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Stand location variance as an indicator of disturbance regime in a monotypic *Tsuga canadensis* forest

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STAND LOCATION VARIANCE AS AN INDICATOR OF DISTURBANCE REGIME IN A
MONOTYPIC TSUGA CANADENSIS FOREST

By

Cole J Doolittle

Honors Scholarship Project

Submitted to the Faculty of

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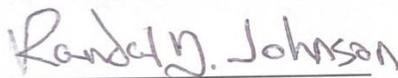
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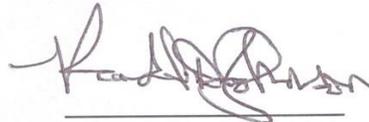
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To my Father, who first taught me to hear the Lord in the song of a Nuthatch, see the Lord in the complexity of an Orchid, and feel the Lord in the strength of an Oak.

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ABSTRACT

Disturbance regimes, which are critical components of forest ecosystems, influence forest morphology, biodiversity, and regeneration. The heterogeneity of disturbance regimes are not well understood on small scales. In this study I analyzed tree cores from five sites within a *Tsuga canadensis* (Eastern hemlock) forest in northern Wisconsin to investigate disturbance regimes through mean growth release criteria. This study investigated the following questions: 1) Are disturbance regimes in *T. canadensis* stand level or site specific? 2) If disturbances are site specific, is site location an indicator of disturbance regime? 3) Do site characteristics such as density and tree diameter at breast height (DBH) influence disturbance regime? I found that *T. canadensis* disturbance regimes are site specific and depend greatly on forest geomorphology, and that density and tree diameter may be weak predictors of disturbance regime. Moreover, I observed a correlation between high intensity release, defined as large increases in ring growth, and low disturbance size, defined as a low proportion of trees with release record, suggesting that *T. canadensis* may have a differential evolutionary response to gap disturbances dependent on gap size. Though confined to one geographic location, this evidence suggests that *T. canadensis* disturbance regimes are complex, site specific, and predict growth strategies which ultimately influence forest morphology. The site specificity of *T. canadensis* disturbance regimes suggest that ecological and management studies, which often assume disturbance homogeneity, may miss important site differences.

Keywords: *dendrochronology, windfall, northwoods, disturbance regime, eastern hemlock, monotypic forest, growth strategy, natural history, release*

INTRODUCTION

Disturbance Regimes

Disturbance processes are important drivers of vegetation dynamics across much of Eastern North American Forests (Attiwill 1994, Janowiak et. al 2014). Classically, a disturbance is defined as a “discrete event that disrupts the ecosystem, community, or population structure and changes the resources, substrate availability or physical environment” (White and Pickett 1985). In these Eastern forest systems, where water does not limit production, wind and fire disturbance regimes drive vegetation dynamics (Canham and Loucks 1984, Attiwill 1994). In this region 30% of late successional species compositions such as *Tsuga canadensis* (Eastern hemlock) may be replaced every 20 years as a result of windfall disturbance (Frelich and Lorimer 1991).

The Northwoods of UNDERC-East (University of Notre Dame Environmental Research Center) are a part of the Laurentian Mixed Forest System which covers the majority of the northern Great Lakes region (Cleland et al. 1997). This system is characterized by secondary temperate broadleaf and mixed boreal transition forests (McNab et. al 2007, Janowiak et. al 2014). *T. canadensis*, a late-successional evergreen tree species, is both shade-tolerant and well adapted to the cool temperate climate of the Northwoods. The cycle of disturbance-mediated gap creation and understory sapling recruitment in *T. canadensis* stands maintains a species-rich seedbank as well as habitat for gap-dependent forest species (Attiwill 1994). Due to the importance of gap dynamics in *T. canadensis* stands, and the relatively long life of *T. canadensis*, they provide an excellent model for studying disturbance regimes in the Northwoods

(Rooney 2008). At UNDERC, *T. canadensis* is found in remnant old growth forests (Figure 1). While a majority of forest stands at UNDERC have historically been repeatedly logged and do not predate the mid 1950's, the unlogged *T. canadensis* plot dates back to the 1790's. This old-growth plot provides a rare opportunity to study disturbance with little interference from anthropogenic land use.



Figure 1: Forest Composition at UNDERC-East in Land O'Lakes, Wisconsin. The Hemlock stand assessed in this study (yellow) is found by Crampton Lake in the southeast section of UNDERC-East. Map created by Bethany Blakely, University of Notre Dame.

Wind and fire are historically the most common forms of disturbance in the Northwoods (Frelich and Reich 1995a, Janowiak et. al 2014). Wind disturbance events are responsible for influencing the canopy structure and creating light gaps within a mature forest (Frelich and Reich 1995a, White and Host 2008). Fire, while once a common component of Northwoods disturbance regimes, has become effectively extirpated from the Northwoods. Since 1910 the frequency of regional fires has been dramatically reduced by anthropogenic intervention (Schulte and Mladenoff 2005, Heinselman 1973). Studies estimate that pre-European settlement natural and native inhabitant driven fire disturbance regimes included stand-killing fires on a rotation of 50 – 100 years while modern research estimates the rotation period between such fires is now 500 – 1000 years (Heinselman 1973). Unlike wind, fire does destroy understory seedlings, and therefore can affect species composition (Davis 1996). After a fire disturbance event, the ability for a forest stand to retain the pre-fire species composition is referred to as compositional stability, or compositional “memory” (Frelich and Reich 1995). Hardwood-hemlock and White pine forests show relatively weak species compositional stability, and therefore experience more compositional changes following fire disturbance (Frelich and Reich 1995a). The presence of a near-monotypic *T. canadensis* forest on UNDERC’s property indicates a lack of stand-killing fire disturbance since establishment, which would encourage a polytypic canopy. Therefore, it is assumed that observing disturbance regimes through tree dating is analogous to observing non-stand replacing windfall events throughout the history of the *T. canadensis* forest. Wind gap-creating disturbance events, which remove old trees

and promote understory tree growth, are important drivers of vegetation composition in forest ecosystems worldwide (Attiwill 1994, Janowiak et al. 2014).

The Northwoods and many other Eastern forest systems experience large scale fragmentation due to anthropogenic land use. Habitat fragmentation is one of the main contributors to native species loss and compromises many natural ecosystem processes including natural disturbance regimes (Wilcox and Murphy 1985). Small remnants of fragmented native forests are driven primarily by external (i.e. anthropogenic land use, pollution), not internal, factors (i.e. static disturbance regimes, decomposition; Saunders et al. 1991). These fragmented forested landscapes are more susceptible to external factors leading to increased ecological degradation and exotic invasion resulting in dynamic shifts in disturbance regime (Heilman et al. 2002, Rejmánek 1919). Disturbance regimes on a local site scale are not well understood, as a vast majority of research is done on forest or regional scales. However, understanding the localized disturbance regimes is critical for continued management of species diversity and old-growth characteristics within fragmented forest systems. At UNDERC, disturbance regime specificity within the *T. canadensis* forest may exist due to topography. Specifically, site specific disturbances may be determined by changes in elevation sheltering or exposure within *T. canadensis* plots to the predominant disturbance factor - wind. Fetch, a measure of the distance that wind has to pick up speed over water, was used in this study to test sites with potentially differential wind regimes. The presence of disturbance regime site specificity within UNDERC's *T. canadensis* forests would suggest

that these monotypic forest systems have site specific responses to altered wind conditions prevalent in fragmented forests.

Climate Change

Climate change also drives ecological shifts in forest ecosystems. As the climate warms, weather patterns become more unpredictable and violent, creating more windstorms with the potential to induce disturbance (Dale 2001). Extreme precipitation and temperature deviation from median values are known to predict understory disturbances, but the data are inconclusive on overstory disturbance dynamics (Elliot and Root 2006). Since disturbance regimes in the Northwoods are important drivers of forest composition and succession, any changes in disturbance frequency or intensity could have consequences for future forest composition. Therefore, understanding the forest disturbance structure and the impacts of climate change on disturbance in the Northwoods provides insight into the health and resiliency of this important ecosystem. As our climate continues to rapidly change, a history of disturbance incidence will become crucial to understanding modern forest systems.

Dendrochronology

A chronological timeline of disturbance events can be recorded through analysis of tree rings (Frelich 1995a). Increment boring, a common dendrochronological tool, allows the collection of tree cores with minimal damage to the tree (Stokes and Smiley 1968). Analyzing growth patterns in tree rings reveals periods of stagnation followed by rapid growth, called releases, where a tree responded to a sudden increase in light and resource availability (Stokes and Smiley 1968). A release response is indicative of large

increases in resource (light) availability, which in Eastern forests is typically created through windfall disturbance events.

This study constructed a timeline of release events throughout the history of an old growth *T. canadensis* forest on UNDERC property using tree cores from five sites, cross dating, and comparing stand density characteristics. Sites were selected for heterogeneity in microtopography. Once constructed, this timeline was used to assess the size and intensity of release events within each microtopographic area.

Furthermore, local climate data (yearly precipitation and temperature) were compared with the resulting disturbance timeline. I addressed the following questions: 1) Are disturbance regimes in the *T. canadensis* forest of UNDERC forest level or site specific? 2) If disturbance regimes are site specific, is stand location a predictor of disturbance frequency? 3) Do site characteristics such as density and diameter at breast height (DBH) influence disturbance regimes? I hypothesized that disturbance regimes are site specific within the *T. canadensis* forest and that stand location influences disturbance frequency. Specifically, I expected lowland habitat within the *T. canadensis* forest topography to sustain both more frequent and larger disturbances compared to the interior and sheltered sites. I additionally hypothesized that sites with high tree density and large tree diameter experienced more frequent and more intense disturbance regime patterns.

METHODS

Experimental Procedure – Field Core Collection:

Five plots within the *T. canadensis* forest stand east of Crampton Lake were chosen on UNDERC-East property in Land O' Lakes, Wisconsin. The *T. canadensis* plots at UNDERC were located in the southeastern corner of the property and are not accessible by road (Figure 2). Each plot met one of the following criteria: wind exposed forest-lake edge (LOW), wind protected forest-lake edge (EDS), forest interior (INT), forest-forest edge (FFE), or forest ridge (RID; Figure 3). All trees at each plot within a 10m radius were measured for diameter at breast height (DBH) and distance to plot center. Additionally, all *T. canadensis* trees over 15cm DBH within the 10m radius were cored using a Haglof Increment Borer. Each *T. canadensis* cored was numbered and tagged using aluminum nails and tree tags. Cores were secured in straws and returned to the lab for analysis. GPS coordinates were recorded at each plot center. Site maps were created using ArcGIS (ESRI 2011).

Experimental Procedure – Core Preparation, Mounting, and Scanning:

Once returned to the lab, cores were dried for 48hrs in a 50°C oven and mounted onto wood panels. Each core was hand sanded to a high polish in accordance with standard dendrochronological procedures using 100, 200, 320, 400, and 600 grit sandpaper (Black and Abrams 2003, Nagel et. al 2007, Stokes and Smiley 1968, Spletchna 2005). Each core was visually cross dated and scanned by an HP Scanjet G3110 into a .jpg file at 1200 dpi. Once scanned, the distances between rings in each

core were transformed into a .pos file using CooRecorder and saved as a .rwl file using CDendro (Cybis Elektronik 2010). Digital cross dating using COFECHA was performed to recheck dating sequences as previously described (Grissino-Mayer 2001). Problems in core dating were solved using CooRecorder until correlation values for each site reached ecologically acceptable levels (>0.5 ; Cybis Elektronik 2010). Cores with persistent dating problems were omitted to ensure consistent dating across all analyzed cores.

Site Descriptions and Sample Size:

The 107 trees cored were split between the sites as follows: RID = 22, LOW = 29, EDS = 21, INT = 26, and FFE = 13 (Figure 2). Of these trees, 31 were omitted due to COFECHA identified errors split between the sites as follow: RID = 9, LOW = 9, EDS = 8, INT = 4, and FFE = 2. Final sample size for data analysis was 76 trees. I had trouble hitting the pith in some trees due to natural pith decay. In some cases when approaching the pith, the core lost its rigidity and became unreadable due to this decay. Therefore, while some entire site records date to the late 1790's, the confidently cross-dated section of the records collected in this study only date back to the late 1800's or early 1900's.

Ridge (RID) Site Analysis: Ridge was selected due to its relatively high elevation. The RID site is situated on top of a small plateau met by steep declines to Crampton Lake on the West, North, and East edge and a steep decline to the forest interior on the Southern

edge. Of the initial 22 ridge tree cores, nine were omitted due to persistent dating problems for a final sample size of 13 cores (series intercorrelation = 0.692). The 1,709 tree rings were cross dated back to 1820. The mean core age was 132.0 years.

Exposed Lowland Edge (LOW) Site Analysis: This low exposed edge was chosen due to its low elevation and Western exposure to wind off Crampton Lake. Of the initial 29 low tree cores, nine were omitted due to persistent dating problems for a final sample size of 20 cores (series intercorrelation = 0.583). The 2,346 tree rings were cross dated back to 1850. The mean core age was 102.0 years.

Protected Forest Edge (EDS) Site Analysis: This protected edge was chosen due to its proximity to Crampton Lake to mirror LOW. Unlike LOW, EDS was protected from predominant winds due to a western elevation increase. Of the initial 21 protected forest edge tree cores, eight were omitted due to persistent dating problems for a final sample size of 13 cores (series intercorrelation = 0.572). The 1,529 tree rings were cross dated back to 1830. The mean core age was 109.0 years.

Interior (INT) Site Analysis: The interior site was chosen due to its distance from any edge. Of the initial 26 interior tree cores, four were omitted due to persistent dating problems for a final sample size of 22 cores (series intercorrelation = 0.635). The 1,060 tree rings were cross dated back to 1860. The mean core age was 61.0 years.

Forest-Forest Edge (FFE) Site Analysis: This forest-forest edge site was chosen due to its location on the transition boundary from monotypic *Tsuga canadensis* forest to a polytypic mixed hardwood forest. Of the initial 13 forest-forest edge tree cores, two were omitted due to persistent dating problems for a final sample size of 11 cores (series intercorrelation = 0.547). The 778 tree rings were cross dated back to 1900. The mean core age was 70.0 years.

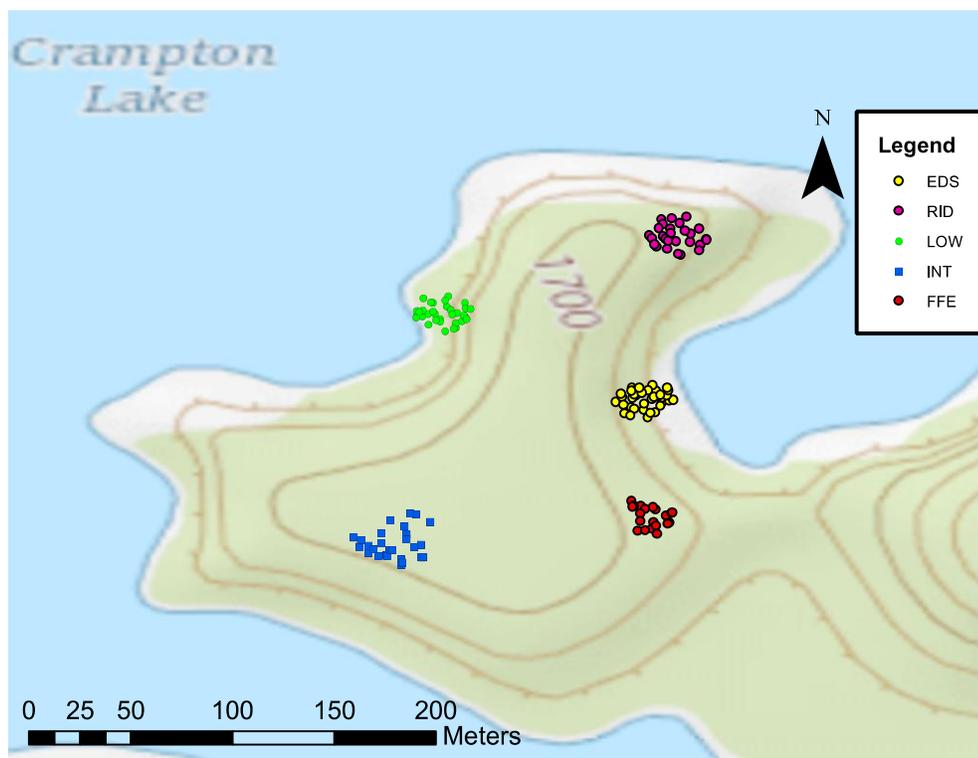


Figure 2: Distribution and Classification of Hemlock Stand Sites at UNDERC-East. Figure shows coring sites on topographic map. LOW site chosen for exposure to prevailing wind fetch. EDS site protected from prevailing winds by microtopography. INT site protected from prevailing winds by surrounding trees. RID site moderately protected by trees, but moderately exposed due to microtopography. FFE site selected at protected edge of hemlock stand. Map created in ArcGIS.

Statistical Analysis:

Release events were identified from ring width data (.rwl outputs from CDendro) for each site using RStudio 1.1 and the TRADER package (RStudio Team 2015, Altman et al. 2014). Release events were based on growth averaging methods (Nowacki and Abrams 1997). Moderate and severe release events were defined as >50% growth increase and >90% growth increase; respectively. All release events must have met growth increase criteria for five consecutive years, and releases were limited to one per five-year span to limit false positive results.

Intensity of release per site was calculated from the means of percent growth increase from each disturbance of each site. These datasets failed the Shapiro-Wilk normality test ($W=0.943$, $p=0.003$) and were therefore analyzed using a Kruskal-Wallis rank sum test. Post-hoc analysis was completed using Dunn's Test, a non-parametric pairwise multiple comparison procedure based on rank sums.

Proportion of trees with release events per disturbance by site were calculated by dividing the number of trees releasing per disturbance by the total number of core records in that year. These datasets also failed the Shapiro-Wilk normality test ($W=.80495$, $p=5.621e-09$). However, parametric analysis was possible after \log_{10} transformation (Shapiro-Wilk, $W=.96775$, $p=0.0388$). A one-way ANOVA allowed analysis of the transformed data, and post-hoc analysis was completed using Tukey's Honestly Significant Difference (HSD) analysis.

Diameter at breast height per site was analyzed using a one-way ANOVA, with post-hoc analysis completed using Tukey's HSD analysis. In all cases, $p < 0.05$ was considered statistically significant.

RESULTS

In analyzing the disturbance intensity, and therefore heterogeneity, I found clear variance. These data are nonparametric and analyzed via the Dunn post-hoc test for nonparametric data (Kruskal-Wallis, $\chi^2=33.4$, $df=4$, $p=9.89e-07$). The intensity of release at individual sites was significantly higher at LOW than EDS; $z=-3.743$, $p=0.0015$; FFE; $z=4.145$, $p=0.0003$; and RID; $z=3.987$, $p=0.0006$; (Figure 3).

T. canadensis disturbance proportion, another measure of heterogeneity, also showed clear variance. These data are parametric and were therefore analyzed using a one-way ANOVA; $df=4$, $F=4.02$, $p=0.0519$. The proportion of trees with detectable release events per disturbance was significantly lower at LOW than EDS; Tukey HSD $p=0.0269$; and FFE; Tukey HSD $p=0.0264$; (Figure 4).

Diameter at breast height (DBH), measured for consistency across the five sites, showed variance between two sites. These data were parametric in nature, and therefore analyzed using a one-way ANOVA; $df=4$, $F=675.9$ $p=0.0023$. Diameter at breast height (DBH) was significantly lower at EDS than INT; Tukey HSD $p=0.0009$ (Figure 5).

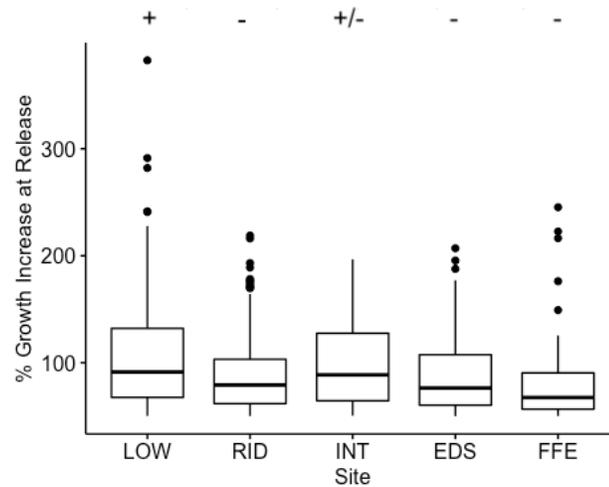


Figure 3: Differences in *T. canadensis* release intensity measured by percent growth increase. Results of Kruskal-Wallis nonparametric analysis reveal a significant difference between the intensity of release at LOW, EDS, FFE, and RID. Kruskal-Wallis: $\chi^2=33.4$, $df=4$, $p=9.89e-07$; Dunn's Test, LOW-EDS $p=0.0015$, LOW-FFE $p=0.0003$, LOW-RID $p=0.0006$. Bars with different symbology (+, -) are statistically different.

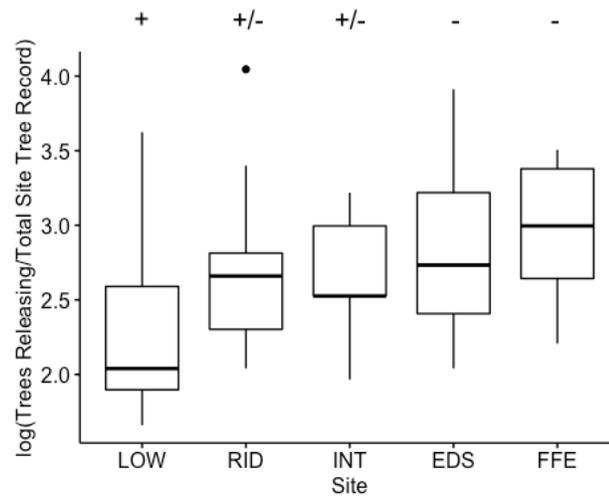


Figure 4: Differences in proportion of *T. canadensis* releasing at each site (log proportion). Log transformed results of one-way ANOVA reveal a significant difference between the proportion of trees that release at LOW, EDS, and FFE. 1-Way ANOVA, $df=4$, $F=4.02$, $p=0.0519$; Tukey HSD, LOW-EDS $p=0.0269$, LOW-FFE $p=0.0264$. Bars with different symbology (+, -) are statistically different.

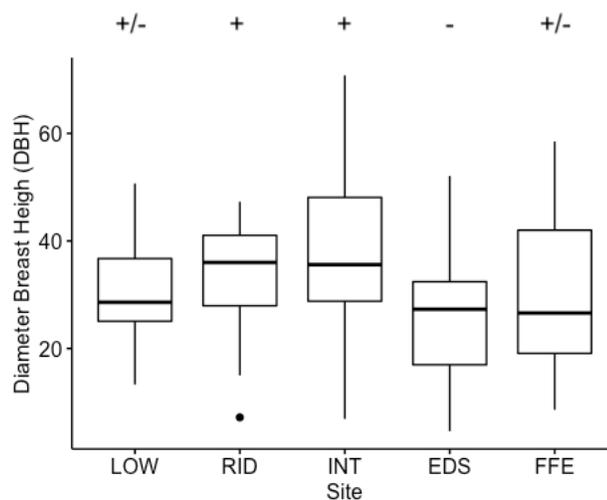


Figure 5: Differences in *T. canadensis* diameter at breast height at each site (diameter, cm). Results of one-way ANOVA reveal significant differences between DBH at INT and EDS; 1-Way ANOVA, $df=4$, $F=675.9$, $p=0.0023$; Tukey HSD, INT-EDS $p=0.0009$. While significant, these results are not consistent with disturbance size and intensity data which suggests that DBH variance was not a significant factor in the disturbance study. Bars with different symbology (+, -) are statistically different.

DISCUSSION

There are differences in disturbance intensity, frequency, and size across *T. canadensis* forest sites at Crampton Lake. The evidence supports the hypothesis that disturbance regimes in monotypic *T. canadensis* forests are site specific and vary over forest topography. Previous research suggests that information on disturbance regimes in individual forests is necessary for both scientific study and land management (Lorimer and Frelich 1989). However, data presented here suggest that scientific study and land management should account for disturbance intensity, frequency, and size fluctuation throughout a smaller ecological scale.

The high intensity of release at LOW compared to EDS, FFE, and RID suggests that site location plays an important role in disturbance regimes (Figure 3). Stronger intensity release events may represent large gap sizes. Larger gaps allow more light to penetrate to understory branches of canopy trees and dramatically increase light availability to understory flora. Therefore, I would expect, due to the comparatively high intensity of releases at LOW, that disturbances on the exposed edge create relatively larger gaps. However, disturbance records appear in a proportionally lower number of cores at the exposed edge (LOW; mean: 11.2% than the sheltered edge (EDS; mean: 18.4%) and forest-forest edge (FFE; mean: 21.3%) sites (Figure 4). The enigmatic suggestion from these data is that release events detected in tree growth at the exposed edges were large releases, but not very common across trees. It is possible that there is a response within *T. canadensis* that accounts for the mismatched disturbance size and release intensity results.

The disturbance size record suggests that there may be a differential response to light availability in *T. canadensis*. When presented with a moderate increase in light from a small gap, *T. canadensis* may respond by focusing growth in the apical meristem to reach higher where more light is available. Additionally, when presented with open canopy light availability *T. canadensis* may focus more energy into branch and needle development, allocation strategies which are both less visible in the core record than stem allocation. Previous research suggests that this life history strategy, first documented in *Acer* and *Betula* spp., may exist in *T. canadensis* saplings (Logan 1965, Vasilias and Aarssen 2000). However, this is the first time it has been documented in mature *T. canadensis* within an unmanaged forest. Differential growth strategies in *T. canadensis* are not yet well understood. Further study into these strategies could document *T. canadensis* in gap environments and attempt to quantify the ideal light conditions for *T. canadensis* regeneration. Additionally, comparing direct observation on growth strategy to tree ring analysis would provide insight into the accuracy of post-gap determination of release intensity and disturbance size. This differential response, supported by my results, offers a plausible explanation as to why high intensity release events align with a proportionally smaller disturbance event.

Another possibility is that young, understory *T. canadensis* trees may simply not be successful under direct light conditions. Adapting to shade-tolerance may come with the trade-off of direct light productivity. The specific adaptation strategy of *T. canadensis* is unclear and understanding this complex physiological response will require more study. Furthermore, this study focused on one *T. canadensis* forest.

Further study should include comparisons between *T. canadensis* forests across similar regions to determine if evidence presented here is indicative of all *T. canadensis* forests or unique to the UNDERC-East forest.

Diameter at breast height (DBH) also differs significantly across the sites (Figure 5). The interior sites, INT (mean: 27.8) and RID (mean: 33.4), have significantly larger trees than the sheltered edge (EDS; mean: 25.2). I expected DBH to inversely correlate with site density. Larger trees with a wider diameter leave less room for competition. RID (26 trees/10m rad.) and INT (27 trees/10m rad.) are slightly less dense than EDS (36 trees/10m rad.), which supported the hypothesis. However, it is important to note that only one plot for each of these categories was measured. A larger sample size is necessary to increase confidence in this relationship.

It must be noted that each site had cores removed due to persistent dating problems. In these cases, even after software analysis using Coorecorder and COFECHA there was a low confidence value that these cores aligned with the forest's historical record. There are three reasons why dating problems persisted in this study: resolution, false rings, and natural decay. Resolution, or the detail within the finalized core scans, was 400 dpi. This means that for years with particularly small rings it was difficult to define, or resolve, such a small ring growth. False rings, which are rings created by a tree in response to abrupt environmental shifts such as a cold spike or insect infestation, are identical to typical seasonal rings and could have skewed core interpretation if not properly identified. Finally, cores with natural decay were moist and often could not be sanded leading to assumptions of ring presence and width. These three complications

could have contributed to a cascade of inaccurate dating potentially resulting in a cross dated core with a low confidence value. Since there was no pattern detected in the location or size of these problematic cores they were removed from the final record in accordance with established dendrochronological procedure (Black and Abrams 2003).

As forests become more fragmented, understanding disturbance on a localized, site level is critical. Rapid changes in forest morphology due to anthropogenic interactions likely have large effects on the disturbance regime and therefore forest structure. Additionally, growth strategies and disturbance regimes may differ across forests with various aging structures. Understanding the importance of age structure on disturbance regime could provide insight into the negative impacts of fragmentation and how to manage *T. canadensis* ecosystems.

Documenting disturbance regime is a daunting task. This research offered evidence that disturbance regimes are localized to specific geomorphic regions within a *T. canadensis* forest. These specific geomorphic regions interact with differential growth strategies of *T. canadensis* to shape the overall forest morphology. Documenting these site, disturbance, and tree interactions is critical for any ecologist or management officer looking to preserve old-growth characteristics of a *T. canadensis* forest. This study suggests that assuming a homogenous forest disturbance structure is an unrealistic management practice. Managing a forest based on the assumption of disturbance homogeneity may have adverse consequences for areas of the forest with unique disturbance regimes – decreasing productivity, biodiversity, and sustainability. As the Northwoods continues to be fragmented, it can be expected that disturbance

regimes will change rapidly and unpredictably in conjunction with topography, climate, and anthropogenic land use. The destabilization of fragile, localized disturbance regimes will have numerous detrimental effects on ecosystem functions.

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