long-term ecosystem resilience and the intens ity, severity, and frequency of disturbance (Cm1:is and Gough 2018).

Acknowledgements

Funding for this research was provided by the National Science Foundation (NSF; DEB1-457675). We thank the many participants on the !SE team who helped with the ice application and associated fieldwork and laboratory work, especially Ian Halm, Geoff Schwaner, Gabe Winant, Gary Hawley, Christopher Hansen, and Brendan Leonardi. This manuscript is a contribution of the Hubbard Broo k Ecosystem Study. Hubbard Brook is part of the Long-Term Ecological Research (LTER) network, which is supported by the NSF (DEB-1633026). The HBEF is operated and maintained by the United States Department of Agriculture, Forest Service, Northern Research Station, Newt ow n Square , Pa.

References

Amiro , B., Barr,A.,Barr,J., Black,T., Bracno, R.,Brown, M.,et al. 2010.Ecosystem cart>on <lioxi<le fluxes after <listurl>ance in forests of Noren America. J. Geophys. Res. Biogeosci 115(G4).<loi:10.1029/2010J G001390.

Arii, K., an<! Lechowicz, M.J. 2007 . Changes in un<lerstory light regime in a l>eecn-maple forestafterasevere ice storm.can.J.For . Res. 37(9): 1770-1776. <loi:10.1139 /X0?-024.

Atkins,J., Bohrer, G., Fahey, R., Har<liman, B., Gough, C., Morin,T.,et al. 2018a. forescr. ecosystem an<! canopy structural complexity metrics from LIDAR [onl in e]. R package version 1.0.1. Availal>le from nccps:f/CRAN.R-projecLOrg/package=forestr.

Atkins,J., Fahey, R.,Har<liman , B., an<!Gough , C. 2018b. Forest canopy structural complexity and light al>sorption relationships at Che sul>continental scale. J.Geophys. Res. Biogeosci. 123(4):1387-1405. doi:10.1002/2017JG04256.

Beaudet, M., Brisson, J., Messier, C., and Gravel, D. 2007. Effect of a major ice stonn on understory light conditions in an old-growth *Acer-FagUS* forest panem of recovery over seven years. For. Ecol Manage. 242(2-3): 553- 557. doi:10.1016/j.foreco.2007.01.068.

Buma, B. 2015. Disturl>ance inter acti ons: Characterization, prediction, and Che potential for cascading effects.Ecospnere, 6(4):l-15.doi:to.1890{ES15-00058.l.

Buma, B., and Wessman, C. 2011. Disturbance interactions can impact resilience mechanisms of forests. Ecospnere, 2(5):1-13. doi:10.1890/ESU-00038.1.

Canham, C.D. 1988. An index for un<lerstory light levels in and around canopy gaps. Ecology, 69(5): 1634-1638. doi:to .2307/1941664.

Cannon, J.B., Peterson, C.J., O'Brien, J.J., an<! Brewer, J.S. 2017. A review and dassification of interactions l>etween forest<listurl>ance fromwin<!an<! fire . For. Ecol. Manage.406 : 381-390. doi:10.1016/j.foreco.2017.07.03.5

cannon,J.B., Henderson, S.K., Bailey, M.H.,and Peterson , C.J. 2019. Interactions l>etween wind and fire disturl>ance in forests: competing amplifying and l>uffering effects . For. Ecol. Manage. 436: 117-128. doi:10.1016/j.foreco.2019.01.015.

Cheng, C.S., I.i, G., and Auld, H. 2m1. Possil>le impacts of dimace Change on freezing rain usingdownscale<!future climatescenarios: up<late<I for eastern Canada. Atmos.-Ocean, 49(1): 8-21. <loi :10 .1080/07055900.2011.555728 .

Cohen, W.B., Yang, Z., Stenman, S.V., Schroeder, TA., Bell, D.M., Masek, J.G., et al. 2016. Forest disturbance across Che conterminous United States from 1985-2012: cne emerging dominance of forest dedine. For. Ecol. Manage. 360: 242-252. doi:10.1016j.foreco.2015.10.042

Cooper-Ellis, S., Foster , D.R.,Carlton, G.,and I.ezl>erg, A-1999.Forestresponseco catastrophic win<!: results from an experimental hurricane. Ecology, 80(8): 2683-2696. <loi: 10.1890/0012-96 58(1999)080[2683: FRTCWRJ2.0.CO;2 .

Curtis, P.S., and Gough, C.M. 2018. Forest aging, <listurbance and Che carl>on cyd e. New Phytol.219: 1188-1193. doi:10.1111/nph.15227. PMID:29767850 .

Duguay, S.M., Arii, ,K. Hooper, M., and Lechowicz , M.J. 2001. Ice stonn <lamage and early recovery in an old-growth forest. Environ. Monie. Assess. 67(1-2): 97-108. doi:10.1023/A:1006464511158. PMID:11339708.

Ehl>recnc , M., Schall, P.,Jucnn eim, J., Ammer, C. ,an<!Sei<lel, D. 2016. Effective numl>er of layers: a new measure for quantifying tnree--<limensional stand structure l>ased on sampling with terrestrial LIDAR. For . Ecol. Mana ge. 380: 212-223. doi:to.1016/j.foreco.2016.09..003

Ehl>recht, M., Sehail, ,P. Ammer, C., and Seidel, D. 2017. Quantifying stand structural complexity and its relationship with forest management, tree speciesdiversityand microdimace.Agric.For. Meteorol. 242:l- 9. <loi:10.1016/j.agrfonn et.2017 .04.012 .

Ellsworcn , D ., and Reich, P. 1993. ca nopy structure and vertical paccems of photosynthesisand relate<!leaftraitsin a deciduousforest. Oecologia, 96(2): 169-178. doi:10.1007/BF00317729. PMID:28313412.

Fah ey, R.T., Fotis, A-T., and Woo<ls, K.D. 2015. Quantifying canopy complexity and effects on productivity and resilience in late-successional hemlock-hardwood forests. Ecol. App l. 25(3): 834-847. <loi: to.1890/14-1012.1. P MID: 26214927.

Fahey, R.T., Stuart-Hai'ntjens, E.J., Gough , C.M., De I.a Cruz, A-, Stockton, E., Vogel, C.S., and Curtis, P.S. 2016. Evaluating forest sul>canopy response to moderate severity disturbance and contril>ution to ecosystem-level produc• tivity and resilience. For. Ecol. Manage. 376:135-147.doi:10.1016£j.fureco.2016.06.001.

Fahey, R.,T. Atkins,J.W., Gough, C.M., Har<liman , B.S., Nave, LE., Tallant, J.M., et al. 2019. Defining a spectrum of integrative trait-l>a se <Ivegetation canopy Structural types. Ecol. Len . 22: 2049-2059. <loi :10.1111/e le.13388 . P MID: 31523909.

Flower,C.E.,and Gonzalez-Meler, MA 2015. Responses of tem perate forest pro-<luctivity to insect and pathogen <listurbances. Annu. Rev. Plant Biol. 66: 547-569. doi:10.1146/ann urev-arplan t-043014-115540. PMID:25580836 .

Foster, D.R., Knight, D.H., an<!Franklin,J.F. 1998. landscape panems an<! lega• des resulting from large, infrequent forest <listur l>ances . Ecosystem,s 1(6): 497- 510. do i:10.1007/s100219900046.

Fotis,A.T.,Morin,T.H.,Fahey,R.T.,Har<liman,B.S.,Bohrer,G.,an<!Curtis,P.S. 2018. Forest structure in space and time: l>iotic and al>iotic de terminants of canopycomplexity and their effects on net primary productivity. Agric. For. Meteorol. 250-251: 181-191. doi:10.1016/j.agrfomet.2017.12.251.

Frelicn, LE. 2002. Forest <lynamics and <listurl>ance regimes: studies from tem• perate evergreen-<leciduous forests.Gaml>ridge U nivers ity Press .

Frelicn, L.,E. an<! Reicn, P.B. 1999. Minireviews: neighl>orhood effects, <listur • l>anceseverity,and communitystal>ility in forests.Ecosystems , 2(2):151-166. <loi :to .to07/s100219900066 .

Gough,C.M.,Har<liman,B.S.,Nave,L.,Bohrer,G.,Maurer,K.D.,Vogel, C.S.,et al 2013. Sustained carl>on uptake and storagefollowing moderate disturbance in a Greatlakesforest.Ecol. Appl.23:1202-1215. doi:10.1890/12-1554..1PMID: 23967586 .

Gough, C.M. Curtis, P.S., Har<liman , B.S ., Scheuermann, C.M., and Bond-1.aml>erty, B. 2016. Distur l>ance , com p lexity, and success ion of ne e ecosystem production in North America's temperate deciduous forests. Ecospnere, 7(6): e01375. <loi: 10. 100 2fecs2.1375 .

Gough, C.M., Atkins, J.W., Fahey, R.T., and Har<liman, B.S. 2019. High races of primaryproduction in structurallycomplexforests. Ecology, 100(10): e02864. <loi :10. 1002/ecy.2864 . PMID:31397885.

Gyakum, J.R., an<! Roel>l>er, P.J. 2001. The 1998 ice stonn - analysis of a planetary•scaleevent.Mon.WeatherRev.129(12):2983-2997.doi:10.1175/1520.0493(2001)129<2983:TISAOA>2.0.C0;2.

Halpi,n C.R., and Lorim,er C.G. 2016. Trajectories and resilience of stand structure in response to variable disturbance severities in northern hardwoods. For. Ecol. Manage. 365: 69-82. doi:10.1016/j.foreco.2016.01.016

Hanson,J.J, and Lorimer, C.G. 2007. Forest structure and light regimes following moderate wind stonns: implications for multi-cohort management. Ecol. Appl. 17(5): 1325-1340. doi:10.1890/06-1067.1 PMID:17708211.

Hardiman, B,S Bohrer, G. Gough, C.M, Vogel, C.S., and Curtis, P.S. 2011. The role of canopy structural complexity in wood net primary production of a maturing northern deciduous forest. Ecology, 92(9):1818-1827. doi:10.1890/10.2192.1. PMID:21939078.

Hardiman, B.S., Bohre r, G., Gough, C.M,. and Curtis,P.S. 2013. canopy structural changes following widespread mortality of canopy dominant trees. Forests, 4(3): 537-552. doi:10.3390/f4030537

Hardy J.P., Melloh, R., Koenig, G. Marks, D. Winstral, A., Pomeroy, J.W., and Link,T. 2004. Solar radiation transmission through conifer canopies. Agric. For. Meteorol. 126(3-4): 257-270. doi:10.1016/j.agrformet.2004.06.012

Houlton, B.Z. , Driscoll, C.T., Fahey , T.J., Likens, G.E., Groffman, P.M., Bernhardt, E.S., and Huso, D.C. 2003. Nitrogen dynamics in ice storm-damaged forestecosystems:implications for nitrogenlimitation theory.Ecosystems, 6(5): 431-443. doi:10.1007/s1002-1002-0198-.1

Irland , LC. 2000. Ice stonns and forest impacts. Sci. Total Environ. 262(3): 231-242. doi:10.1016/S0048-9697(00)00525-8 PMID:11087029.

JohnStone,J.F., Allen, C.D., Franklin,J.F.,Frelich, LE., Harvey, B.J., Higuera, P.E., et al. 2016. Changin g disturbance regimes, ecological memory, and forest resilience. Front. Ecol Environ. 14(7): 369-378. doi:10.1002/fee.1311

Jones , J.J., Pither , J.P., Debruyn, R.D., and Roberts on , R.J. 2001. Modelin g ice storm damage to a mature, mixed-species hardwood forest in eastern Ontario. Ecoscience, 8(4):513-521. doi:10.1080/11956860.2001.11682681.

Kraemer, M.J., and Nyland, R.D. 2010. Hardwood crown injuries and rebuilding following ice stonns: a literature review. USDA For. Serv. Gen. Teeh. Rep. NRS-60. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, Pa. doi:10.2737/NRs-GTR-60.

Lesak, A.A., Radeloff, V.C,. Hawbaker, T.J., Pidgeon, A.M., Gobakken , T., and Contrucci, K. 2011. Modelin g forest songbird species richness using LiDAR-derived measures of forest structure. Remote Sens. Environ. 115(11): 2823-2835. doi:10.1016/j.rse.2011.01.02.5

Lucash, M.S.,SCheller,R.M.,Sturtevant, B.R., Gustafson,E.J,. Kretchun,A.M., and Foster, J.R. 2018. More than the sum ofits parts: how disturbance interactions shape forest dynamics underclimate change. Ecosphere, 9(6): e02293. doi:10.1002/ecs2.2293

MacArth ur, R.H., and Hom , H.S.1969. Foliage profile byvertical measurements. Ecology, 50(5):802- 804. doi:10.2307/1933693.

McCune, B.,and Mefford, M.J. 2006. PC-ORD. Multivariate analysis of ecological data.Version 5.31. MjM Software Design, Gleneden Beaeh, Ore.

Millwar d, A.A., and Kraft,C.E. 2004. Physical influences of landscape on a large-extent ecologicaldisturbance: thenortheastern NorthAmerican ice stormof 1998.Landsc. Ecol19(1):99-111. doi:10.1023/B:LAND.0000018369.41798.2f .

Mitchell, S. 2013. Wind as a natural disturbance agent in forests: a synthesis. Forestry, 86(2): 147-157. doi:10.1093/forestry/cps058

Nage,lTA.,Firm, D.,Rozenbergar, D., and Kobal, M.2016.Patternsand driversof ice storm damage in temperate forests of Central Europe. Eur.J. For. Res. 135(3): 519- 530. doi:10.1007/s10342-016-0950.2.

Nave, L.,Gough , C., Maurer, K., Bohrer , G., Hardiman, B., LeMoine, J.,et al. 2011. Disturbance and the resilience of coupled carbon and nitrogen cycting in a north temperate forest.J. Geophys. Res. Biogeosci. 116:G04016. doi:10.1029/2011JG001758

Nock, CA.,Lecigne, B., Taugourdeau, 0., Greene, D.F,. Dauzat,J., Delagrange,S., and Messier, C. 2016. Linking ice accretion and crown structure: towards a model of the effect of freezing rain on tree canopies. Ann. Bot. 117(7): 1163-1173. doi:10.1093/aob/mcw059. PMID:27107412

Olthof, I., King, D.J., and Lautenschlager , R. 2003. Overstory and understoryleaf area index as indicators of forest response to ice storm damage. Ecol. Indic. 3(1): 49-64. doi:10.1016/S1470.160X(03)00o.4.

Parker, G.G., and Brown, M.J. 2000 . Forest canopy stratification - is it useful? Am. Nat. 155(4): 473-484. doi:10.1086/303340 PMID:10753075.

Parker, G.,G. Harding, D,J. and Berger, M.L. 2004. A portable LIDAR system for rapid description of forest canopy structure.J.Appl. Ecol.41(4): 755-767. doi:10.1111/j.0021-8901.2004.00925.x.

Peterson, C.J. 2000. Damage and recovery of tree species after two different tornadoes in the same old groWth forest: a comparison of infrequent wind disturbances. For. Ecol. Manage. 135(1-3): 237-252. doi:10.1016/S0378-1127(00)00283-8.

Peterson, C.J.2007.Consistent influenceof treediameterand specieson damagein nine eastern North America tornado blowdowns. For. Ecol Manage. 250(1-2): 96-108. doI:10.1016/j.foreco.2007.03.013.

Reieh , P., Ellsworth , D., Kloeppel, B., Fownes, J., and Gower, S. 1990. Vertical variation in canopy structure and CO_2 exchange of oak-maple forests: influenceof ozone, nitrogen,and other factors on simulatedcanopycarbongain. Tree Physiol. 7(1-2-3-4):329-345. doi:10.1093/treephys/7.1-2-3-4.329 PMID: 14972927.

Reyes, G.P., and Kneeshaw, D. 2008. Moderate-severitydisturbance dynamics in *Ables balsamea - Bellla* spp. forests: the relative importance ofdisturbance type and localstand and site Characteristics on woody vegetation response. Ecoscience, 15(2): 241-249. doi:10.2980/15-2-308.2

Reyes,G.P., Kneeshaw , D., De Grandpre , L.,and Leduc , A. 2010.Changes in woody vegetation abundance and diversity after natural disturbances causing dif. ferent levels of mortality. J. Veg. Sci. 21(2): 406-417. doi:10.1111/j.1654-1103.2009.01152.X.

Rhoads, A.G,. Hamburg, S.P., Fahey, T.J., Siccama, T.G., Hane, E.N., Battles, J., et al. 2002. Effects of an intense ice storm on the structure of a northern hardwood forest. Gan.J. For. Res. 32(10):1763-1775. doi :10.1139/x02-089.

Roberts , M.R. 2007. A conceptual model to characterize disturbance severity in forest harvests. For. Ecol. Manage. 242(1): 58-64. doi:10.1016/j.foreco.2007.01.043.

Rustad, LE., and cam pbell, J.L. 2012. A novel ice storm manipulation experiment in a northern hardwood foresL can.J. For. Res. 42(10): 1810-1818. doi: 10.1139/x2012-120.

Seheuerma nn , C.M., Nave, L.E., Fahey, R.T., Nadelhoffer , K.J., and Gough, C.M. 2018. Effects of canopystructureand speciesdiversityon primaryproduction in upper Great Lakes forests. Oecologia, 188(2):405-415. doi:10.1007/s00442-018-4236-.x PMID:30076540.

Stephens , S.L., Moghaddas , J.J., Edm inste r, C., Fied le r, C.E., Haase , S., Harrington, M., et al. 2009. Fire treatment effects on vegetation stru cture, fuels, and potential fire severity in western US forests. Ecol Appl. 19(2): 305-320. doi:10.1890/07-1755..1 PMID:19323192.

Stuart-Ha tjens , E.J.,Curtis, P.S,.Fahey,RT , Vogel,C.S,.and Gough, C.M. 2015. Net primary productionofa temperatedeciduous forestexhibitsa threshold response to increasing disturbance severity. Ecology, 96 (9): 2478- 2487. doi: 10.1890/14-1810.1 PMID:26594704.

Swaminathan, R. Sridharan, M. and Hayhoe K. 2018. A computational frame• work for modelling and analyzing ice storms. arXiv preprint. arXiv: 1805.04907.

Takahashi, K., Arii, K., and Lechowicz, M.J. 2007. Quantitative and qualitative effectsofa severe icestormon an old-groWth beeeh-maple foresL can.J. For. Res. 37(3): 598-606. doi:10.113/9X06-266.

Turcotte, R.M., Elliorr, T.R., Fajvan, MA. , Park, Y.·L.,Snider , DA. , and Tobin , P.C. 2012. Effects of ice storm damageon hardwood survival and groWth in Ohio. North. J. Appl. For. 29(2): 53-59. doi:10.5849/njaf.10-053.

Turner, M.G., and Romme, W.H. 1994. Landscape dynamics in crown fire ecosystems. Landsc. Ecol. 9(1): 59-77. doi:10.1007/BF00135079.

Weeks , B.C., Hamburg, S.P., and Vadeboncoeur , MA. 2009. Ice storm effects on the canopy structure ofa northern hardwood forest after 8 years. Can.J. For. Res. 39{8): 1475-1483. doi:10.1139/X09-07.6

Woods, K.D. 2004. Intermediate disturbance in a late-successional hemlock - northern hardwood foresLJ. Ecol. 92(3): 464- 476. doi:10.Ull[j.0022-0477.2004.00881.x.