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## Aspen-dominated forest response to drought in the Lake States

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**Aspen-dominated forest response to drought in the Lake States**

by

**Julia Schwager**

A thesis submitted to the graduate faculty  
in partial fulfillment of the requirements for the degree of

**MASTER OF SCIENCE**

Major: Forestry

Program of Study Committee:  
Miranda Curzon, Major Professor  
Thomas Isenhart  
Brian Palik

The student author, whose presentation of the scholarship herein was approved by the program of study committee, is solely responsible for the content of this thesis. The Graduate College will ensure this thesis is globally accessible and will not permit alterations after a degree is conferred.

Iowa State University

Ames, Iowa

2020

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## **DEDICATION**

To my family and friends, I would like to extend my deepest gratitude for your unwavering support over the last 2.5 years. Thank you for cheering me on and always believing in me. I am especially indebted to Michael, who walked alongside me every step of the way, even when we were separated by several states and a mountain range or two.

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**NOMENCLATURE**

LTSP	Long-Term Soil Productivity
CPT	Compaction
OMR	Organic matter removal
C0	No additional compaction
C1	Moderate compaction
C2	Severe compaction
SOH	Stem-only harvest
WTH	Whole-tree harvest
FFR	Forest floor removal

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**ABSTRACT**

The Long Term Soil Productivity (LTSP) program was founded to examine the effects of soil disturbance, specifically impacts to soil organic matter and soil compaction, on fundamental forest productivity. Both have significant impacts on forest ecosystem function and are heavily influenced by management activities. The LTSP study design includes nine core combinations of organic matter removal and soil compaction. As treatment severity increases, potential net primary productivity is expected to decrease. This study takes place on the LTSP installation in the northern lower peninsula of Michigan, on the Huron National Forest where aspen-birch forest was clear-cut harvested and treated according to LTSP principles in early 1994. Current projections predict warmer temperatures, potentially longer growing seasons, and greater variability in precipitation that together have the potential to increase water stress for tree species, including aspen. The objectives of this study included answering the following questions related to forest response to stress, both anthropogenic and climate-related: 1) How do soil compaction, organic matter removal, and their potential interaction impact stand-level forest growth response to drought in 2012, and 2) how are individual trees responding to drought in 2012 given factors such as size, species, and crowding in addition to treatment effects?

Our work showed that there were no stand-scale growth responses to the 2012 drought associated with treatments, but species responses varied. At the individual tree scale, factors such as diameter, species, and crowding were better indicators of drought resistance, resilience, and recovery to drought than treatments.

This research has particular value within a landscape that has a long history of management and will likely continue to provide conventional timber products, even as global environmental change introduces new stressors for forests. Additionally, as demand for more

sustainable energy sources increases, bioenergy feedstocks may be increasingly sourced from these forests. As a result, aspen stands in the Lake States may be expected to meet greater demand. This could mean more frequent harvest, an increased likelihood of soil compaction, and an increase in the biomass removed if residues are utilized for bioenergy feedstocks or other comparable products, thus understanding the long-term effects of such disturbances on stand growth and response to climate conditions is increasingly important.

## CHAPTER 1. INTRODUCTION TO THE THESIS

The Long-Term Soil Productivity (LTSP) study was initiated by the USDA Forest Service in the early 1990s to examine the impacts of organic matter removal and soil compaction on site productivity across a variety of production forests (Powers, 2006). The LTSP study design includes nine treatments, created by crossing three levels of organic matter removal (stem-only harvest, whole-tree harvest, and whole-tree harvest plus forest floor removal) with three levels of soil compaction (none, light, and heavy) (Powers, 2006). Both organic matter removal and soil compaction have significant impacts on forest ecosystem function and are heavily influenced by management activities. Nearly 30 years after the LTSP study was initiated, the same basic questions about impacts to site productivity remain relevant.

In the Lake States, numerous factors including changing market demands, increasing pressure to accomplish harvests during a less predictable and shorter winter season, and other changes to climatic conditions increase the urgency of understanding management impacts on local forest productivity. Quaking aspen is the most abundant tree species in the Lake States region (Hillard, 2018) and is extremely important to the regional economy. If the demand for more sustainable energy sources increases, bioenergy feedstocks may be increasingly sourced from these forests (Berger *et al.*, 2013). As a result, aspen stands in the Lake States may be expected to meet greater demand which could mean more frequent harvest, an increased likelihood of soil compaction, and an increase in the biomass removed if residues are utilized for bioenergy feedstocks or other comparable products (Berger *et al.*, 2013). In addition, as the climate becomes warmer and drier in many regions across the continent, aspen stands could potentially experience significant changes in their abundance on the Lake States landscape

(Worrall *et al.*, 2015), especially given changing dynamics with climate and native defoliators like forest tent caterpillars (Reinikainen *et al.*, 2012).

This study aims to evaluate the impacts of soil compaction and organic matter removal on aspen dominated forest responses to drought at both the stand scale and the individual tree scale using tree cores and climate data. Understanding how aspen forest systems respond to anthropogenic disturbances within the context of changing climate conditions and other stressors will help managers maintain sustainable levels of aspen-birch forest types on the landscape.

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## CHAPTER 2. ASPEN-DOMINATED FOREST RESPONSE TO DROUGHT IN THE LAKE STATES

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### Abstract

The Long Term Soil Productivity (LTSP) program was founded to examine the effects of soil disturbance, specifically impacts to soil organic matter and soil compaction, on fundamental forest productivity. This project takes place on the LTSP installation in the northern lower peninsula of Michigan, on the Huron National Forest which has a primary composition of aspen-birch forest type that was clear-cut harvested and treated according to LTSP principles in early 1994. This project examines the stand-scale and individual tree scale response of this forest to a region-wide drought that occurred in 2012. The ecological indices of resistance, resilience, and recovery and tree cores collected from the site in 2018 were used to evaluate drought responses.

Our work showed that there were no stand-scale growth responses to the 2012 drought associated with treatments, but species responses varied. At the individual tree scale, model selection showed that size, species, the interaction between size and species, and the interaction between crowding and species were better indicators of drought resistance and recovery to drought than treatments and their interaction, and drought resilience was best modeled by size, species, crowding, the interaction between size and species, and the interaction between crowding and species.

### Introduction

Quaking aspen (*Populus tremuloides* Michx.) is the most widely distributed native tree in North America (Jones and DeByle, 1985; Burns, 1990) and the most abundant tree species in the Lake States region (Hillard, 2018). Both quaking and bigtooth (*P. grandidentata*) aspen are

ecologically important to region's forests, providing ecosystem services such as soil and hydrologic cycle stabilization, carbon storage, habitat for species that require various successional stages across the landscape, and regional climate regulation (Brinkman and Roe, 1975; Alban and Perala, 1992). Despite aspen's adaptability as a species, recent declines across its range suggest factors such as a changing climate, altered land uses, and increasing management intensity have the potential to influence the species' vulnerability on the landscape (Rogers *et al.*, 2013).

Beyond holding immense ecological and social value, aspen-dominated forests also play an important role in the economy of the Great Lakes region and are some of the most heavily manipulated forests in the midwestern United States. The rising demand for more sustainable energy sources and other products (e.g. textiles produced from wood fiber) may increase the market demand for aspen. Aspen trees are frequently harvested for pulp, plywood, sawlogs, boxes and crates, bioenergy feedstocks and in some cases as value-added co-products (Brinkman and Roe, 1975; Devappa *et al.*, 2015). There is still debate about the economic efficiency of greater reliance on biofuels, including questions about the sustainability of large-scale biomass removal for use as energy (Becker *et al.*, 2009), but as innovations in biofuel production make the process more economically feasible, forest managers may begin to harvest on shorter rotations and collect a greater volume of biomass per tree (Berger *et al.*, 2013). This could entail more compacted soils due to increased heavy machinery presence and less slash in the form of branches and tops left on the ground. Removing harvest residues for use as bioenergy feedstocks has potential to negatively impact productivity, but impacts vary with site quality (Thiffault *et al.*, 2011; Berger *et al.*, 2013; Curzon *et al.*, 2014; Slesak *et al.*, 2017). Lower quality sites with sandy soils can be more negatively impacted by greater levels of organic matter removal due to

lowered soil nutrient availability and water-holding capacity (Curzon *et al.*, 2014; Curzon *et al.*, 2020). Forests on sandy soils could see increased negative effects from harvest residue removal, and these effects could increase over time following multiple harvests (Walmsley *et al.*, 2009).

As the climate becomes warmer and drier in many regions across the continent, aspen stands may experience dramatic changes in their abundance across the landscape (Worrall *et al.*, 2015). Water limitation has been the driving factor behind most large-scale Sudden Aspen Decline (SAD) events in the western United States (Frey *et al.*, 2004; Rehfeldt *et al.*, 2009; Worrall *et al.*, 2013). In the Lake States, where forest tent caterpillar defoliation events often compound drought-induced stress (Man and Rice, 2010; Reinikainen *et al.*, 2012), dieback events can occur in as few as 6 years (Shields and Bockheim, 1981). Although large-scale SAD events occur most commonly and have been studied more in-depth in western regions of North America (Worrall *et al.*, 2013), a warmer and drier climate has the potential to negatively affect aspen stands across their entire range. Thus, understanding the impacts of management on aspen response to stressors such as drought will be key to maintaining this important resource into the future (Hogg *et al.*, 2002; Millar *et al.*, 2007).

Given aspen's widespread presence across the northern hemisphere and its contributions to myriad ecosystem services, maintaining adaptive capacity of aspen-birch type forests in the face of a changing climate and altered land uses is of increasing concern to resource managers (Rogers *et al.*, 2020). Understanding how these systems respond to disturbances can help ensure they will persist on the landscape and maintain their functional role (Sánchez-Pinillos *et al.*, 2019). Resistance, resilience, and recovery are commonly used to measure responses to disturbance. Resistance can be defined as a system or individual's ability to maintain ecological performance during a disturbance, resilience is the ability to return to pre-disturbance

performance levels, and recovery is the relationship between post-disturbance performance and performance during the disturbance (Lloret *et al.*, 2011). Previous work has demonstrated that management has potential to influence these disturbance responses in other forest types (Kohler *et al.*, 2010; D'Amato *et al.*, 2013; Duveneck and Scheller, 2016), but less is known about aspen-dominated forest ecosystems.

The Long-term Soil Productivity (LTSP) study was established in the early 1990s by the USDA Forest Service to assess whether and to what extent disturbance associated with harvest (specifically, organic matter removal and soil compaction) might negatively impact the major forest ecosystems of the United States. An installation of this study in aspen-dominated forest at the Huron-Manistee National Forest provided an experimental setting for testing questions about management impacts on drought response on sandy soils. The level of organic matter removal has potential to impact forests through reductions in nutrient availability (Berger *et al.*, 2013) as well as decreased soil moisture (Roberts *et al.*, 2005). Through reduced soil porosity, compaction has potential to negatively impact water-holding capacity and restrict gas exchange which can affect root growth (Frey *et al.*, 2009).

In line with reductions in standing biomass production observed following whole-tree harvest on this site (Curzon *et al.*, 2020), I expected greater levels of organic matter removal to negatively impact drought response of aspen-dominated stands because of the potential for lower nutrient availability and a lessened “mulching effect” (Powers, 2002). At the scale of individual trees, I also expected greater organic matter removal to reduce resistance and resilience of tree growth to drought but hypothesized that responses would also be influenced by species because species’ responses to drought differ depending on traits and functional roles related to water and

nutrient acquisition (Drobyshev *et al.*, 2013; Grossiord, 2020) as well as tree size and crowding (Martinez-Vilalta *et al.*, 2012; Fien *et al.*, 2019).

## Methods

### Study Area

Field sampling took place on the Huron-Manistee National Forest in northeastern lower Michigan, USA (44° 38' N, 83° 32' W). Mean annual precipitation at the site is 75 cm and mean annual temperature is 6.2°C. Forest stands were dominated by *P. tremuloides* and *P. grandidentata* with lesser components of *Acer rubrum*, *Quercus rubra*, and *Pinus strobus* prior to harvest in early 1994 when experimental treatments were applied. The impacts of two factors, organic matter removal and compaction, were examined by fully crossing three levels of each factor, resulting in nine treatments. Levels of organic matter removal included stem-only harvest (SOH), whole-tree harvest (WTH), and whole-tree plus forest floor removal (FFR). Levels of compaction included no additional (C0), moderate (C1; up to 15% increase in bulk density), and heavy (C2; up to 30% increase in bulk density) (Stone *et al.*, 1999). Each experimental treatment was replicated three times for a total of 27 treated plots. Soils at the Huron-Manistee site are acidic and relatively infertile, having developed from outwash sands and composed of 93% sand, 6% silt, and 1% clay (Stone *et al.*, 1999; Slesak *et al.*, 2017).

### Sample collection and processing

I sampled overstory vegetation June-August, 2018 during the 25th growing season post-harvest. This involved stem-mapping all trees greater than 10 cm in diameter at breast height (DBH, 1.37 m) in 500 m<sup>2</sup> circular plots (12.6 m radius) centered within the 27 existing 40 m x 40 m (0.4 ha) treatment plots (Figure 1). Data recorded for each tree included species, crown class, general condition, and DBH. All sampled trees were permanently tagged and spray-painted to indicate where DBH had been measured. In addition, cores were collected at breast height from

all living trees greater than 10 cm DBH located within an 8 m radius of plot center using increment borers.

Cores were mounted using standard procedures (Stokes, 1968) and then sanded at progressively finer grit to provide polished and flat viewing surfaces (Stokes, 1968; Speer, 2010). Once dated, ring widths were measured using a Velmex measuring stage. Then, dating was checked for accuracy using the COFECHA program (Holmes, 1983).

### **Climate data**

The National Drought Mitigation Center Drought Atlas was used to identify periods of drought in the region by examining Palmer Drought Severity Index (PDSI) values during the most recent 10 years of growth. PDSI is a widely used drought index that takes into account precipitation, temperature, and availability of water in the soil (Palmer, 1965; Alley, 1985). Historical records (MIDNR) as well as PDSI values from the nearest drought atlas station (Hale Loud Dam) ranging from -2.0 to -3.33 indicated a moderate to severe drought occurred during the growing season at the Huron-Manistee NF in 2012 also observed elsewhere in the region (D'Amato *et al.*, 2013).

### **Analysis**

Once dating had been completed, annual ring widths were used to reconstruct diameter growth over time. First, the diameter inside bark was estimated based on DBH recorded during the 2018 growing season (Dixon *et al.*, 2007). Then, the diameter inside bark for each year was estimated by substituting annual diameter growth (2 x ring width) from the diameter observed for the following year. Following reconstruction of annual diameter inside bark, the diameter outside bark was estimated and added (Dixon *et al.*, 2007). Lastly, we used species-specific allometric equations developed for forests in the same geographical region (Perala and Alban, 1994) to estimate above-ground biomass for each tree at the end of each growing season based on

reconstructed DBH. Annual growth was then quantified as the above-ground biomass added during a growing season (Foster *et al.*, 2016).

Because 2012 drought response was reconstructed using cores extracted from trees surviving to 2018, I was not able to account for growth of trees that may have died in the intervening period. However, using periodic data collected by the USFS in 2013 and again in 2018, I was able to show that little to no mortality occurred in trees (DBH  $\geq$  10 cm) and the mortality that occurred in the sapling layer (DBH < 10 cm) did not differ among treatments (Curzon *et al.* in prep). Therefore, we assume that any growth not captured in this analysis by relying on surviving trees is not biased.

To quantify individual trees' resistance ( $R_t$ ) to drought, average growth from the years during the drought was compared to average growth during the five years prior to drought (Kohler *et al.*, 2010; D'Amato *et al.*, 2013) using biomass increments (BI):

$$R_t = BI_D / BI_{pre}$$

where  $BI_D$  was the stand-level or individual tree biomass increment during the drought and  $BI_{pre}$  was annual stand-level or individual tree biomass increment averaged over the five years prior to the drought. To quantify resilience ( $R_s$ ), averaged growth during the five years following the drought was compared to averaged growth during the five years prior to the drought (Kohler *et al.*, 2010; D'Amato *et al.*, 2013):

$$R_s = BI_{post} / BI_{pre}$$

where  $BI_{post}$  was the averaged population-level biomass increment during the five years following the drought. To quantify recovery ( $R_c$ ), averaged growth from the five years following the drought was compared to averaged growth during the drought (Kohler *et al.*, 2010; Lloret *et al.*, 2011):

$$R_c = BI_{post} / BI_D .$$

Crowding, ( $CI_H$ ) used to characterize growing conditions within a 5 m neighborhood of each tree was calculated as:

$$CI_H = \sum_{j=1}^n \left[ \frac{d_j}{d_i} \right] \frac{1}{R_{ij}}$$

where  $d_i$  = DBH in cm of subject tree  $i$ ,  $d_j$  = DBH in cm of competitor tree  $j$ ,  $R_{ij}$  = distance in m between subject tree  $i$  and competing tree  $j$ , and  $n$  = number of neighbors within a 5 m radius (Hegyi, 1974).

Superposed Epoch Analysis (SEA) was used to establish whether the 2012 drought observed through historical documents (MIDNR) and appropriate PDSI indices had an impact on tree growth at the Huron NF. Before SEA, raw ring widths were detrended for each species using a modified negative exponential smoothing spline (Perkins *et al.*, 2018). The resulting ring width index (RWI) was then detrended again using a default smoothing spline to create a chronology for each species with a large enough sample size. This included *Prunus serotina* (n=8), *Quercus rubra* (n=41), *Acer rubrum* (n=15), *Pinus resinosa* (n=6), *Pinus strobus* (n=13), *Populus grandidentata* (n=290), and *Populus tremuloides* (n=89).

Mixed effects analysis of variance (ANOVA) was then used to determine whether organic matter removal, compaction, and their interaction impacted stand-level resistance, resilience, and recovery to drought. A random effect was included for block.

Lastly, I assessed which combination of factors (tree size, crowding, species, and treatment) best predicted drought responses of individual trees through the selection of linear models. Candidate models differed, but potential fixed effects included tree size (DBH) prior to drought, crowding during drought ( $CI_H$ ), species, species x DBH, species x  $CI_H$ , and treatment. Size and crowding were standardized (mean = 0, SD = 1) to allow for comparison of the effects

of the two predictors. Models were assessed using Akaike's information criterion (AIC<sub>C</sub>) value and ranked accordingly. Homoscedasticity and the normality of residuals were assessed to confirm assumptions.

## Results

### Tree-scale drought response

SEA revealed varied species-level responses to drought. Across treatments, *P. strobus* and *P. resinosa* experienced decreased growth rates in 2012, but *P. strobus* recovered with statistically significant growth in 2013, while *P. resinosa* growth did not recover until 2015 (Figure 2). *P. grandidentata* (Figure A1) and *P. tremuloides* (Figure 2) showed increased growth rates during the drought. Even though growth was not obviously depressed during 2012, *Q. rubra* responded with strong growth rates the following growing season (Figure A1). While some species (e.g. *A. rubrum*) did not show a significant growth reduction in 2012 (Figure A1), the responses of *P. strobus*, *P. resinosa*, and others confirm drought conditions during 2012 impacted tree growth.

### Individual tree resistance, resilience, and recovery to drought

Model selection indicated that crowding, tree size, species, and associated interactions were better predictors of all measures of drought response than organic matter removal, compaction, or their interaction (Table 1). The best model for resistance indicated it was significantly impacted by size and species (Table 1). Larger trees were generally less resistant than smaller trees, and relative to *Q. rubra*, species that were significantly less resistant to the 2012 drought included *A. rubrum*, *P. resinosa*, *P. strobus*, *P. grandidentata*, and *P. tremuloides*. Species-specific slopes for DBH and crowding demonstrated that larger *P. resinosa* are less resistant and larger *P. grandidentata* are more resistant to drought than smaller trees (Figure B1)

and that crowding negatively affects *P. resinosa* but positively affects *P. strobus* resistance to drought (Figure B2).

Resilience to drought depended on tree size, species, and crowding (Table 1). Relative to *Q. rubra*, *P. resinosa*, *P. strobus*, and *P. tremuloides* exhibited lower resilience to the 2012 drought. Larger trees were significantly less resilient to drought regardless of species, but species-specific slopes for DBH showed that larger *P. resinosa*, *P. strobus*, and *P. grandidentata* are significantly less resilient to drought (Figure B3). Greater levels of crowding led to higher drought resilience in all species, and species-specific slopes for crowding also showed significantly higher resilience in *P. strobus* (Figure B4).

Similarly to resistance, recovery following drought was significantly impacted by tree size and species (Table 1). *Pinus strobus* showed greater recovery rates following drought than other species. Larger species showed less recovery in general, and a species-specific slope for DBH indicated that larger *P. strobus* exhibit lower rates of recovery than smaller trees (Figure B5). The influence of crowding also varied by species with *P. resinosa* recovery increasing with greater crowding while *P. strobus* shows less recovery to drought with increasing crowding (Figure B6).

## Discussion

Contrary to expectations, data did not suggest an impact of organic matter removal or compaction treatments on the stand-level resistance, resilience, or recovery of aspen-dominated forests to drought as indicated by annual above-ground biomass production even though a subset of species showed a significant response to the 2012 drought across the site, confirming it had impacted tree growth.

There has been intense interest in the scientific community in recent years regarding how species diversity affects drought responses in forests (Ammer, 2019; Grossiord, 2020). Studies have shown complementary effects of mixed stands can lead to reductions in competition due to temporal and spatial differences in water uptake (Hooper, 1998; Forrester and Bauhus, 2016) and facilitative mechanisms such as reduced herbivory vulnerability (Jactel and Brockerhoff, 2007) and hydraulic redistribution of soil water (Hao *et al.*, 2013) in mixed stands can improve forests' drought resistance and resilience. However, there is also potential for negative effects due to these traits in the form of increased productivity levels and evapotranspiration, which equates to increased water stress (Forrester, 2015), making it difficult to draw broad conclusions across forest types (Grossiord, 2020). Different responses can also be observed within the same forest type but at different localities (Forrester *et al.*, 2016), which can make expanding results from individual species to the stand scale less useful. It is possible some kind of community response (whether interacting species or below-ground sharing of resources) may have mitigated drought effects at the stand scale at the Huron, but including diversity ( $H'$ ) as a covariate in initial tests showed no significant effects (results not reported).

My hypotheses about organic matter removal were based on the assumption that those treatments would result in less soil organic matter which contributes to water-holding capacity and lower nutrient availability which can impact drought response and recovery (although evidence is mixed) (Gessler *et al.*, 2017). However, previous analyses from the same LTSP site showed little to no significant difference among treatments in soil nutrients (Slesak *et al.*, 2017). This may explain why I did not see a drought response associated with treatments. In addition, despite expectations that the two most abundant species across the study (*P. grandidentata* and *P. tremuloides*) would be impacted by the 2012 drought (as well as treatments), SEA analysis did

not detect significant drought responses for either. The two aspen species dominated post-treatment stands, and the absence of a significant drought response in these species may explain why little difference was observed among treatments at the stand-scale.

My results at the Huron NF demonstrate that individual trees responded differently to drought stress due to factors such as size, species, and crowding. Both white and red pine responded clearly to the dry conditions characterizing the 2012 growing season as expected. The absence of a clear response of other, typically more drought-sensitive species (e.g. *P. tremuloides*) was surprising, but the increased growth seen in *P. grandidentata* and *P. tremuloides* during the drought might be explained by a recent forest tent caterpillar outbreak that began in 2008 in northern lower Michigan (Rozendaal and Kobe, 2014). Outbreaks tend to occur in decadal intervals and last for 3-6 years (Man and Rice, 2010). This could have caused compensatory growth responses (Robison and Raffa, 1994) during the following years in species such as *P. grandidentata*, *P. tremuloides*, *Q. rubra*, and *A. rubrum*, which are all preferred food sources for FTC (Schowalter, 2017). Although there are conflicting reports on how climate impacts FTC outbreak timing and severity, some studies have shown that drought intensity during the previous summer and incident solar radiation of the current year can affect the severity of FTC outbreaks (Haynes *et al.*, 2018). In this case, the suspected FTC outbreak preceded drought, but future monitoring of this site has potential to increase knowledge of how these stressors interact, particularly considering severe FTC outbreaks have the potential to lead to *Populus* mortality and subsequent changes in stand development and composition of Lake States forests (Cooke *et al.*, 2009; Man and Rice, 2010; Reinikainen *et al.*, 2012).

Tree size and species were important predictors of all three drought responses I analyzed and crowding was important in the case of resilience. Compared to smaller stems, larger *P.*

*resinosa* were less resistant and less resilient to drought, and larger *P. strobus* were less resilient and exhibited less recovery to drought during the 5-year period examined. Other work that explored relationships between *Pinus sylvestris* (Scots pine) tree-level characteristics and drought response also showed that faster-growing (larger) trees were more negatively affected during the drought period and exhibited lower resilience (Martinez-Vilalta *et al.*, 2012).

Mean drought tolerances for each species (Table A2) did not always aid in interpretation of species responses. For example, even though it has a higher mean drought tolerance than *Q. rubrum* (Ülo and Fernando, 2006), *P. resinosa* were less resistant and less resilient to the 2012 drought relative to *Q. rubrum*. Other species that are less drought tolerant than *Q. rubrum*, such as *P. grandidentata*, *P. tremuloides*, *A. rubrum*, and *P. strobus* were also less resistant, and *P. tremuloides*, and *P. strobus* were less resilient to drought. Interactions between the 2012 drought and FTC outbreaks around 2008 could be contributing to these responses, especially in species that are hosts of FTC, as growth would be lowered due to defoliation prior to the drought year (resistance, resilience, and recovery indices all involve comparison of growth during and after drought with growth prior to drought). Other drivers could include differences in how species respond to drought including whether they are isohydric or anisohydric. Isohydric species, such as *P. tremuloides* and *P. grandidentata* regulate their response to moisture deficit by closing their stomata, while anisohydric species, like *Q. rubrum*, maintain transpiration levels throughout the drought (Abrams, 1990; Galvez *et al.*, 2011). The clonal aspect of interconnected root systems in *Populus* species could also influence how *P. grandidentata* and *P. tremuloides* respond to the drought as connected root systems have been shown to reduce the negative impacts of drought stress through the sharing of resources (Kokouvi Emmanuel *et al.*, 2016; Bretfeld *et al.*, 2017).

Long-term studies like LTSP are valuable for understanding how forests will respond to management actions over time, and could become even more important as we try to predict forest responses to climate change and manage for adaptive systems (Lindenmayer *et al.*, 2012). The Huron NF LTSP installation is about halfway through a typical rotation age and additional questions that could be addressed with further analysis of the data I collected in 2018 include whether and how drought and FTC outbreaks interact to effect tree growth and stand productivity as the stands mature, whether timing of drought, defoliation and other potential stressors during the development of a stand impacts growth, and what role species diversity plays in growth responses to climate events like drought. It would also be useful to analyze the data collected from the Chippewa NF and Ottawa NF and to determine how these other Lake States LTSP installations compare to responses at the Huron NF. This could provide insight on how forests with different soil texture respond to drought following harvest with varying levels of OMR and CPT.

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## Tables

Table 1. Model selection results for resistance, resilience, and recovery to drought. Factors include tree size (DBH), species (SPP), crowding (CI<sub>H</sub>), and treatments, where CPT=compaction and OMR=organic matter removal. Effect sizes are provided for top-ranking models. Models are ranked by AICC values. Bold text indicates significant effects (p<0.05).

<b>Resistance Models</b>	<b>Model Rank</b>	<b>AIC<sub>c</sub></b>	<b>Delta</b>	<b>R<sup>2</sup></b>
Fixed effects				
<b>-0.2687DBH + 1.4872SPP + 0.0267CI<sub>H</sub> + SPP*DBH + SPP* CI<sub>H</sub></b>	1	452.1	0	0.42
DBH + SPP	2	576.9	124.8	0.11
<b>DBH + SPP + CI<sub>H</sub></b>	3	579.9	127.8	0.12
<b>CI<sub>H</sub> + SPP</b>	4	596.3	144.2	0.10
DBH + SPP + OMR + CPT + OMR*CPT	5	596.6	144.5	0.13
<b>DBH + SPP + CI<sub>H</sub> + OMR + CPT + OMR*CPT</b>	6	598.9	146.8	0.14
<b>DBH + CI<sub>H</sub></b>	7	605.1	153.0	0.04
<b>CI<sub>H</sub> + SPP + OMR + CPT + OMR*CPT</b>	8	613.9	161.8	0.12
Null	9	615.4	163.3	0.05
<b>DBH + CI<sub>H</sub> + OMR + CPT + OMR*CPT</b>	10	624.3	172.2	0.06
<hr/>				
<b>Resilience Models</b>	<b>Model Rank</b>	<b>AICC</b>	<b>Delta</b>	<b>R<sup>2</sup></b>
Fixed effects				
<b>-0.4940DBH + 1.6727SPP + 0.03423CI<sub>H</sub> + SPP*DBH + SPP* CI<sub>H</sub></b>	1	843.9	0	0.66
<b>CI<sub>H</sub></b>	2	1055.7	211.8	0.38
<b>DBH + SPP</b>	3	1058	214.1	0.39
<b>DBH + SPP + CI<sub>H</sub></b>	4	1063.5	219.6	0.39
<b>DBH + SPP + OMR + CPT + OMR*CPT</b>	5	1065.2	221.3	0.40
<b>DBH + SPP + CI<sub>H</sub> + OMR + CPT + OMR*CPT</b>	6	1083.9	240.0	0.36
<b>CI<sub>H</sub> + SPP</b>	7	1088.2	244.3	0.36
<b>CI<sub>H</sub> + SPP + OMR + CPT + OMR*CPT</b>	8	1139.2	295.3	0.29
<b>DBH + CI<sub>H</sub></b>	9	1141.6	297.7	0.30
<b>DBH + CI<sub>H</sub> + OMR + CPT + OMR*CPT</b>	10	1201.7	357.8	0.19
Null				
<hr/>				
<b>Recovery Models</b>	<b>Model Rank</b>	<b>AICC</b>	<b>Delta</b>	<b>R<sup>2</sup></b>
Fixed effects				
<b>-0.0592DBH + 1.1325SPP + 0.0028CI<sub>H</sub> + SPP*DBH + SPP* CI<sub>H</sub></b>	1	1371.4	0	0.71
<b>CI<sub>H</sub> + SPP</b>	2	1513.8	198.7	0.54
<b>DBH + SPP + CI<sub>H</sub></b>	3	1514.3	199.2	0.55
<b>CI<sub>H</sub> + SPP + OMR + CPT + OMR*CPT</b>	4	1517.9	202.8	0.55
<b>DBH + SPP</b>	5	1517.9	202.8	0.54
<b>DBH + SPP + CI<sub>H</sub> + OMR + CPT + OMR*CPT</b>	6	1519.3	204.2	0.55
<b>DBH + SPP + OMR + CPT + OMR*CPT</b>	7	1522.6	207.5	0.54
<b>DBH + CI<sub>H</sub> + OMR + CPT + OMR*CPT</b>	8	1816.9	501.8	0.20
<b>DBH + CI<sub>H</sub></b>	9	1826.2	511.1	0.20
Null	10	1847.3	532.2	0.16

## Figures

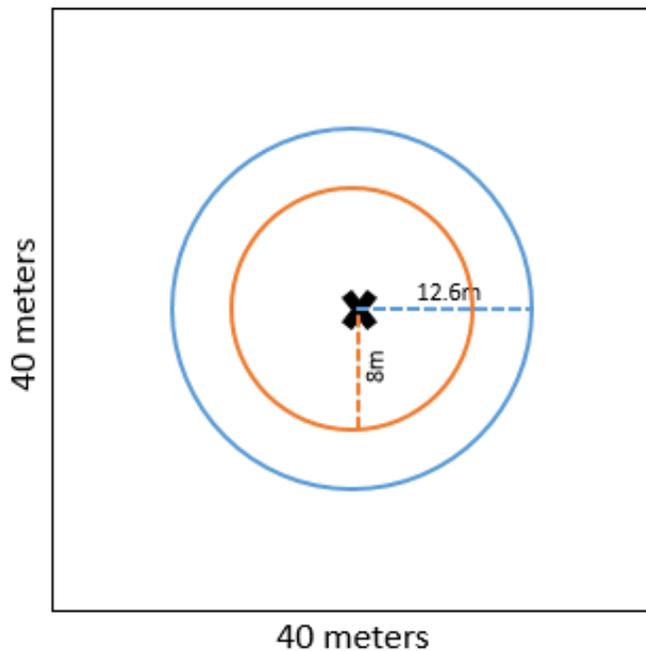


Figure 1. Diagram illustrating treatment plot and sampling design. All trees DBH > 10 cm DBH were stem mapped within a 12.6 m radius (area within blue circle) of the center of the treated plot. Additionally, cores were collected from all living trees greater than 10 cm DBH located within an 8 m radius of plot center (area within orange circle).

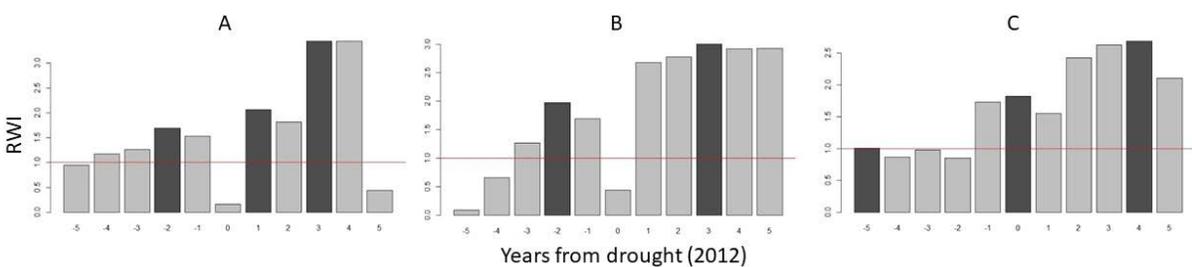


Figure 2. Superposed epoch analysis results for individual species' growth responses to drought. Species represented include *Pinus strobus* (panel A), *Pinus resinosa* (panel B), and *Populus tremuloides* (panel C). Bars indicate relative mean growth over the selected period, where bar color indicates significance of the departure from the chronology's mean ring width index (RWI) value. Light grey bars indicate growth was not significantly different from mean RWI and dark grey bars indicate growth was significantly different from mean RWI.

### Appendix A. Supplemental Tables

Table A1. Tree-ring statistics for series analyzed in this study (R<sub>BAR</sub>=mean correlation coefficient among tree-ring series).

Species	Number of cores	Start year	Mean tree ring width, SD (mm)	R <sub>BAR</sub>	Mean sensitivity
ACRU	15	1995	2.16 (0.721)	0.411	0.265
PIRE	6	2005	3.68 (1.341)	0.768	0.445
PIST	12	2000	3.54 (1.430)	0.62	0.528
POGR	287	1995	2.51 (0.887)	0.536	0.307
POTR	85	1995	2.19 (0.893)	0.524	0.342
PRSE	8	1996	2.20 (0.936)	0.313	0.314
QURU	39	1997	2.44 (0.720)	0.506	0.276

### Appendix B. Supplemental Figures

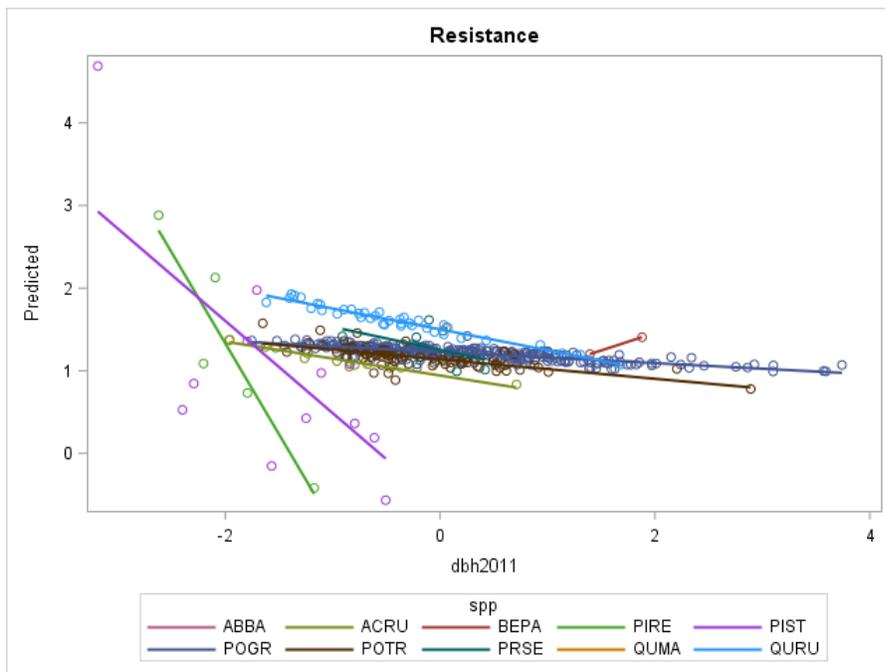


Figure B1. Plot showing the effects of the interaction between size and species on drought resistance.

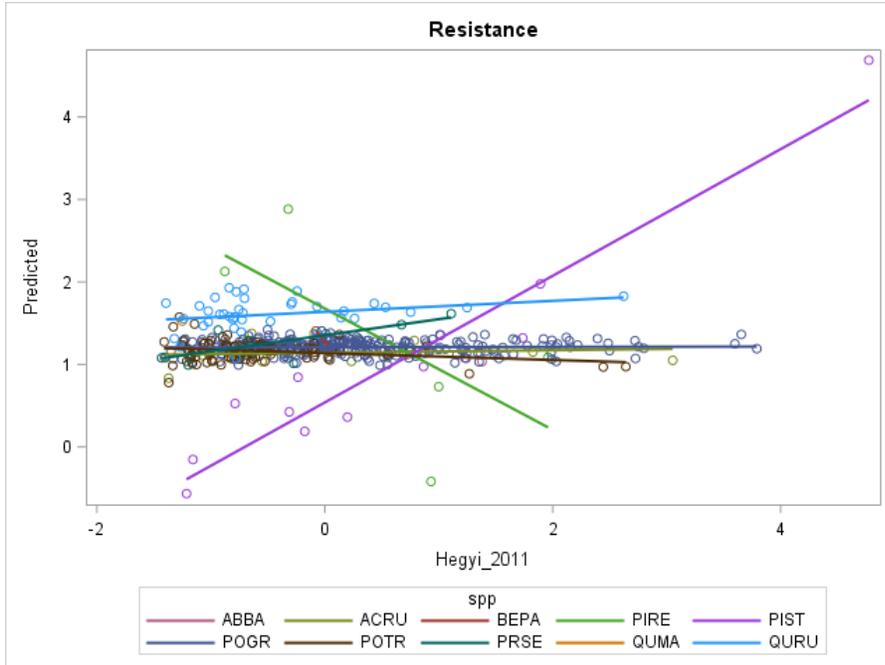


Figure B2. Plot showing the effects of the interaction between crowding (“Hegyi\_2011”) and species on drought resistance.

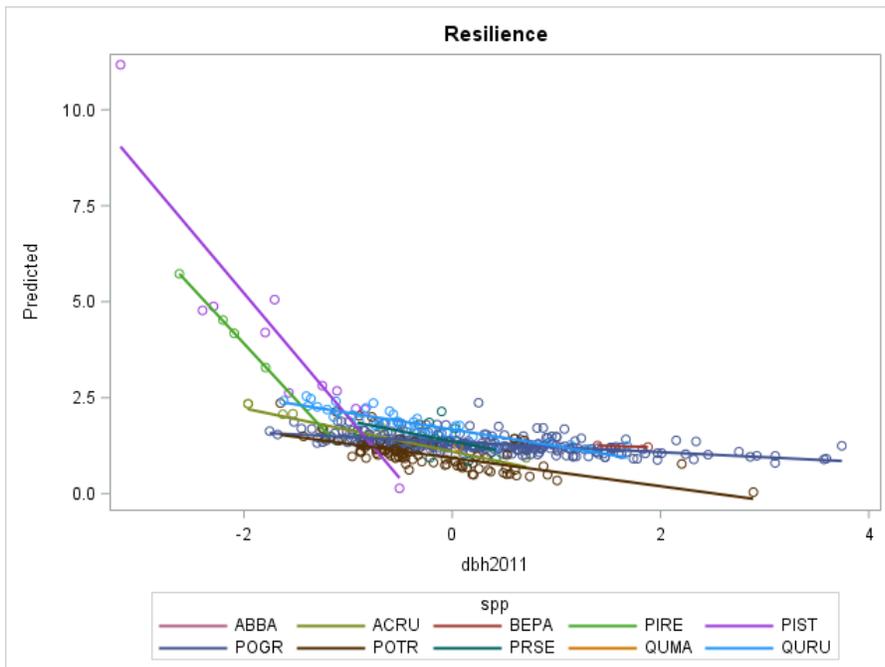


Figure B3. Plot showing the effects of the interaction between size and species on drought resilience.

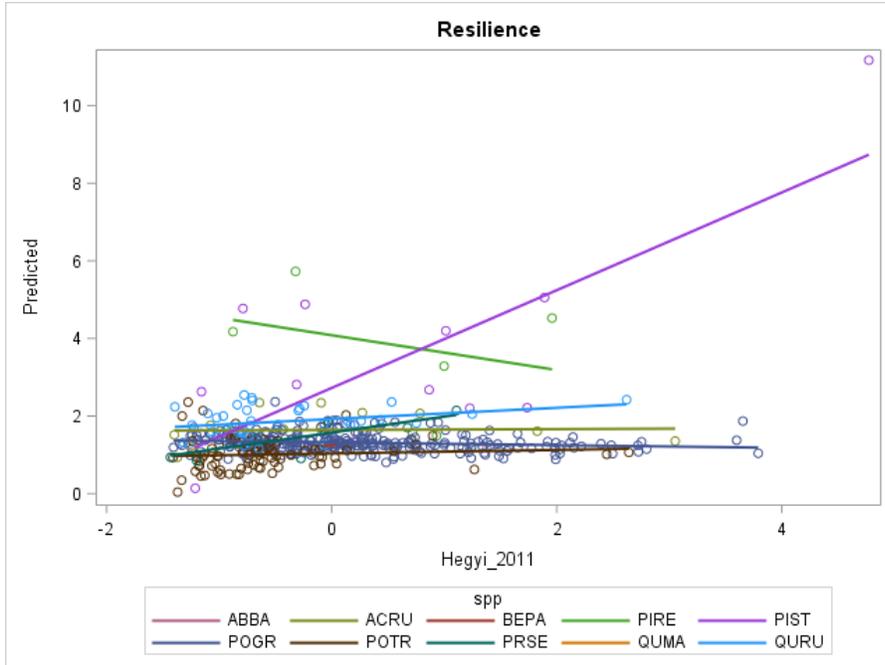


Figure B4. Plot showing the effects of the interaction between crowding (“Hegyi\_2011”) and species on drought resilience.

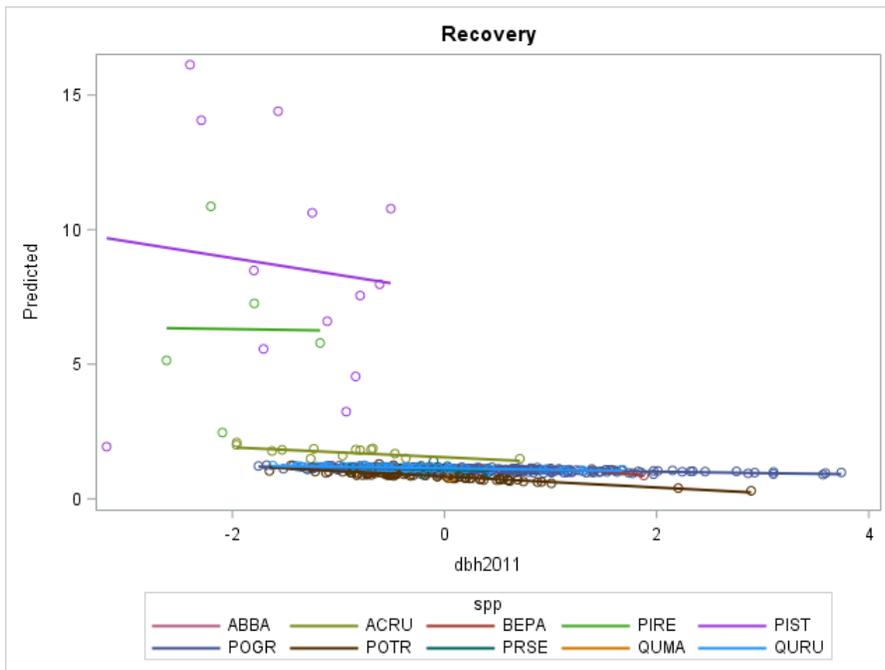


Figure B5. Plot showing the effects of the interaction between size and species on drought recovery.

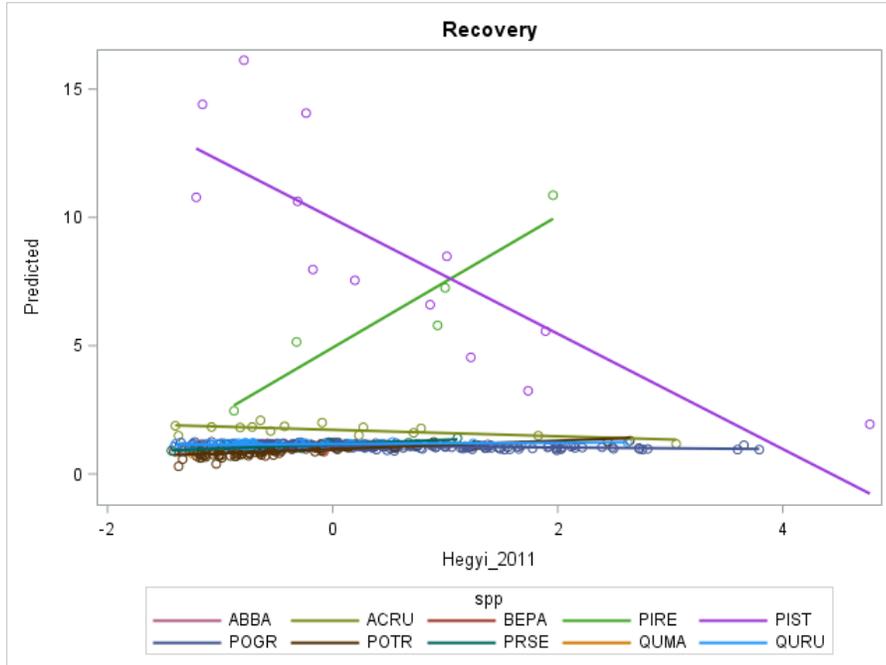


Figure B6. Plot showing the effects of the interaction between crowding (“Hegyi\_2011”) and species on drought recovery.

### CHAPTER 3. GENERAL CONCLUSIONS

Although our results showed no significant differences in drought response associated with treatments at the stand-scale, we know that species matters. Species like red pine and white pine showed the clearest response to the 2012 drought, with significant reductions in growth in 2012 that didn't reach pre-drought levels until two or three years later. Others, like bigtooth and quaking aspen (the two most abundant species in the study) did not experience significant reductions in growth during the drought, but did exhibit lower than average growth in some of the years prior to the drought. This could be due to FTC outbreaks in the region around those years, which could explain why a clear drought response is not apparent for these species (SEA and resistance, resilience, and recovery indices include relative measures of growth). It also means that treatments could affect drought response, but other factors obscured that response.

At the individual tree scale, factors such as size, species, crowding, and the interactions between size x species, and crowding x species were better indicators of drought response than treatments. Larger trees were less resistant, less resilient, and showed less recovery to drought than smaller trees. Species showed varied responses, with some responding significantly better or worse than others. *A. rubrum*, *P. resinosa*, *P. strobus*, *P. grandidentata*, and *P. tremuloides* were significantly less resistant to drought relative to *Q. rubra*; both *Pinus* species as well as *P. tremuloides* exhibited less resilience to drought relative to *Q. rubra*; and *P. strobus* was the only species to show more recovery to the 2012 drought relative to *Q. rubra*. Species at the site also responded differently given their size and crowding levels.

Understanding how aspen-birch forests in the Lake States respond to climate stressors will aid in maintaining this forest type on the landscape and at levels that can continue to be utilized for production. This project could serve as a baseline for comparison for future work at

the other two Lake States LTSP installations, which have already been sampled. Continued monitoring of stand and individual tree responses would also be useful later in stand development, especially given the fact that larger trees responded to the 2012 drought differently than their smaller counterparts. Long-term studies like the LTSP study will continue to provide valuable insights for adaptive management strategies as climate and anthropogenic disturbances evolve over time.