

Site Specific Responses to Disturbance Regime in a Monotypic *Tsuga canadensis* Forest

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Abstract

Disturbance regimes, which are critical components of forest ecosystems, are not well understood on small scales. In this paper I analyze tree cores to understand disturbance regimes through average growth release criteria. Five sites within a *Tsuga canadensis* (Eastern hemlock) forest. This study asks 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 (DBH) influence disturbance regime? 4) Does *T. canadensis* release intensity correlate with disturbance size? I found that disturbance regimes in *T. canadensis* are site specific and depend greatly on forest geomorphology. Density and tree diameter may be weak predictors of disturbance regime. Additionally, the correlations revealed between high intensity release and low disturbance size suggests 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

Introduction

Disturbance regimes play a critical role in the life, health, and prosperity of forest ecosystems. Typically, a disturbance is defined as “a relative discrete event that disrupts the ecosystem, community, or population structure and change the resources, substrate availability or physical environment” (White and Pickett 1985). Canopy gap-creating disturbance events, which remove old trees and promote understory tree growth, are important driver of forest vegetation ubiquitous in forest ecosystems worldwide (Attiwill 1994, Janowiak et. al 2014). Both understory species diversity, an indicator of ecosystem health, and composition complexity are maintained by these gap-disturbances events (Hartshorn 1980, Yamamoto 1992). These factors make gap disturbances critical for overstory and understory competition dynamics, diversity, and health (Janowiak et al. 2014).

Disturbance processes are important drivers of vegetation dynamics across much of Eastern North American Forests. 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* 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; Figure 1). 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. While a majority of forest stands at UNDERC are relatively young the old *T. canadensis* plot provides an opportunity to study disturbance with little interference from anthropogenic land use.

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 driven fire disturbances 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 indicate a lack of stand-killing fire disturbance since establishment, which would encourage a polytypic canopy. Therefore, we can make the assumption that observing disturbance regimes through tree dating is analogous to observing non-stand replacing windfall events throughout the history of the *T. canadensis* forest.

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 by primarily external (i.e. anthropogenic land use, pollution, climate), not internal, factors (i.e. disturbance regimes, decomposition; Saunders et al. 1991). These fragmented forested landscapes are more susceptible to ecological degradation, exotic invasion, and disturbance regime shifts (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 both topography and climate. Specifically, site specific disturbances may be determined by changes in elevation sheltering or exposing *T. canadensis* plots to the predominant disturbance factor; wind. The presence of disturbance regime site specificity within UNDERC's *T. canadensis* forests would suggest that these monotypic forest systems would have site specific responses to fragmentation.

In modern times, climate changes can drive 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). 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 both the baseline impact of forest disturbance and the impacts of climate change on disturbance in the Northwoods would provide insight into the health and resiliency of this important ecosystem. As our climate continues to rapidly change an understanding of how forests worked in the past will become critical to understand modern forest systems.

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

(local, stand, regional) there was a disturbance event. This study aims to construct a timeline of release events throughout the history of an old growth *T. canadensis* forest on UNDERC property using tree core cross dating and stand characteristics. In doing so, I hope to address the following questions: 1) Are disturbance regimes in the *T. canadensis* forest of UNDERC forest-level or site-specific? 2) If they are site specific, is stand location a predictor of disturbance frequency? 3) Do site characteristics such as density and tree diameter (DBH) influence disturbance regime? and 4) Does *T. canadensis* release intensity correlate with disturbance size? I hypothesize that disturbance regimes are site specific within the *T. canadensis* forest and that stand location influences disturbance frequency. Specifically, we expect lowland habitat within the *T. canadensis* forest topography to sustain both more frequent and larger disturbances compared to the interior and sheltered sites. Additionally, I hypothesize that sites with high tree density and large tree diameter experience 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 (Figure 3). The *T. canadensis* plots at UNDERC are located in the southeastern corner of the property and are not accessible by road (Figure 2). Each plot met one of the following criteria: exposed forest-lake edge (LOW), 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 10 meter radius were measured for diameter at breast height and distance to plot center. Additionally, all *T. canadensis* trees over 15cm DBH within the 10-meter 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 48 hours 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, Splechna 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 (Grissino-Mayer 2001). Problems in core dating were solved using CooRecorder until correlation values were $>.500$. Cores with persistent dating problems were omitted to ensure consistent dating across all analyzed cores.

Site Descriptions and Sample Size Analysis

107 trees were cored split between the sites as follows: RID = 22, LOW = 29, EDS = 21, INT = 26, and FFE = 13. 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. We had trouble hitting the pit in some trees due to rot, this contributed to a short confidently cross-dated core record for some sites.

Ridge (RID) Site Analysis: Ridge was chosen due to its relatively high elevation. The RID site is situated 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 9 were omitted due to persistent dating problems for a final sample size of 13 cores (series intercorrelation = 0.692). 1709 tree rings were cross dated back to 1820. The mean core age is 132.0 years.

Exposed Lowland Edge (LOW) Site Analysis: This low exposed edge was chosen due to its low elevation and exposure Western edge to wind off Crampton Lake. Of the initial 29 low tree cores 9 were omitted due to persistent dating problems for a final sample size of 20 cores (series intercorrelation = 0.583). 2346 tree rings were cross dated back to 1850. The mean core age is 102.0 years.

Protected Forest Edge (EDS) Site Cross Dating Analysis: This protected edge was chosen due to its proximity to Crampton Lake to mirror LOW. Unlike LOW, EDS is protected from predominant winds due to a western elevation increase. Of the initial 21 protected forest edge tree cores 8 were omitted due to persistent dating problems for a final sample size of 13 cores (series intercorrelation = 0.572). 1529 tree rings were cross dated back to 1830. The mean core age is 109.0 years.

Interior (INT) Site Analysis: The interior site was chosen due to its relatively average elevation and large distance from any edge. Of the initial 26 interior tree cores 4 were omitted due to

persistent dating problems for a final sample size of 22 cores (series intercorrelation = 0.635). 1060 tree rings were cross dated back to 1860. The mean core age is 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 2 were omitted due to persistent dating problems for a final sample size of 11 cores (series intercorrelation = 0.547). 778 tree rings were cross dated back to 1900. The mean core age is 70.0 years.

Statistical Treatment of Data

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 event 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 5 consecutive years, and releases were limited to 1 per 5-year span to limit false positive results.

Intensity of release per site was calculated from the means of % 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 comparisons 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 ($W=8.0495$, $p=5.621e-09$). However, parametric analysis was possible after \log_{10} transformation (Shapiro-Wilk, $W=96775$, $p=0.0388$). A 1-Way ANOVA allowed analysis of the transformed data. Post-hoc analysis was completed using Tukey's Honestly Significant Difference (HSD) analysis.

Diameter at breast height per site was analyzed using a 1-way ANOVA. Post-hoc analysis was completed using Tukey's Honestly Significant Difference (HSD) analysis.

Intensity of release over decades from 1910-2000 was calculated by sorting % growth increase data by 10-year period. These data failed the Shapiro-Wilk normality test ($W=0.94268$, $p=0.0031$) and were therefore analyzed using a Kruskal-Wallis rank sum test.

Results

The intensity of release was significantly higher at LOW than EDS (mean + SE; LOW, 1.057 ± 0.026 ; EDS, 0.882 ± 0.028 ; Kruskal-Wallis, $\chi^2=33.4$, $df=4$, $p=9.89e-07$; Dunn's Test, $z=-3.743$, $p=0.0015$; Figure 6), FFE (mean + SE; LOW, 1.057 ± 0.026 ; FFE, 0.842 ± 0.060 ; Kruskal-Wallis, $\chi^2=33.4$, $df=4$, $p=9.89e-07$; Dunn's Test, $z=4.145$, $p=0.0003$; Figure 6), and RID (mean + SE; LOW, 1.57 ± 0.026 ; RID, 0.884 ± 0.023 ; Kruskal-Wallis, $\chi^2=33.4$, $df=4$, $p=9.89e-07$; Dunn's Test, $z=3.987$, $p=0.0006$; Figure 6).

The proportion of trees with detectable release events per disturbance was significantly lower at LOW than EDS (mean + SE; LOW, 11.253 ± 0.309 ; EDS, 18.458 ± 2.992 ; 1-Way ANOVA, $df=4$, $F=4.02$, $p=0.0519$; Tukey HSD $p=0.0269$; Figure 7), and FFE (mean + SE; LOW, 11.253 ± 0.309 ; FFE, 21.375 ± 1.699 ; 1-Way ANOVA, $df=4$, $F=4.02$, $p=0.0519$; Tukey HSD $p=0.0264$; Figure 7).

Diameter at breast height (DBH) was significantly lower at EDS than INT (mean + SE; INT, 27.881 ± 0.631 ; EDS, 25.243 ± 0.317 ; 1-Way ANOVA, $df=4$, $F=675.9$ $p=0.0023$; Tukey HSD $p=0.0009$; Figure 8), and RID (mean + SE; RID, 33.470 ± 0.393 ; EDS, 25.243 ± 0.317 ; 1-Way ANOVA, $df=4$, $F=675.9$, $p=0.0023$; Tukey HSD $p=0.0757$; Figure 8). Diameter at breast height was significantly lower at EDS than INT (-2.638cm^2) and RID (-8.227cm^2).

There was no significant difference between the intensity of disturbance events over decade periods from 1910-2000 (Kruskal-Wallis, $df = 8$, $p = 0.1125$; Figure 9).

Discussion

It is clear that there are a number of statistically significant differences in disturbance intensity, frequency, and size across *T. canadensis* forest sites. This evidence supports my 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, evidence presented here suggests that scientific study and land management should account for disturbance intensity, frequency, and size fluctuation throughout specific sites.

The high intensity of release at LOW compared to EDS, FFE, and RID suggests that site location plays an important role in disturbance regime (Figure 6). Stronger intensity release events are theoretically indicative of large gap size. Larger gaps present more light to understory branches of canopy trees and dramatically increase light availability to understory flora. Therefore, we would expect, due to the relative 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: 11.253) than the sheltered edge (EDS; mean: 18.458) and forest-forest edge (FFE; mean: 21.375) sites (Figure 7). The enigmatic suggestion from this 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 trunk cambium 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, Vasiliauskas 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 observe *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 response, supported by my findings, offers a plausible explanation as to why high intensity release events correlate with a proportionally smaller disturbance event. Another possibility is that young, understory *T. canadensis* trees may simply not be successful under direct light conditions. In other words, 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.

Diameter at breast height (DBH) also differs significantly across the sites. The interior sites, INT (mean: 27.881) and RID (mean: 33.47), have significantly larger trees than the sheltered edge (EDS; mean: 25.243; Figure 8). I expected DBH to inversely correlate with site density. Theoretically, 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 my hypothesis (Figure 5). However, it is important to note that only one plot for each of these categories was measured. While the inverse correlation hypothesis seems to be supported, a larger sample size is necessary to increase confidence in this correlation.

There seems to be no correlation between the intensity of release and decade throughout the 1900s. Disturbances experienced by *T. canadensis* stands today are of relatively equal intensity to those experienced over the past century (Figure 9). This evidence rejects the hypothesis that *T. canadensis* disturbance intensity can be used as a model indicator of climate change over the past 100 years. There is evidence that suggests that climatic sensitivity of tree rings is lost at Northern latitudes (Briffa et al. 1998). This could be a confounding factor in why no relationship between intensity and decade was revealed. However, it is possible that a reconstruction of climate using precipitation and temperature records could yield interesting correlations between ring growth and climate change. Qualitatively it seems that certain decades (1930's, 1950's) with low precipitation have relatively numerous disturbances (Figure 10). To confirm such qualitative analysis we would need to compare precipitation and temperature data with core widths to shed light on the possibility that low precipitation contributes to frequent

disturbance events. Nevertheless, data presented here offers some reassurance that northern *T. canadensis* dominated forests may be insulated from the more dramatic effects of changing disturbance regimes resulting from a warming climate for the time being.

It is important to acknowledge that while 76 trees is a significant sample size it does not offer a complete interpretation of the overall forest disturbance structure. Additionally, the omission of 31 trees from the initial 107 indicates the possibility of significant error in the dating sequence. A significant number of false or missing rings could have played a large role in skewing data interpretation of disturbance. 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 forest presented in this study.

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 damages of fragmentation and how to manage *T. canadensis* ecosystems.

Understanding disturbance regime is a daunting task. This research offers evidence that disturbance regimes are localized to specific geomorphic regions within a *T. canadensis* forest. These specific geomorphic regions interact with *T. canadensis* differential growth strategies to shape the overall forest morphology. Understanding 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

regime structure a dangerous and 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 we can expect disturbance regimes to 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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Appendix A: Figures

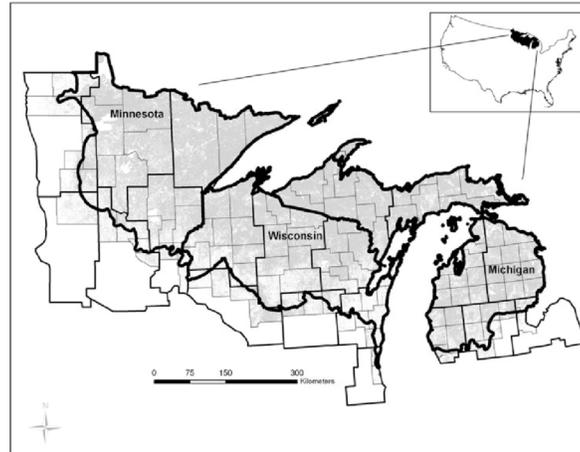


Figure 1: Ecological Province 212. Map showing the counties falling at least partly within Ecological Province 212. Shading indicates forest cover. Map created by Gustafson and Sturtevant.

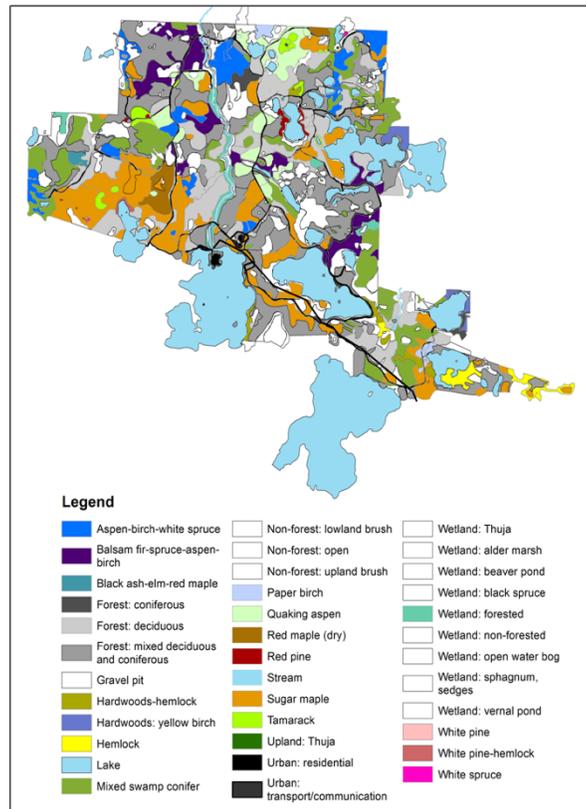


Figure 2: UNDERC Forest Composition. Map created by Bethany Blakely. Crampton Lake in Southeast section of map, yellow indicates Hemlock stand.

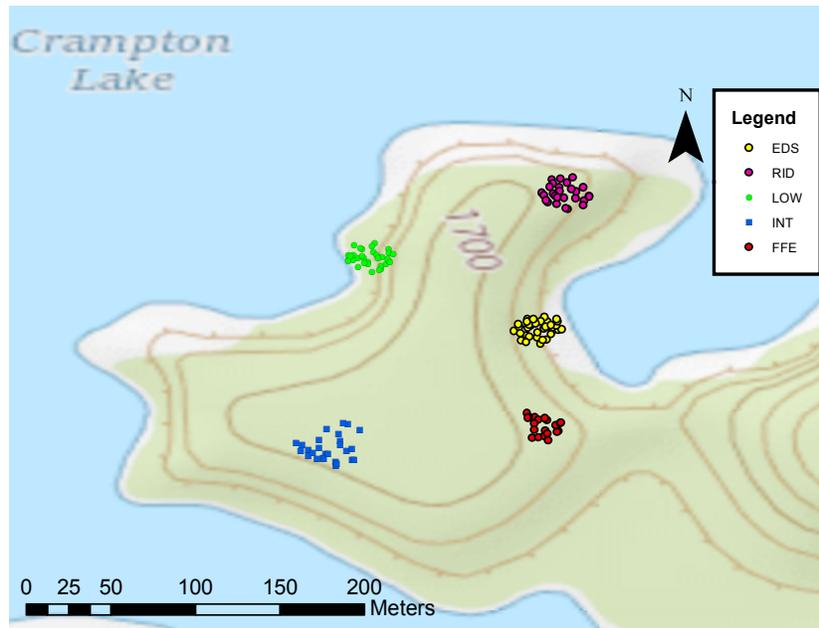


Figure 3: UNDERC Core Collection Map (Meters). Map showing coring sites on topographic map. Map created in ArcGIS.

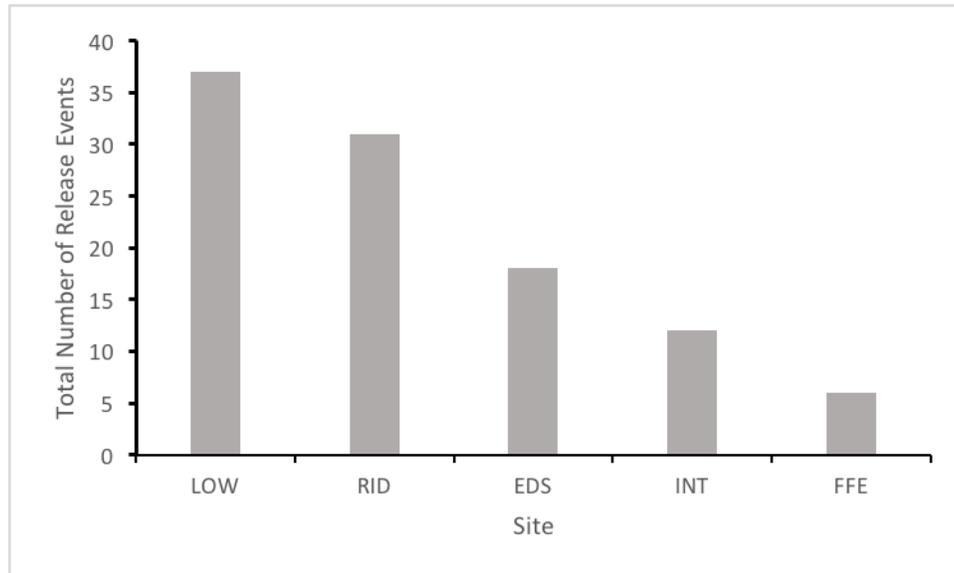


Figure 4: *T. canadensis* Release Events Observed at Each Site. Raw recorded data of release events sorted by site.

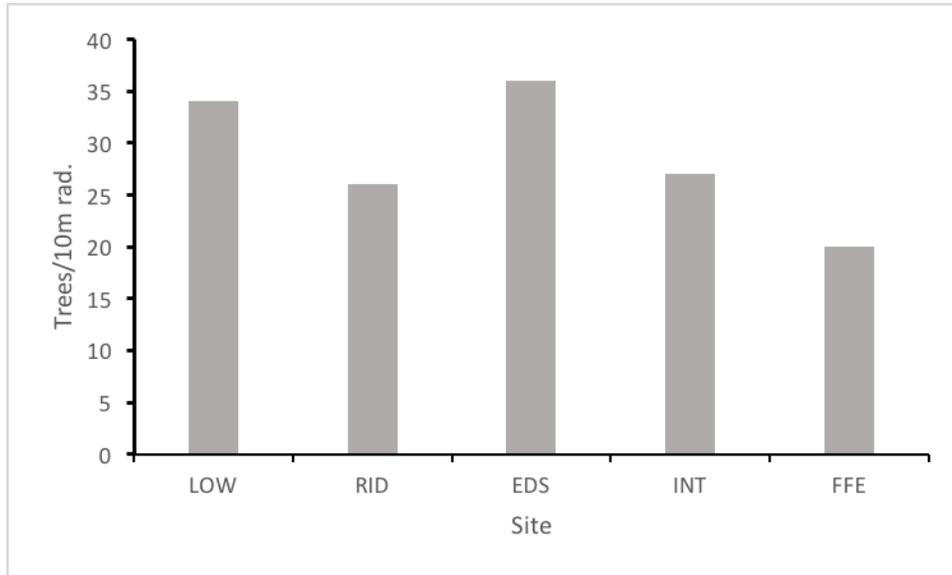


Figure 5: *T. canadensis* Density of Each Site (radius, cm). Raw recorded data of tree density within the 10m test radius.

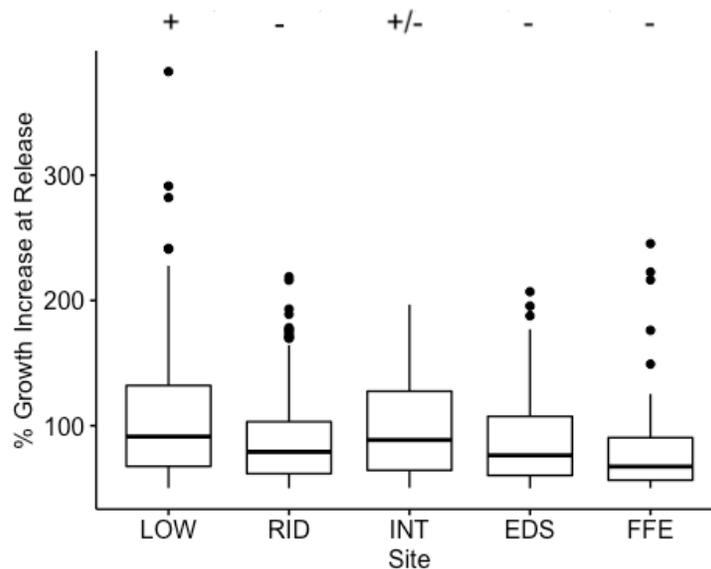


Figure 6: Differences in *T. canadensis* release intensity measured by % growth increase (%). Results of Kruskal-Wallis nonparametric analysis reveal a significant difference between the intensity of release at LOW, EDS, FFE, and RID. Kruskal-Wallis: $\chi^2=33.4$, $df=4$, $p=9.89e-07$; Dunn's Test, LOW-EDS $p=0.0015$, LOW-FFE $p=0.0003$, LOW-RID $p=0.0006$.

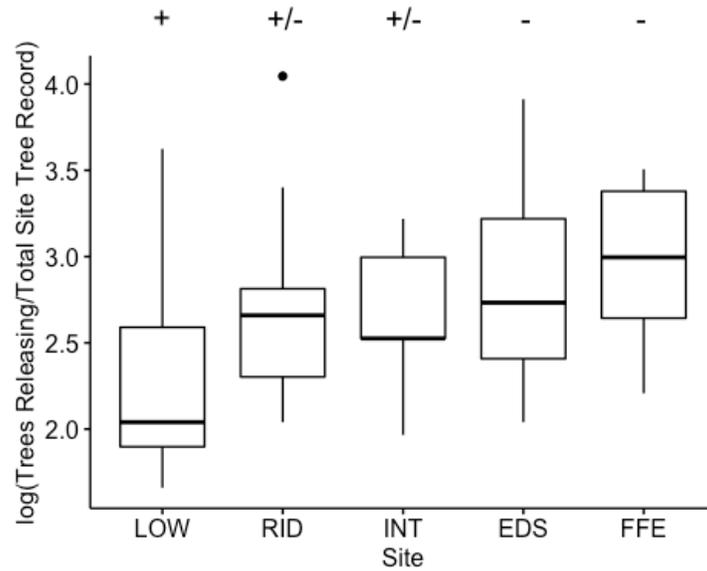


Figure 7: Differences in proportion of *T. canadensis* releasing at each site (log proportion). Log transformed results of 1-way ANOVA reveal a significant difference between the proportion of trees that release at LOW, EDS, and FFE. 1-Way ANOVA, $df=4$, $F=4.02$, $p=0.0519$; Tukey HSD, LOW-EDS $p=0.0269$, LOW-FFE $p=0.0264$.

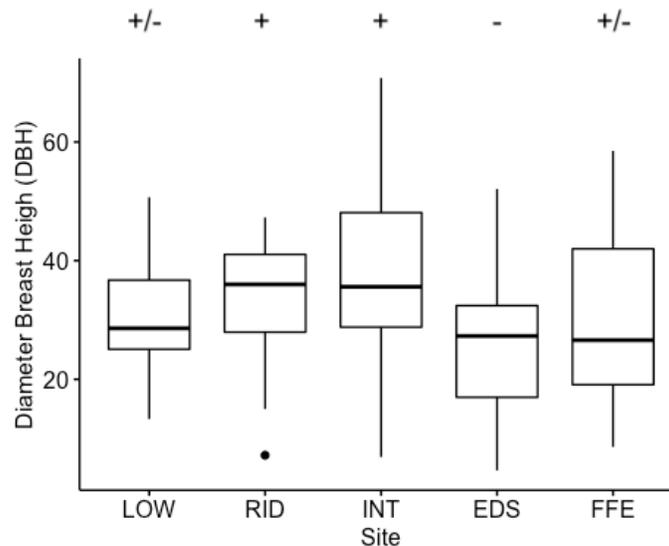


Figure 8: Differences in *T. canadensis* diameter breast height at each site (diameter, cm). Results of 1-way ANOVA reveal significant differences between DBH at INT, RID, and EDS. ; 1-Way ANOVA, $df=4$, $F=675.9$, $p=0.0023$; Tukey HSD, INT-EDS $p=0.0009$, RID-EDS $p=0.0757$.

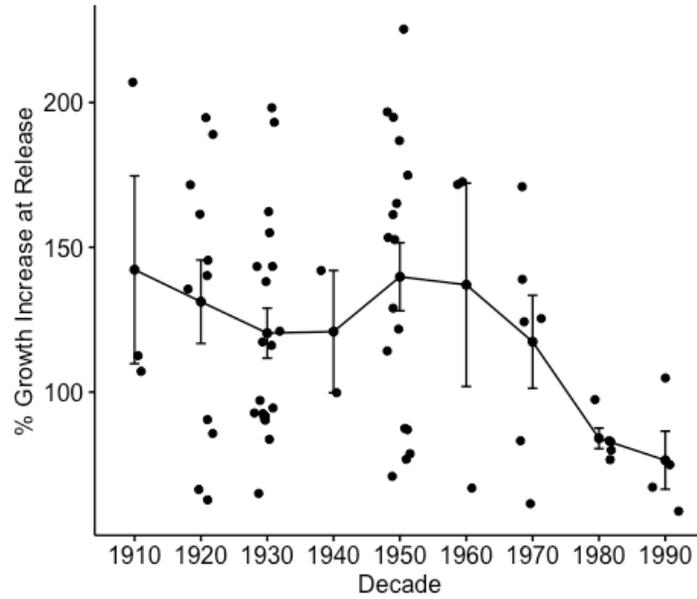


Figure 9: *T. canadensis* Release Intensity measured from 1910-2000 (year). Results of Kruskal-Wallis nonparametric analysis reveal no significant relationship between decade and release intensity. Kruskal-Wallis, $df = 8$, $p = 0.1125$.

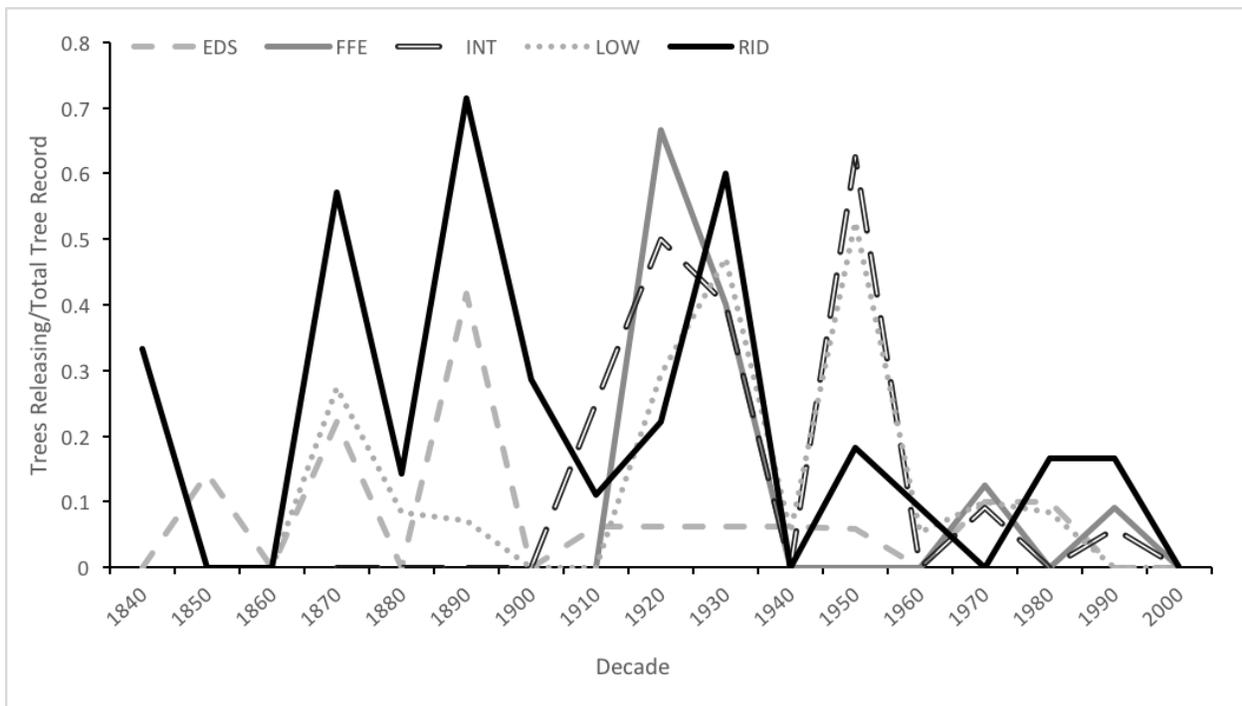


Figure 10: *T. canadensis* release proportion by decade and site. Raw data visualizing proportion of trees that release in each decade.