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## Exploring The Abiotic And Biotic Drivers Of Leaf Litter And Wood Decomposition In Response To Changing Climates And Associated Adaptive Management Regimes In Northeastern Forests

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EXPLORING THE ABIOTIC AND BIOTIC DRIVERS OF LEAF LITTER AND  
WOOD DECOMPOSITION IN RESPONSE TO CHANGING CLIMATES AND  
ASSOCIATED ADAPTIVE MANAGEMENT REGIMES IN NORTHEASTERN  
FORESTS

A Thesis Presented

By

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## ABSTRACT

Global climate change will have substantial impacts on future forest dynamics motivating forest managers, landowners, and decision-makers to adopt new, adaptive approaches to forest management. For instance, extreme precipitation events, including severe droughts and high-rainfall events, are projected to alter regional hydrological cycles within the Northeast with potential implications for important ecosystem processes and forest functions. In response to the challenges posed by changing climates, novel adaptation frameworks have been suggested to assist forest adaptation to climate change; however, little is known about the potential cascading effects of global climate change and associated adaptive management regimes on key ecosystem processes, including forest decomposition.

In this thesis, we conducted two studies, one examining the effects of future extreme precipitation scenarios and another investigating various adaptive management strategies on leaf litter and wood decomposition within Northeastern forests. The first study investigated the effects of projected extreme precipitation scenarios on leaf litter and wood decomposition rates using a precipitation manipulation experiment. Results indicate that wood decomposition rates will be disrupted during prolonged droughts or intense precipitation events whereas leaf litter will not be significantly affected. The second study quantified the impacts of various adaptive management strategies applied to northern hardwood ecosystems on wood decomposition rates and nutrient dynamics across a gradient of increasing harvest severity. Wood stake mass loss did not broadly differ between adaptive management treatments but was negatively influenced by increasing harvest severity. Additionally, wood stake carbon, but not nitrogen, was greater in areas experiencing harvesting, but not nitrogen, suggesting that canopy gap formation with deadwood retention may enhance the potential for forest carbon sequestration, particularly in the short-term. Collectively, the results of this thesis suggest that shifts in future forest dynamics, due to changing climates and associated adaptive management regimes, will have significant implications for forest functions, such as forest carbon sequestration and cycling, by influencing wood decomposition.

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## CHAPTER 1: INTRODUCTION

The impacts of global climate change on future forest dynamics are anticipated to be substantial. Specifically, extreme disturbance events associated with precipitation patterns are projected to become more frequent and intense (Alexander et al. 2006). In the Northeastern United States, forests have already experienced increased instances of flooding and drought, which have impacted their productivity and functioning (Allen et al. 2010, Huang et al. 2021). Consequently, it is expected that extreme precipitation events will have significant implications for ecosystem processes, like forest decomposition, that are driven by climate conditions.

The challenges posed by climate change have prompted forest managers and landowners to adopt new approaches to forest management. For instance, adaptive silvicultural strategies have been developed into a management framework that is designed to assist forest adaptation to changing forest conditions based on an adaptation gradient of *resistance*, *resilience*, and *transition* (Millar et al. 2007, Nagel et al. 2017). Deliberately altering harvest severity is a recognized management strategy that enhances ecosystem resilience and resistance to future climate change and other disturbances by increasing ecosystem heterogeneity, but these strategies have unknown implications for leaf litter and wood decomposition (D'Amato et al. 2011).

Forest decomposition plays a major role in forest functions, specifically C storage and biogeochemical cycling (Laiho and Prescott 1999, Woodall et al. 2015). Historically, models have successfully predicted large-scale variations in decomposition using only climate and substrate quality; however, more recent studies have identified the influence

of microbial communities and their decomposer activities on decomposition trends at smaller spatial scales (Adair et al. 2008, Kubartova et al. 2015). Additionally, less is generally known about wood decomposition and further, how it will respond to shifting future forest dynamics (Russell et al. 2015). Thus, climate change and shifting disturbance regimes, including forest harvesting, can potentially result in significant changes to litter and wood decomposition with implications for forest functions.

The objective of this thesis is to identify the impacts of changing climates and shifting adaptive management regimes on leaf litter and wood decomposition in Northeastern forests. In chapter 2, we assess the impacts of various future extreme precipitation scenarios on leaf litter and wood decomposition rates using a precipitation manipulation experiment. In chapter 3, we quantify the effects of various levels of harvest severity on wood decomposition rates and nutrient dynamics to identify the implications of shifting adaptive management regimes on critical ecosystem processes. The final chapter is a summary of these findings and future management recommendations. This chapter also highlights limitations from the above chapters and potential future directions for research.

## **CHAPTER 2: IMPACTS OF EXTREME PRECIPITATION EVENTS ON LEAF LITTER AND WOOD DECOMPOSITION**

### **2.1. Abstract**

Global hydrological cycles are projected to shift under future climate change scenarios due to an increase in the frequency and intensity of extreme precipitation events with likely consequences for important ecosystem processes that are driven by climate, such as forest decomposition. Our objective for this study was to determine the effects of varying future extreme precipitation scenarios, including drought and extreme rainfall events, on leaf litter and wood decomposition rates. We used a precipitation manipulation experiment to demonstrate that various future extreme precipitation scenarios will significantly impact wood but not leaf litter decomposition and that variations in substrate quality will contribute to differences in decomposition rates. After three years, wood decomposition rates were 53% greater under historic rainfall patterns for the Northeast compared to the drought regime and 32% greater compared to the high rainfall regime. Furthermore, labile litter and wood substrates decomposed, on average, 75% and 17% more rapidly than recalcitrant substrate types, respectively. Thus, our findings, suggesting a potentially greater sensitivity of wood decomposition to changing precipitation regimes compared to leaf litter, underline the possible significant impacts of projected extreme precipitation scenarios for forest functions. This encompasses forest carbon cycling and sequestration, given that wood represents a substantial source of forest carbon.

### **2.2. Introduction**

Global hydrological cycles are projected to shift under future climate change scenarios due to an increase in the frequency and intensity of extreme precipitation events

with likely consequences for important ecosystem processes like decomposition (Guilbert et al. 2015). For example, average annual precipitation in the Northeast United States has increased each decade since the late 1900s (Huang et al. 2021). In addition, the region is projected to experience more frequent and intense precipitation events with longer drying periods in between (Allen et al. 2010, Sun et al. 2007). Extreme precipitation events, including severe droughts and intense flooding, have already had numerous economic, social, and ecological consequences within the region (Alexander et al. 2006). Therefore, determining the impacts of future extreme precipitation scenarios on forest processes such as decomposition is essential to understanding and anticipating the effects of climate change on important forest ecosystem functions, such as carbon cycling and sequestration.

Climatic conditions are commonly recognized as key drivers of forest decomposition rates (Dai et al. 2021, Dyer et al. 1990). In cases where temperature is not limiting, decomposition and respiration rates are positively correlated with the moisture content of the decomposing material and the surrounding micro-environment (Aerts 1997, Boddy 1983, Cisneros-Dozal et al. 2007, Crockatt and Bebbber 2014, Herrmann and Bauhus 2013, Lee et al. 2014). For instance, mesocosm studies have demonstrated that soil moisture regulates enzyme production by fungi to influence CWM decomposition, and larger-scale syntheses have found a dominating influence of climate on leaf, root, and wood decomposition (A'Bear et al. 2014, Adair et al. 2008, Smith et al. 2011, Zanne et al. 2022).

In addition to climate, substrate quality significantly contributes to variations in forest decomposition rates due to differences in the chemical composition and physical

structure of leaf litter and CWM (Cornwell et al. 2008, Jomura et al. 2022, Strickland et al. 2009). In general, litter is primarily composed of organic forms of carbon (C), including cellulose and hemicellulose, and is relatively high in nitrogen (N), making it a relatively labile source of organic material. In contrast, CWM is high in lignin, a complex polymer that is difficult to decompose (Aber et al. 1990, Kahl et al. 2017, Meentemeyer 1978). Variations in chemical composition of leaves and CWM, often described using C:N ratios or lignin content, also contribute to differences in decomposition rates among differing species of substrates and influence the composition of microbial decomposers inhabiting and decomposing the substrate (Ge et al. 2013, Liu et al. 2013, Weedon et al. 2009). For example, high-quality substrate composed of easily degradable compounds can support a high diversity of decomposer organisms. Conversely, low-quality substrate often supports a low diversity of organisms that specialize in decomposing more complex compounds (Freschet et al. 2012, Hättenschwiler et al. 2005, Kahl et al. 2017, Weedon et al. 2009). Consequently, climate and substrate quality interact to affect decomposition, thus, shifts in moisture conditions will have varying impacts on leaf litter and CWM decomposition due to differences in substrate quality (Bradford et al. 2017, Dai et al. 2021).

Given the importance of moisture in affecting leaf litter and CWM decomposition rates, future shifts in precipitation scenarios will play a major role in forest decomposition (Dyer et al. 1990, Salamanca et al. 2003, Su et al. 2023). For example, Lensing and Wise (2007) found that high-rainfall events accelerated litter decomposition rates by 50%. Direct impacts of rainfall on litter and CWM include the leaching of soluble compounds during the initial stages of decomposition (Swift et al. 1979).

Leaching of soluble substances, like phenolics, carbohydrates, and amino acids from decomposing organic material potentially benefits ecosystem productivity by distributing important ecosystem nutrients through the soil, but excess rainfall may result in nutrient loss due to the removal of leached materials below the rooting zone and into groundwater (Kuehne et al. 2008, Parsons et al. 1990, Tietema and Wessel 1994). Rainfall indirectly affects litter and CWM decomposition by regulating microbial activities that contribute to the degradation of organic material. The activities of saprophytic fungi are moisture-limited and include the production of hydrolytic and oxidative extracellular enzymes that allow for the breakdown of recalcitrant components that make up litter and wood like lignin, cellulose, and hemicellulose (A'Bear et al. 2014, Sinsabaugh et al. 2008). Moisture also drives heterotrophic respiration as higher moisture levels increase respirational C loss in both litter and wood (Ataka et al. 2014, Herrmann and Bauhus 2013). Thus, shifts in moisture conditions and precipitation events will impact the rate at which litter and wood decompose in forested ecosystems.

Shifting hydrological cycles will have significant implications for forest functioning such as C storage potential or biogeochemical cycles. Extreme precipitation events, including intense rainfall or droughts, may have contrasting effects on the rate at which leaf litter and CWM decompose due to altered micro-climatic moisture conditions and the resulting influence on microbial activities; however, these dynamics have been little studied. Our objective for this study was to determine the effects of varying future extreme precipitation scenarios, including drought and extreme rainfall events, on leaf litter and CWM decomposition rates using a precipitation manipulation experiment. The questions we sought to answer were (1) how will leaf litter and CWM decomposition

rates respond to various future extreme precipitation scenarios; and (2) under future extreme precipitation scenarios, how will moisture and substrate quality interact to affect leaf litter and CWM decomposition rates? We hypothesized that (1) heavy magnitude extreme precipitation events will accelerate leaf litter and CWM decomposition rates, particularly of labile substrates due to enhanced leaching of soluble compounds; and (2) extreme drying periods (i.e., drought) will slow or hinder leaf litter and CWM decomposition rates.

## **2.4. Methods**

### *2.4.1. Study Site*

This study was conducted at the University of Vermont Jericho Research Forest (44.445° N, 73.003° W). The portion of the 192-ha experimental forest used for this work is primarily comprised of naturally regenerated second-growth northern hardwood forests and is dominated by maple (*Acer spp.*), birch (*Betula spp.*), American beech (*Fagus grandifolia*), eastern white pine (*Pinus strobus*), northern red oak (*Quercus rubra*), and eastern hemlock (*Tsuga canadensis*), with minor components of various deciduous and coniferous species. Soils are sandy glaciofluvial deposits at this site. Mean annual temperature ranges from  $-7^{\circ}$  C (January) to  $21^{\circ}$  C (July) and annual precipitation is 107.5 cm (NOAA, 2020). The experiment took place within 0.1-ha canopy gaps created during winter of 2017-2018.

### *2.4.2. Experimental Design*

To determine the effects of future extreme precipitation scenarios on leaf litter and wood decomposition, we conducted a precipitation manipulation experiment that was active for two years, during the 2018 and 2019 growing seasons as described by Clark and

D'Amato (2023). The experiment included a 27-m<sup>2</sup> precipitation manipulation shelter placed in the central portion of three recently created 0.1 ha canopy gaps. Precipitation treatments were applied within each shelter to emulate various combinations of extreme drought and/or episodic rainfall scenarios projected for this region and are summarized as follows:

1. Historic (control): “typical” rainfall, calculated as the median daily volume and frequency of nontrace rainfall (>1-mm totally daily rainfall) using a 100-year daily meteorological record (1917-2017). This treatment represents our experimental control.
2. Drought: “once-in-a-century” (1<sup>st</sup> percentile) growing season drought (1917-2017), calculated using the 95<sup>th</sup> percentile of consecutive rainless days (>1-mm total daily rainfall) for each growing season month.
3. Inundation: historic rainfall punctuated by periodic, high volume (95<sup>th</sup> percentile) extreme precipitation events based on regional precipitation projections under future climate change.

Each experimental precipitation treatment unit was applied beneath shelter canopies (N =3; one replicate per precipitation treatment per shelter) and contained tea bags and wood stakes to quantify the effects of extreme precipitation or drought on leaf litter and wood decomposition rates.

To study leaf decomposition, green and rooibos tea in tetrahedron-shaped synthetic tea bags were oven dried at 75°C for 48 hours (Keuskamp et al. 2013). Each tea bag was weighed and numbered with a unique ID. Within each treatment, 12 bags per tea type were buried pairwise at a depth of 8-cm in June 2018. At five intervals over the

course of approximately 24 months (~ 2 years), tea bags from each treatment were collected, oven dried, and weighed to determine mass remaining and decomposition rates over time.

To study wood decomposition, wood stakes were manufactured in size to 2.54 x 2.54 x 20 cm from locally harvested sugar maple (*Acer saccharum*) and quaking aspen (*Populus tremuloides*) wood and oven dried at 75°C for eight days (Fraver et al. 2018). Each stake was weighed and numbered with a unique ID. Within each treatment, eight stakes per species were positioned pairwise (10-cm apart) on the ground surface in June 2018. At five intervals over three years, six stakes per species per treatment were collected, oven dried, and weighed to determine mass loss over time.

#### 2.4.3. Statistical Analyses

To determine the response of leaf litter decomposition rates to extreme precipitation events, we fit the asymptotic decomposition model ( $X=A + [1-A]e^{-k_a t}$ ) to the proportion of leaf litter mass remaining, where  $X$  is the proportion of initial mass remaining at time  $t$ ,  $A$  is the fraction of the initial mass with a decomposition rate of zero, while the remaining fraction ( $1-A$ ) decomposes with a rate of  $k_a$  (Berg 2000, Hobbie et al. 2012).

To determine the effects of extreme precipitation events on leaf litter decomposition rates, we compared decomposition model parameters – the decomposition rate,  $k_a$ , and the fraction of litter that does not decompose,  $A$  – using the aov function in the ‘stats’ package in R to perform an analysis of variance (ANOVA) (R Core Team, 2021). We fit a linear model to measure interactions between treatment and tea type to determine the effects of extreme precipitation events and substrate quality on leaf litter

decomposition rates and the fraction of substrate whose decomposition rate was, or approached, zero ( $k_a$ ,  $A$ ). Our final models included decomposition model parameters as response variables and interactions between treatment and tea type as predictor variables using the lme function in the ‘nlme’ package (R Core Team, 2021). Constant variance structures were applied to account for heterogeneity in variance across treatments. In cases in which there was a significant main effect, a post hoc analysis was performed using the Tukey-Kramer methods to identify where differences in decomposition model parameters existed between the treatments.

Estimates for wood stake decomposition rates were calculated by dividing the final dry weight of the stakes from the initial weight and multiplying by 100 to determine the percentage of mass remaining over time. To determine the effects of extreme precipitation events on wood decomposition, we performed an ANOVA with mass remaining as the response variable and treatment as the predictor variable. Our final mixed-effects model included interactions between treatment, number of seasons stakes were left in the field, and species on mass loss with plot as the random variable. A constant variance structure was applied to account for heterogeneity in variance across the number of seasons stakes were left in the field.

## **2.5. Results**

### *2.5.1. Leaf Litter Decomposition*

Future extreme precipitation scenarios did not significantly impact initial rates of tea bag decomposition ( $k_a$ ) or the fraction of substrate whose decomposition rate was, or approached, zero ( $A$ ) (Figure 2.1) ( $F = 2.616$ ,  $P = 0.122$ ;  $F = 1.273$ ,  $P = 0.322$ , respectively). Although the interactions between treatment and tea type for both model

parameters ( $k_a$ ,  $A$ ) were marginally significant ( $F = 2.8994$ ,  $P = 0.102$ ;  $F = 3.5109$ ,  $P = 0.070$ , respectively), a post hoc analysis revealed that  $k_a$  of green tea was significantly greater within the drought treatment than the control ( $P = 0.022$ ) and that  $A$  of green tea was significantly greater within the drought than the inundation treatment ( $P = 0.053$ ). As hypothesized, there were significant differences between leaf litter substrate types for both model parameters (Figure 2.1). For  $k_a$ , green tea ranged from 0.040 to 0.067 and was greater than  $k_a$  of red tea, which ranged from 0.009 to 0.018 ( $F = 591.6587$ ,  $P < 0.001$ ). For  $A$ , green tea ranged from 0.230 to 0.331 and was significantly lower than red tea, which ranged from 0.386 to 0.494 ( $F = 370.3932$ ,  $P < 0.001$ ). Post-hoc analyses did not determine significant differences across the treatment types for  $k_a$  or  $A$ .

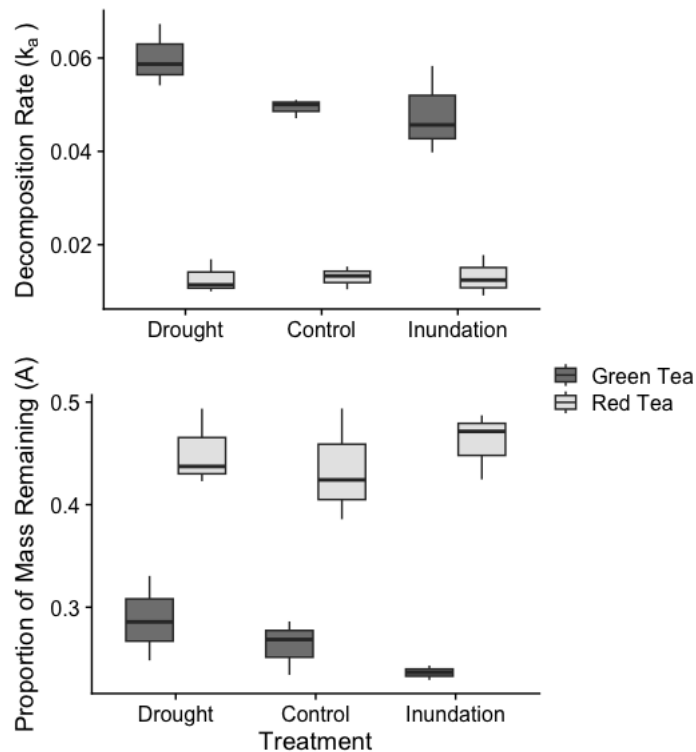


Figure 2.1. Decomposition model parameters obtained from fitting an asymptotic model to show differences between leaf litter substrate types

### 2.5.2. *Wood Decomposition*

Treatment effects on the remaining mass of wood stakes were significantly dependent on the number of years stakes were left in the field ( $F = 3.4$ ,  $P = 0.015$ ) (Figure 2.2 A). After the first year, mass remaining within the inundation treatment was 1.4% lower compared to the control ( $P = 0.003$ ), although there was no significant difference observed after the second year. Mass remaining after the third year was 32% lower within the control than the inundation ( $P = 0.0205$ ) treatment. The mean mass remaining of wood stakes after three years within the drought, control, and inundation treatments were 87.4%, 57.0%, and 75.5%, respectively. Differences in decomposition rates between sugar maple and aspen stakes did not occur until after the second year of the experiment (Figure 2.2 B). After the second and third years, aspen stakes had significantly less mass remaining than sugar maple stakes ( $P = 0.0418$ ,  $0.0001$ ). Mean starting and final mass of wood stakes were 73.014 g and 69.814 g, respectively.

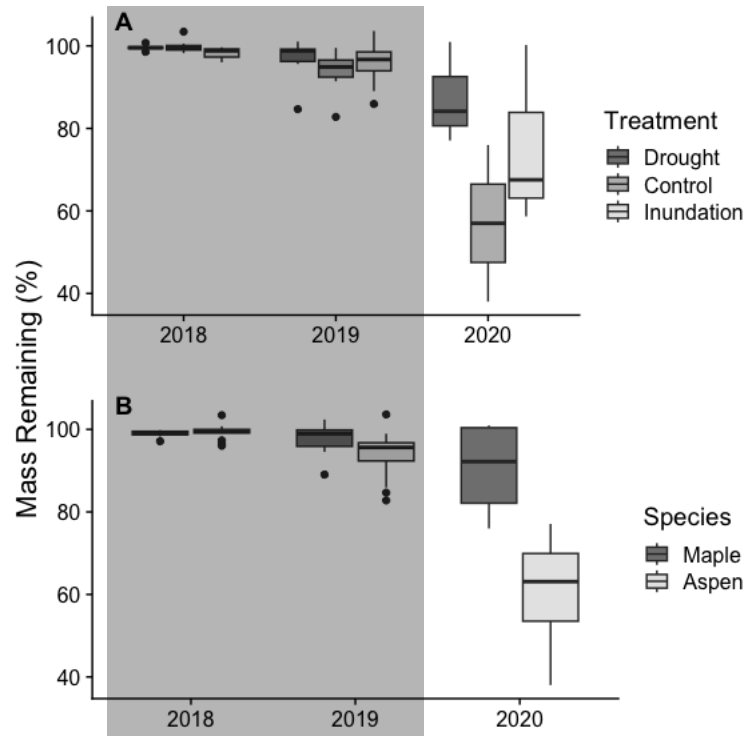


Figure 2.2. Mass remaining (%) of wood stakes over three years (A) by treatment types and (B) between stake species. The shaded portion represents the years the experiment was active.

## 2.6. Discussion

Global climate change will have substantial impacts on future forest dynamics and alter regional hydrological cycles. Forest functions, including C cycling and storage potential, may be disrupted during prolonged droughts or intense precipitation events due to shifts in forest decomposition. We used a precipitation manipulation experiment to demonstrate that various future extreme precipitation scenarios will significantly impact wood but not leaf litter decomposition.

### 2.6.1. Decomposition Rates

Our results suggest that the various future extreme precipitation scenarios projected to impact Northeastern forests will not interrupt leaf litter decomposition. These findings contradict previous studies that found increasing precipitation significantly

accelerates leaf litter decomposition due to greater leaching from high-rainfall events (Lensing and Wise 2007, Salamanca et al. 2003). Furthermore, drought effects on labile leaf litter substrates accelerated decomposition of the labile fractions but also resulted in a greater asymptotic mass remaining, or a greater 'slowly decomposing' fraction (Hobbie et al. 2012). These results are consistent with Berg and Ekbohm (1991) who found nutrient rich litter exhibited multiple stages of decomposition where the labile fractions of litter decomposed more rapidly during the initial stages (12-18 months) than the later stages (3-4 years).

In contrast to leaf litter, our results indicate that projected extreme precipitation scenarios will significantly impact wood decomposition. Short-term exposure to high-rainfall events accelerated wood decomposition but the effects were much greater over longer time periods. After three years, historic rainfall patterns that are typical for the Northeast had a greater effect on wood decomposition than high-rainfall events. In these instances, high-rainfall events and overall greater precipitation potentially disrupted microbial decomposer activities likely creating anaerobic conditions, whereas moderate or little to no precipitation provided consistent moisture conditions that were more suitable for microbial organisms within leaf litter and CWM (A'Bear et al. 2014, Boddy et al. 1983).

### *2.6.2 Substrate Quality*

As expected, labile leaf litter substrates decomposed more rapidly than recalcitrant leaf litter substrates. Climate and substrate quality are strong predictors of decomposition rates throughout multiple ecosystems and act synergistically to control the process of decomposition (Adair et al. 2008). At global scales, temperature and moisture

are highly related to decomposition rates but within individual ecosystems, chemical composition of the decomposing substrate becomes a better predictor and is often expressed in terms of C and N concentrations or ratios and lignin content (Aerts et al. 1997, Gholz et al. 2000). Labile leaf litter substrates tend to have higher N concentrations and lower lignin contents making them more decomposable, therefore, it is not surprising that green tea had greater decomposition rates than red tea (Aber et al. 1990, Meentemeyer 1978).

Similarly, wood decomposition rates differed between sugar maple and aspen stakes. After the second year of the experiment, aspen stakes decomposed more rapidly than sugar maple stakes, likely due to differences in chemical composition and wood traits. These results agree with the established idea that differences in wood physical, chemical, and structural properties across tree species and their interactions with microbial communities contribute to variations in their general decomposability (Forrester et al. 2023, Weedon et al. 2009). Furthermore, previous studies have observed an initial lag time (~2 years) before decomposition rates increased rapidly for aspen species compared to maple species having longer initial lag times (~6-10 years) (Freschet et al. 2012, Johnson et al. 2014). This lag time is potentially due to the initial phases of decomposition when microbial organisms colonize the substrate and can be impacted by wood physical and structural traits (Harmon et al. 1986, Swift et al. 1979). Thus, the micro-environment provided by low-density and nutrient rich wood may be more habitable and accessible for microbial decomposers, specifically fungi, and accelerate the initial stages of wood decomposition.

### *2.6.3. Study Limitations*

Limitations of this study include small sample sizes and the short length of the experiment. Overall, our study was comprised of approximately 48 tea bags per tea bag type and 32 wood stakes per species that were situated throughout the various treatment types. Over three years, the tea bags and stakes were collected to measure decomposition rates; however, some samples were unable to be recovered or processed due to various reasons (e.g., missing tags for identification or broken samples that were too fragmented). This resulted in a reduced sample size for some treatments and in the third year of the experiment. Consequently, our dataset exhibited extreme heterogeneity in variances across the treatment types and prevented us from analyzing all four extreme precipitation scenarios. Our solution was to remove a precipitation treatment (the episodic treatment) from our wood stake analysis that had the least datapoints available and to keep analyses consistent, the episodic treatment was also removed from the tea bag dataset.

Additionally, we were unable to test a three-way interaction between treatment, number of years stakes were left in the field, and species of wood stakes due to a lack of datapoints during the third year. Although the experiment lasted for only two years, we are presenting wood decomposition data from the third year when the wood stakes were subjected to ambient conditions. Due to the gradual nature of wood decomposition, we interpret our results as indicating a delay in the effects of the treatments. Finally, in the northern forest ecosystem, three years is an extremely short time period that would only capture the initial stages of decomposition. Therefore, the length of the precipitation manipulation experiment may explain our weakly marginal litter decomposition results. Thus, we are unable to infer about the effects of various future extreme precipitation

scenarios over longer time periods; however, the effects could potentially become stronger if the study was carried out for multiple years to also capture the intermediate and advanced stages of decomposition.

#### 2.6.4 Conclusions

Our results provide insight to the ecological impacts of climate change on ecosystem processes that contribute to forest functions including forest C cycling and sequestration. We found that extreme rainfall and drought had little impact on leaf decomposition, but that wood decomposition was sensitive to changing precipitation with drought reducing wood decomposition rates and heavy rainfall increasing decomposition rates. Given that wood is a major source of forest C, these findings have significant implications for forest C storage.

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## **CHAPTER 3: INFLUENCE OF ADAPTIVE MANAGEMENT REGIMES ON WOOD DECOMPOSITION**

### **3.1. Abstract**

Deadwood decomposition is a critical ecosystem process that will be impacted by shifting climate and disturbance regimes, as well as by the adaptive management strategies designed to address the impacts of these changes. Most studies investigating deadwood decomposition in response to forest harvesting disturbance have focused on contrasts between highly disturbed and undisturbed areas leaving key knowledge gaps regarding how decomposition varies across a gradient of disturbance severity within forests that experience multiple forms of adaptive management. The objective of this study was to quantify the impacts of increasing harvest severity across a gradient of adaptive management strategies on wood decomposition rates and nutrient dynamics. Wood stake mass loss was not affected by harvesting treatments when comparing harvested versus unharvested areas, but instead decreased with increasing disturbance severity. Additionally, wood stake carbon was affected by harvesting, with greater carbon concentrations in harvested versus unharvested areas, whereas there were no differences in wood nitrogen concentrations across treatments. Although wood mass loss decreased with harvest severity, the results of this study indicate that deadwood retention within harvested areas may maintain the potential for forest carbon sequestration in deadwood pools, particularly in the short-term.

### **3.2. Introduction**

Deadwood, or coarse woody material (CWM), is an integral component of forested ecosystem structure that plays a major role in ecosystem functions and properties

including carbon (C) storage, biogeochemical cycling, and biodiversity (Boddy 2001, Harmon et al. 1986). CWM increases stand structural and compositional complexity and provides resilience to disturbance and changing forest dynamics through its influence on post-disturbance recovery (Johnstone et al. 2016). CWM also represents a significant, yet recalcitrant, source of carbon (C) that constitutes up to 20% of total aboveground biomass in forested ecosystems (Laiho and Prescott 2004). Accounting for more than 50% of accumulated organic matter in forests, the decomposition of CWM is a fundamental ecosystem process that directly impacts C storage potential and local to regional biogeochemical cycles of C and N (Laiho and Prescott 1999). Lastly, CWM serves as a valuable resource and habitat for many organisms and also acts as a regeneration substrate for some tree species (Dai et al. 2021, Lonsdale et al. 2008). Despite the major role that CWM plays in forested ecosystems, CWM decomposition rates and associated shifts in CWM nutrient dynamics in response to disturbance and adaptive management strategies are not well understood.

Forest decomposition is a biological process that includes the breakdown and transformation of complex dead organic material, including deadwood, into simpler organic and inorganic materials. This process results in the release of C to the atmosphere, C transformation into microbial biomass, and recycling of vital ecosystem nutrients, like N, in forms that can be used for plant and microbial production (Juma 1998). The dominant drivers of wood decomposition can be organized into two main categories: (1) abiotic factors (e.g., climate) and (2) biotic factors (e.g., substrate quality and microbial community composition) (Boddy 1989, Dai et al. 2021). The main abiotic control on wood decomposition is climate. Variations in temperature and moisture

strongly drive CWM decomposition rates and are the most common predictors of this process (Finer et al. 2016). In general, CWM decomposition increases with increasing temperature and moisture, a relationship that can be easily modeled at regional or global scales (Crockatt and Bebbler 2015, Forrester et al. 2012, Kubartova et al. 2015).

The main biotic controls influencing wood decomposition are substrate quality, or the amount and type of C and N compounds that make up the substrate, and microbial community composition, specifically the abundance, diversity, and biomass of wood-decay fungal organisms (Dai et al. 2021, Rayner and Boddy 1988). For example, multiple studies have reported evidence for wood trait-based differences in decomposition rates with the most pronounced differences occurring between hardwood and softwood species (Weedon et al. 2009). In general, hardwoods tend to have greater lignin content, making them a more recalcitrant substrate to decompose and inhabit by fungal organisms (Meentemeyer 1978). At smaller spatial scales, the composition and diversity of wood-decaying fungal communities can impact CWM decomposition rates (Kubartova et al. 2015, Maynard et al. 2017b, Setälä and McLean 2004, Van der Wal et al. 2013). For example, field studies have found that increasing diversity decreases CWM decomposition due to increased competition among fungal species (Fukami et al. 2010, Smith and Peay 2021). Thus, CWM decomposition is driven by complex interactions between various abiotic and biotic factors including climate, substrate quality, and microbial community composition.

As the dominant decomposers of CWM in North America, fungal organisms have significant impacts on CWM nutrient dynamics (Blanchette 1991, Dai et al. 2021, Rayner and Boddy 1988, Tanesaka et al. 1993, Van der Wal et al. 2007). During the process of

decomposition, the C and N concentrations of CWM change as fungi mobilize and translocate nutrients, grow, and respire C (Laiho and Prescott 2004, Magnussen et al 2016). Saprophytic fungi mobilize important ecosystem nutrients by secreting extracellular enzymes that break down complex organic compounds, such as cellulose, lignin, and chitin, into smaller and simpler forms of C and N, thus, regulating the availability and cycling of important nutrients within forested ecosystems (Boddy and Watkinson 1995, Burns et al. 2013, Sinsabaugh et al. 2008). C loss occurs due to microbial respiration and changes the concentration of nutrients relative to C, resulting in decreasing C:N or other C:Nutrient ratios (Boddy and Watkinson 1995, Hermann and Bauhus 2012, Mackensen et al. 2003). N concentrations increase over time within CWM during the initial stages of decomposition due to fungal translocation, where nutrients, like N, are acquired by fungal organisms from CWM and outside sources (e.g., soil or leaf litter) and are stored within fungal mycelium to support growth and survival (Boberg et al. 2014, Boddy and Watkinson 1995, Laiho and Prescott 2004, Laiho and Prescott 1999, Philpott et al. 2014). The activities of saprophytic fungal organisms inhabiting CWM are influenced by micro-climatic conditions, substrate quality, and fungal community composition, therefore, shifts in stand micro-environments associated with disturbances, specifically harvesting, are likely to impact fungal activities and related changes in CWM nutrient dynamics (A'Bear et al. 2014, Boddy 1983).

Forest disturbances impact ecosystem processes, such as decomposition, by altering forest microclimates, substrate availability, and microbial community composition (Borgmann-Winter et al. 2022, Fraver et al. 2002, Prevost and Raymond 2012). In most cases, our understanding of disturbance effects on decomposition is based

on contrasts between highly disturbed and undisturbed areas, but less is known about how this process varies across the gradients of disturbance severity often found in ecosystems experiencing gap- and meso-scale natural disturbances or contemporary management practices that deliberately increase ecosystem heterogeneity for different biodiversity and adaption goals (Palik et al. 2020). For example, CWM decomposition rates tend to be greater following clearcuts; however, Crockatt and Bebbler (2015) found CWM decomposition rates increased when moving from forest edge to core (Finer et al. 2016, Jacobs and Work 2012). These contrasting findings are generally attributed to differences in stand micro-climates, including temperature, moisture, and light conditions, that impact the decomposer activities of microbial organisms (Forrester et al. 2012, Muscolo et al. 2014, Prevost and Raymond 2012, Raymond et al. 2006, Read et al. 2023).

Forest disturbances, including harvesting, can also disrupt the composition and structure of microbial decomposer communities and potentially reduce the general decomposer efficiency of the stand (Boddy et al. 1989, Fukami et al. 2010, Smith and Peay 2021). For instance, the diversity, richness, and biomass of fungal communities in forests that experience high severity harvesting are generally lower compared to forests that experience little to no harvesting (Bassler et al. 2014, Juutilainen et al. 2014, Kuffer and Senn-Irlet 2005, Tomao et al. 2020). This shift in composition can occur due to a reduction of the volume, biomass and decay class of large-diameter CWM and an increase in smaller-diameter debris or slash that is often a result of harvesting (Fraver et al. 2002, Harmon et al. 1986). Consequently, overall decomposition rates may decrease due to the limited availability of organic material for decomposer organisms (Bassler et al. 2010, Kuffer and Senn-Irlet 2005, Lonsdale et al. 2008). However, Brazee et al.

(2014) found that canopy gap formation can support fungal diversity and richness but only when CWM and debris are added to the ecosystem to enhance stand structure.

CWM may potentially act as a sink for N or P, especially following a disturbance-related event, as N and P concentrations generally increase with advancing decomposition in deadwood, a pattern that is likely associated with fungal decomposer activities (Boddy and Watkinson 1995, Krankina et al. 1999, Laiho and Prescott 2004, Philpott et al. 2014, Preston et al. 2012). Indeed, CWM additions to soils can quickly (~1 year) immobilize soil N and reduce soil N availability (Homyak et al. 2008, Lajtha 2020, Piatek 2011). As a result, ecosystem N availability may be reduced in forests with large CWM inputs. Thus, it is critical to investigate the effects of harvesting on CWM decomposition and nutrient dynamics to anticipate the potential implications for forest functions, specifically C storage and biogeochemical cycling.

Forest management regimes are shifting to adapt to, or mitigate, the effects of climate change and these shifts will likely have cascading effects on important ecosystem processes like decomposition (D'Amato et al. 2011). These regimes often include a wide range of harvest severities within and across stands to generate heterogeneity in forest stand micro-environments and potential adaptive pathways (D'Amato and Palik 2021, Wikle and D'Amato 2023). Most studies have reported increases in leaf litter and fine root decomposition following forest harvesting and other disturbances, generally due to increased exposure to solar radiation and precipitation, however, multiple interactions between the abiotic and biotic drivers of decomposition make it difficult to predict how CWM decomposition and nutrient dynamics may respond to increasing harvest severity at the stand-level (Finer et al. 2016, Forrester et al. 2012, Harmon et al. 2011, Ritta

2005). Therefore, this study will investigate the effects of differing levels of harvest severity on wood decomposition rates and changes in CWM C and N concentrations at the stand-level. The primary question we sought to answer was how do different levels of harvest severity impact CWM decomposition rates and nutrient dynamics? We hypothesized that (1) CWM decomposition rates will be highest within high harvest severity (gap) treatments due to increased micro-climatic temperatures that accelerate decomposition; (2) CWM C concentrations will decrease as decomposition advances and be lowest within high harvest severity (gap) treatments due to microbial respiration; and (3) CWM N concentrations will increase as decomposition advances and be highest within high harvest severity (gap) treatments due to fungal translocation.

### **3.3. Methods**

#### *3.3.1. Overview and Study Site*

Our study site is located at Dartmouth College's Second College Grant in New Hampshire (44.89 N, -71.13 W) within an installation of the Adaptive Silviculture for Climate Change (ASCC) experimental network (Nagel et al 2017). Forests at this site are dominated by northern hardwoods including sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), and American beech (*Fagus grandifolia*). Mean annual temperature based on climate data from January-December 2022 is 14 °C and precipitation is 117 cm (NOAA, 2022). Soils are coarse loamy glacially-derived tills and elevations range between 484 – 650 meters (NRCS, 2022). The Second College Grant is owned by Dartmouth College and has historically been managed for timber, wildlife habitat management, recreation, and scientific research and education.

The ASCC project is a collaborative series of experimental silvicultural trials co-produced by managers and scientists across a variety of forest types in the US and Canada that aims to address the role active management plays in mediating forest adaptation to climate change. Treatments for the ASCC project are based on a framework of adaptation responses including resistance, resilience, and transition (Nagel et al. 2017). Our study takes place within the *no action* and *transition* treatments of the ASCC study. Each treatment of the ASCC study was replicated in 4 10-ha units. No active management occurred within the *no action* treatment and represented our unharvested control. The goal of the *transition* treatment is to alter forest compositional and structural conditions to those better adapted to future climate change and those that will reflect future climate and disturbances (Millar et al. 2007, Nagel et al. 2017). The prescription for the transition treatment is a continuous cover irregular shelterwood that contains different degrees of within-stand disturbance severity. A portion of each stand (20%) contains 0.1 ha (small) or 0.4 ha (large) harvest gaps and 20% unharvested aggregate retention patches of 0.1 ha in size. The remaining matrix surrounding these elements was thinned to 16-18 m<sup>2</sup>ha<sup>-1</sup>. Some harvested gaps are planted with future climate-adapted species like bigtooth aspen (*Populus grandidentata*), bitternut hickory (*Carya cordiformis*), black birch (*Betula lenta*), American chestnut (*Castanea dentata*), red spruce (*Picea rubens*), white pine (*Pinus strobus*), black cherry (*Prunus serotina*), northern red oak (*Quercus rubra*), and eastern hemlock (*Tsuga canadensis*) (Clark et al. 2022). Extensive pre- and post-harvest vegetation data was collected from 2017-2022 in plots across each treatment unit.

### 3.3.2. Study Design

Wood decomposition stakes were deployed within the *no action* and *transition* treatments to explore the effects of increasing harvest severity on wood decomposition. Within each replicate of the *no action* treatment, 3 stakes were placed in 7 control plots and within each replicate of the *transition* treatment, 3 stakes were placed in 7 matrix, 2 small-gap, and 2 large-gap plots (Figure 3.1). Overall, 216 stakes were placed throughout the experiment but only 210 were recovered from the field due to loss or full decomposition (e.g., too fragmented for analysis).

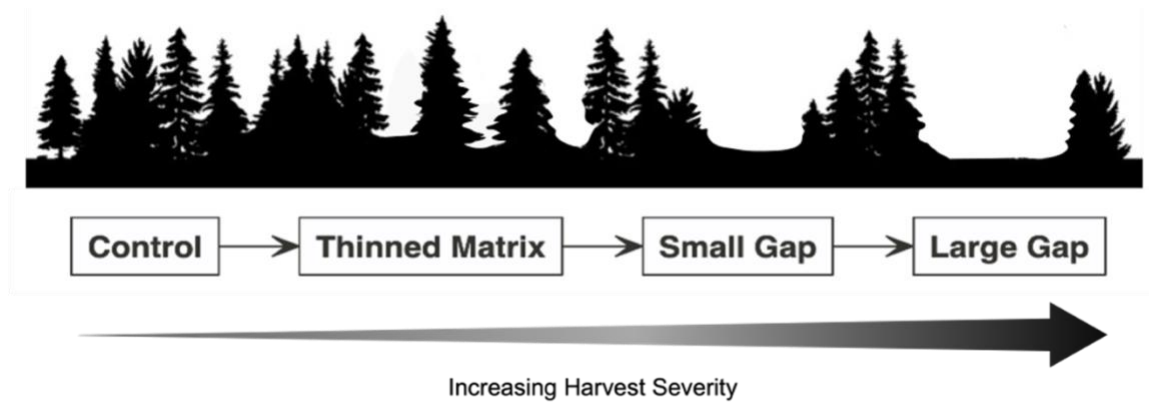


Figure 3.1. Experimental treatments in order of increasing harvest severity.

Stakes were manufactured in size to 2 x 2 x 20 cm from locally harvested, knot- and defect-free sugar maple wood and oven dried at 60° C for 8 days to achieve constant weight (Fraver et al. 2013). Each stake was weighed and uniquely numbered and tagged once dry then placed on the forest floor in summer 2018. After collection in summer 2022, all stakes were cleaned of soil and debris in the laboratory and oven-dried at 60° C for 8 days before being weighed to measure mass loss (%) (Fraver et al. 2018). To measure changes in C:N ratios and concentrations, sawdust was collected from a subset of samples (N = 66, 16 from the control, 16 from the matrix, 19 from the small-gaps, and

15 from the large-gaps) within each treatment by drilling three holes along the length of each stake using a flame-sterilized drill bit before being dried.

### *3.3.3. Carbon and Nitrogen Contents*

Changes in CWM C and N concentrations and ratios were measured to determine how CWM nutrient dynamics change in response to increasing harvest severity. Oven dried sawdust from the stakes were packed into 2 ml polypropylene glass microvials with two 3.5-4 mm clean glass beads and homogenized for 4-5 minutes using a Mini-Beadbeater-96 (BioSpec Products, USA). Concentrations of CWM C, N, and C:N ratios were measured by combustion using a UNICUBE Organic Elemental Analyzer (Elementar, Germany). To have detectable N in these samples, a higher sample mass than typically used for organic samples was run. The C values at this mass fell above the instrument calibration curve. To address this, the recovery rates for samples run above the calibration curve were calculated by running acetanilide and leaf sample standards at similar absolute C values to that of the wood samples (7mg). We found the recovery rate to be >90% for samples run at 7 mg of absolute C, so we did not adjust these samples. However, it is important to report that the C values may be a slight underestimate of the true C (%) values.

### *3.3.4. Statistical Analysis*

Wood stake decomposition rates were calculated by dividing the mass loss of the stakes after four years in the field from the initial dry weight of the stakes, multiplied by 100 to determine the percentage of mass loss over time. C:N ratio changes were calculated similarly using the initial C:N ratio of the stakes before being placed in the field and the post C:N ratio of the stakes after being collected.

Pre- and post-harvest vegetation data was analyzed for changes in biomass, overstory forest structure, and disturbance. We determined amounts of living and dead woody biomass by first calculating volume then converting these values to biomass based on species and decay-class specific wood density values. Tree and woody material biomass were combined to generate a disturbance severity index (DSI) that describes the change in total aboveground biomass at each plot from pre- to one-year post-harvest (Kurth et al. 2020). Overstory basal area was calculated for sugar maple trees as previous studies suggest that the dominant tree species within a forest stand may have significant effects on the surrounding soil dynamics including soil nutrient contents and the composition of microbial communities, both of which strongly drive wood decomposition (Ayres et al. 2009a, Ayres et al. 2009b, Hobbie et al. 2006). We quantified overstory forest structure to calculate canopy cover using post-harvest tree basal area and diameters for each plot. These measurements were used as explanatory environmental variables and averaged by site and tested for differences across treatments using an analysis of variance (ANOVA).

To quantify the impacts of increasing harvest severity on CWM decomposition rates and nutrient dynamics we performed an ANOVA with mass loss (%), C (%), N (%), C:N ratio changes, and absolute C:N ratios as response variables and treatment as the predictor. Analyses were performed in R using the `aov` function in the 'stats' package (R Core Team, 2020). Linear mixed-effects models were used to test abiotic influences affecting CWM decomposition rates and nutrient dynamics using the 'nlme' package in R (Pinheiro et al. 2023). Model selection was based on the Akaike information criterion (AIC) with the model containing the lowest AIC value selected as the best approximating

model in the set. Our final mixed-effect model for CWM decomposition rates included mass loss (%) as the response variable, DSI as a predictor, and plot as the random variable. A power variance structure was applied to DSI as a function of treatment to account for heterogeneity across treatment types. Our final mixed-effect model for CWM nutrient dynamics included C:N ratio changes as the response variable and interactions between treatment, DSI as a predictor variable, and plot as the random variable. A constant variance structure was applied to treatment to account for heterogeneity across treatment types.

### **3.4. Results**

#### *3.4.1. Structural and Compositional Conditions*

The unharvested control and matrix treatments had significantly greater overstory basal areas than the small- and large-gap treatments, which did not differ from each other ( $F = 37.71$ ,  $P < 0.001$ ). Unharvested control and matrix treatments were dominated by sugar maple and the gap treatments were dominated by American beech based on basal area. Disturbance severity was greatest within the small- and large-gaps (DSI ranging from 0.08 to 0.39) compared to the control and matrix (DSI ranging from 0.02 to 0.21) treatments ( $F = 873.8$ ;  $P = < 0.001$ ).

#### *3.4.2. Mass Loss*

Harvesting did not significantly influence wood stake mass loss ( $F = 2.257$ ,  $P = 0.090$ ) but was generally greatest within the unharvested control (Figure 3.2). Mean starting and final mass of wood stakes was 85.841g and 44.547 g, respectively. However, the best approximating mixed-effect model for describing mass loss indicated mass loss was negatively related to DSI (Figure 3.3) ( $F = 6.23$ ,  $P = 0.016$ ).

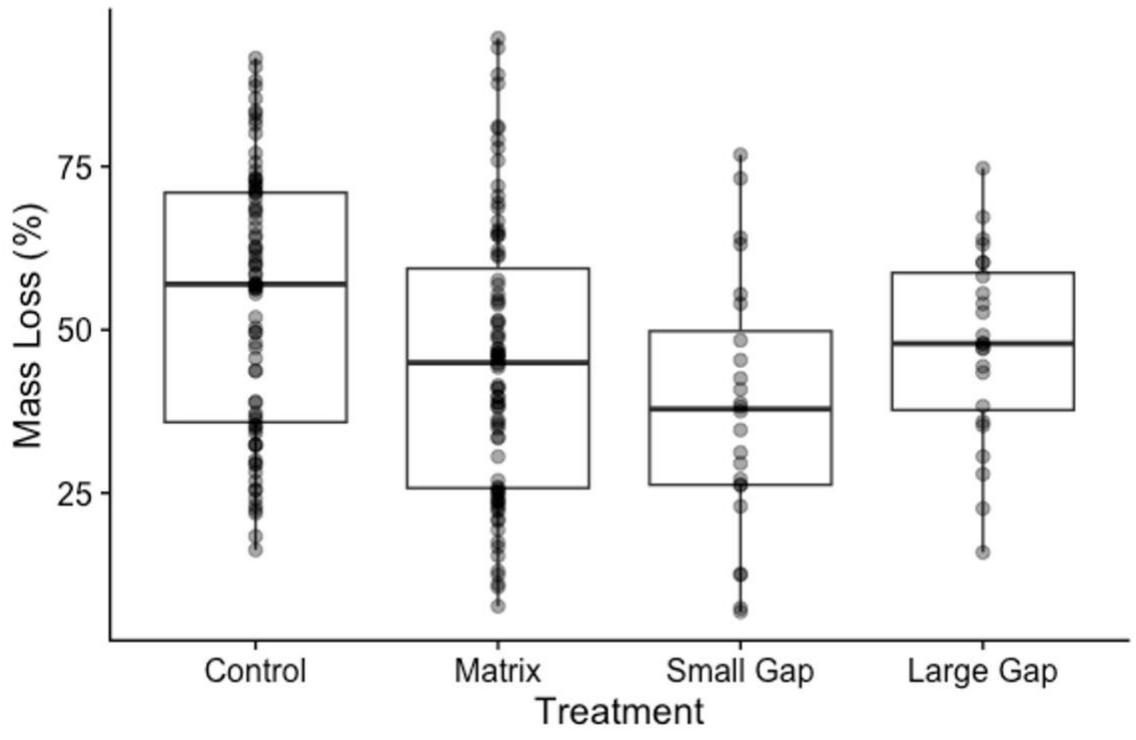


Figure 3.2. Mass loss (%) of wood stakes across the treatment types. Wood stake decomposition rates are generally greatest within the unharvested control.

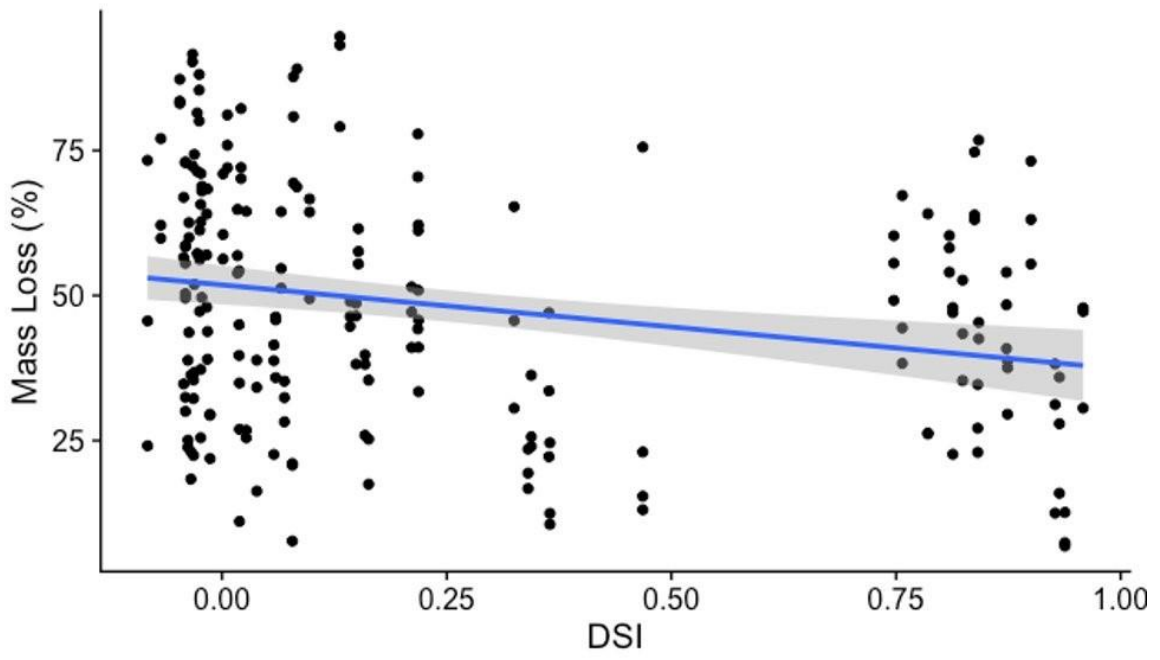


Figure 3.3. Relationship between wood stake mass loss (%) and disturbance severity. Trend line represents linear regression between mass loss as the dependent variable and DSI as the independent variable. The shadowed area indicates the range of the 95% CI of the estimated coefficient.

### 3.4.3. C and N Concentrations and Ratios

Harvesting significantly influenced C (%) of wood stakes (Figure 3.4) ( $F = 6.515$ ,  $P = 0.007$ ). Final wood stake C (%) was 3.2% greater within the large-gap and 8.2% lower within the matrix compared to the control. The best approximating mixed-effect model for wood stake C (%) revealed a marginally significant positive relationship between wood stake C (%) and DSI ( $F = 4.285$ ,  $P = 0.061$ ). Final wood stake C (%) ranged from 29% to 48%. Final N (%) of wood stakes ranged from 0.09% to 0.78% and did not differ across the treatments (Figure 3.4) ( $F = 1.412$ ,  $P = 0.287$ ). Both C (%) and N (%) significantly increased over time (Figure 3.4) ( $F = 9.28$ ,  $P = 0.004$ ;  $F = 83.49$ ,  $P < 0.001$ , respectively). C:N ratios decreased over time but did not differ across the treatments ( $F = 1.274$ ,  $P = 0.302$ ).

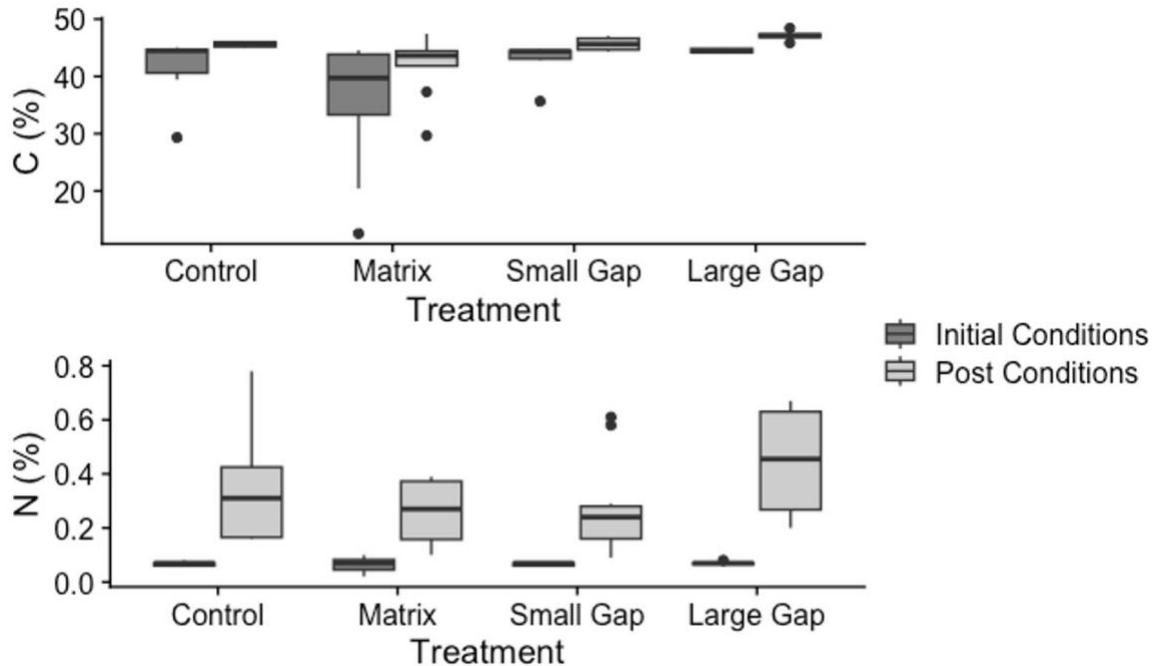


Figure 3.4. Initial and final wood stake C and N concentrations across the treatment types. Wood stake C and N concentrations increase over time and are generally highest within large harvest gaps.

### 3.5. Discussion

The potential impacts of climate change have prompted forest managers and landowners to adopt new, adaptive approaches to forest management. Given the limited levels of experience with these approaches, future forest dynamics under these management regimes and their effects on critical ecosystem processes, specifically wood decomposition, remain unclear. We assessed the effects of a novel adaptation framework on wood decomposition and nutrient dynamics using a gradient of increasing harvest severity and found that wood decomposition rates generally decreased with increasing harvesting severity, a finding counter to many previous comparisons solely contrasting unharvested with high severity treatments. In addition, wood C concentrations were generally greatest in large harvest gaps highlighting the potential for harvesting to influence CWM nutrient dynamics. Collectively, these results underscore the importance of examining wood decomposition across a gradient of disturbance severities given the complex feedbacks between microsite conditions and microbial communities occurring under different levels of canopy cover and harvest-generated disturbance legacies.

#### *3.5.1. Decomposition Rates*

The specific adaptive management strategies investigated in this study (i.e., thinning and canopy gap formation) did not significantly impact wood decomposition rates; however, in contrast to our hypothesis and previous studies, wood stake mass loss was generally greatest within the unharvested control and was negatively related to disturbance severity (i.e., DSI). Although we did not find a significant treatment effect, the significantly negative relationship between mass loss and disturbance severity suggests that harvesting unexpectedly disrupted, or slowed, wood decomposition rates.

Most studies generally observe a positive relationship between gap size, or canopy openness, and wood mass loss due to increased temperatures (Finer et al. 2016, Forrester et al. 2012, Forrester et al. 2023, Griffiths et al. 2021). However, a few studies have identified negative, or negligible, effects of canopy openness on wood decomposition rates with more evidence available for this relationship in leaf litter (Gonzalez et al. 2014, Latterini et al. 2023, Zhang and Zak 1995). In these instances, the localized effects of canopy gaps on micro-climates, specifically a lack of moisture within the decomposing substrate, shifted the composition of microbial communities and altered their associated decomposer activities to influence decomposition rates (Arunachalam and Arunachalam 2000, Brazee et al. 2014, Muscolo et al. 2007). Our findings highlight the need for further investigation into the nuanced relationship between wood decomposition and disturbance, especially at smaller spatial scales.

Previous studies have consistently reported an acceleration of wood decomposition rates and a release of CWM C following disturbance-related events (Finer et al. 2016, Harmon et al. 2011, Woodall et al. 2015). These effects are generally attributed to higher temperatures resulting from increased direct solar radiation and a greater input of CWM (Fraver et al. 2002, Muscolo et al. 2014, Prevost and Raymond, 2012, Toivanen et al. 2012). Although canopy gap creation is known to initially increase soil moisture, this response is temporary and declines over time (Gray et al. 2002). Consequently, moisture might have become limited within the canopy gaps, slowing the physical and chemical degradation of the wood stakes. In contrast, moisture conditions within the unharvested sites remained constant, supporting the growth and activities of decomposer microbial organisms (A’Bear et al. 2014, Boddy 1983). Moreover, the

removal and replacement of large-diameter CWM with smaller-diameter CWM, in the form of slash, potentially altered the availability of habitats and nutrients essential for microbial decomposition (Brazee et al. 2014, Perreault et al. 2021).

The disturbances associated with harvesting had potential impacts on wood decomposition rates by influencing the composition of decomposer organisms. At our study site, Borgmann-Winter et al. (2022) demonstrated that fungal fruiting body diversity and richness were highest within the unharvested sites compared to patch cuts. However, our combined findings appear to contradict the growing body of evidence that suggests wood decomposition rates are negatively correlated with fungal diversity and richness (Fukami et al. 2010, Smith and Peay 2021). This contradiction may indicate a stronger modification to the microbial communities, through changes in the micro-climate and availability of substrate, that led to slower decomposition rates within the harvested gaps compared to the unharvested sites (Latterini et al. 2023).

### *3.5.2. Nutrient Dynamics*

Harvesting had a notable impact on the final concentrations of C in CWM but did not significantly affect N concentrations. Moreover, it was observed that C concentrations were generally highest within the large-gap sites. These results may be indicative of differences in microbial C use efficiency (CUE) between the harvested and unharvested sites due to variations in micro-climatic conditions. During decomposition, microbial organisms break down cellulose through mineralization. As cellulose breaks down, it is released into the atmosphere as carbon dioxide (CO<sub>2</sub>); however, not all carbon (C) is lost as CO<sub>2</sub>. Some C remains in the wood residues and bodies of decomposer organisms, leading to an accumulation of C within CWM as decomposition progresses

(Boberg et al. 2014). The CUE of microbial decomposers is strongly influenced by temperature and precipitation, with CUE generally decreasing as temperatures increase, leading to greater losses of C through respiration (Manzoni et al. 2012, Sinsabaugh et al. 2013). However, limited moisture conditions within large-gaps potentially increased CUE, promoting the growth of microbial organisms and the stabilization of C within CWM.

Furthermore, our findings revealed an increase in C concentrations within our wood stakes as decomposition advanced. While it is common to observe increasing C concentrations within angiosperm bark but not wood, our study suggests the possibility that the CUE of microbial decomposers inhabiting the CWM was enhanced (Harmon et al. 2013). This could have led to a situation where the concentration of C within the wood stakes increased. Additionally, consistent with our hypothesis, substantial quantities of N accumulated within the wood stakes as decomposition advanced. Important macro-nutrients, specifically N and phosphorous, are known to accumulate in CWM over time and are related to the initial chemical composition of the substrate and the activities of microbial decomposers (Laiho and Prescott 2004, Van der Wal et al. 2007). As wood is generally low in N, fungi will translocate N from outside sources to support their growth and survival (Laiho and Prescott 1999, Philpott et al. 2014, Preston et al. 2012).

### *3.5.3. Limitations*

Our study provides an analysis of wood decomposition in response to various adaptive management strategies across varying levels of harvest severity. The inclusion of micro-climatic differences across the treatment types could have provided a more robust and complete analysis. Although we comment on the relationship between forest

structure and stand micro-climate conditions, we are unable to comment on the direct effects of temperature and moisture conditions on wood decomposition rates and nutrient dynamics, including the effects of micro-climatic differences on fungal community composition and associated decomposer activities. Additionally, our study used wood stakes without bark as a proxy for the decomposition of CWM that would be observed for logs with bark. This may explain some of the discrepancies observed between our findings and the findings of previous studies regarding C concentrations of CWM.

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## CHAPTER 4: CONCLUSION

This thesis evaluated leaf litter and wood decomposition within the context of shifting future forest dynamics as a result of changing climates and associated adaptive management regimes. The second chapter measured leaf litter and wood decomposition rates in response to two future extreme precipitation scenarios. Consistent with existing literature, differences in substrate quality contributed to variations in litter and wood decomposition rates as labile substrates decomposed more rapidly than recalcitrant substrates due to species-specific variations in litter and wood traits including C, N, and lignin content or wood density. Our main findings suggest that while leaf litter will not be impacted during the initial stages of decomposition, wood decomposition rates are greater under historical rainfall patterns that are typical for the Northeastern region relative to future projected drought or high-rainfall events over time. Therefore, future extreme precipitation scenarios may potentially disrupt, rather than accelerate, wood decomposition. This study provides insight to the ecological impacts of climate change on ecosystem processes that contribute to forest functions including forest C storage potential and biogeochemical cycling.

In the third chapter, we investigated the impacts of adaptive management strategies on wood decomposition rates and nutrient dynamics. While the specific adaptive management strategies we examined, such as thinning and canopy gap formation, did not significantly affect wood decomposition, the disturbances caused by harvesting unexpectedly disrupted or slowed wood decomposition rates. Contrary to our initial hypotheses, our results indicate a potential stronger modification of microbial communities, likely due to changes in micro-climate and substrate availability, resulting

in slower decomposition rates within the harvested gaps compared to the unharvested sites. Moreover, we observed notable effects of harvesting, disturbance, and time on CWM C concentrations, with large gaps showing the highest concentrations. This suggests that forest C sequestration could potentially be sustained in deadwood pools within managed areas by considering the severity of disturbance caused by the implementation of various adaptive management strategies. Additionally, these findings underscore the need for further investigation into the nuanced relationship between wood decomposition and disturbance.

Forest C cycling and sequestration are key concerns for forest managers and landowners when evaluating management approaches for future climate change scenarios. While it is widely acknowledged that unmanaged forests tend to store more C than managed ones, several adaptive management strategies have proven effective in maintaining and increasing current C stocks in both live and dead wood. Based on the findings from chapter three and existing literature, we recommend retaining CWM of varying sizes and decay classes on-site after harvesting to act as a near-term pool C pool, as we observed significant accumulations of C and N within the wood stakes over time. Together, notably higher C concentrations and slower decomposition rates in the large-gap sites suggests that canopy gap formation with deadwood retention might enhance the potential for forest C sequestration.

There are several opportunities to enhance our understanding of leaf litter and wood decomposition. Further research is required to investigate the interactions between the biotic and abiotic drivers of forest decomposition, particularly within the context of changing future forest dynamics. To build on our current findings, future studies should

continue experiments for longer time periods, including greater sample sizes with samples of varying sizes (e.g., logs), to assess impacts on the intermediate and later stages of decomposition for a better understanding of changing climates and associated adaptive management regimes in the long-term. Furthermore, A major limitation of our second study was a lack of micro-meteorological and fungal composition data, therefore, future studies should directly assess how interactions between micro-climatic conditions, specifically temperature and moisture, and the structure and composition of microbial communities are influencing patterns in wood decomposition rates and nutrient dynamics, especially in response to increasing disturbance severity. Overall, our research emphasizes the need for more comprehensive investigations of litter and wood decomposition across a wider range of disturbance severity gradients as most of our knowledge comes from stark contrasts between undisturbed and highly disturbed harvesting scenarios.

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