2023

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Maya Y. Chandar-Kouba
Bowdoin College

Recommended Citation

Chandar-Kouba, Maya Y., "How do long-term above-ground biomass dynamics vary between different forest stand types at Harvard Forest?" (2023). *Honors Projects*. 403.
https://digitalcommons.bowdoin.edu/honorsprojects/403

How do long-term above-ground biomass dynamics vary between different forest stand types at Harvard Forest?

An Honors Paper for the Department of Biology

Maya Y. Chandar-Kouba

Bowdoin College 2023

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ABSTRACT

Monitoring forest carbon storage is necessary in accurately modelling the global carbon cycle. In the Northeast, terrestrial forests represent a major carbon sink with above-ground biomass (AGB) accounting for 40% of stored forest carbon. Therefore, understanding how AGB varies spatiotemporally is essential in predicting future carbon storage. Repeated measurements in permanent, long-term plots provide an opportunity to examine how carbon stored in AGB is changing over time. I used 29 years of data from the Harvard Forest Environmental Monitoring Systems (HF EMS) Site to determine how stand composition, intrinsic factors, and extrinsic environmental factors influenced rates of carbon storage in AGB over time. Using a partition around medoids (PAM) clustering method, I separated the 34 ground plots at the EMS stand into their respective stand types. I found that each stand type at the HF EMS plots accumulates carbon at consistent rates throughout the study period, although rates of carbon accumulation between stands were significantly different. Red Pine stands experience a rapid decline in biomass in 2018 due to the introduction of the Southern Pine Beetle. Across all stand types, sporadic mortality events determine variations in yearly rates of carbon accumulation, although this has little significant influence on total AGB accumulation. Leaf area index (LAI) and foliar N contents have no effect on growth increments. Extrinsic environmental variables had mixed effects on growth and mortality, highlighting the complexities of predicting forest carbon storage under changing climate conditions.

INTRODUCTION

As climate change accelerates, understanding the nature of carbon sinks and sources has become a global priority. Terrestrial ecosystems account for a large part of the global carbon cycle, taking up about 120 Pg of carbon each year and respiring roughly the same amount back to the atmosphere (Urbanski et al. 2007, Duncanson et al. 2022). Recent attention has turned towards quantifying the carbon storage potential of the forests of the Northeastern United States (Finzi et al. 2020). The Northeastern landscape is dominated by second-growth forests, which have a high carbon storage potential (Urbanski et al. 2007). One component of carbon storage in terrestrial ecosystems is above-ground biomass (AGB), defined as all living biomass that remains above ground (Schuster et al. 2008). AGB accounts for about 40% of carbon stored in Northeastern forests (Finzi et al. 2020).

The Harvard Forest, a long-term ecological research site (LTER) in Petersham, MA, is one of the oldest managed forests in the Northeast (Finzi et al. 2020). Since 1907, the Harvard Forest has served as a research center for students and foresters alike and is now considered to be one of the most studied forests in the world (Urbanski et al. 2007). Three decades of AGB monitoring at the Harvard Forest Environmental Measuring Systems (HF EMS) Site has resulted in an extensive data record. Following my completion of the 2022 field season at Harvard Forest, where I collected annual data records for the HF EMS Site, I gained access to the 29 years of field and atmospheric data from the site. This data allows me to analyze AGB accumulation over time and how accumulation differs among forest stand types, determined by the composition of dominant canopy tree species. Breaking this forest into its stands allows me to understand the relative contributions of each stand type to the total carbon storage in a forest. In addition, the extensive field record at the HF EMS Site allows me to test the effects of various intrinsic factors—including canopy structure and leaf biochemical composition—and extrinsic factors—changing precipitation, temperature, drought, snowpack, and growing season length—on AGB accumulation among stand types.

The magnitude of AGB carbon storage in terrestrial ecosystems tends to fluctuate over time (Schuster et al. 2008). The AGB of a forest can be calculated using the following formula:

$$AGB = \text{growth of living stems} + \text{recruitment} - \text{mortality}$$

Variations in AGB carbon storage can stem from forest attributes including age, species composition, and environmental conditions (Urbanski et al. 2007). It is generally accepted that yearly rates of carbon sequestration in forest AGB, also called aboveground woody increment (AGWI), are high in early successional stages but will eventually peak and decline as the forest ages (Xu et al. 2012, Berger et al. 2004). This peak and decline of AGB has been observed in temperate forests with a similar age and species composition to the Harvard Forest (Schuster et al. 2008, Berger et al. 2004).

Age-related declines in carbon sequestration in AGB have been attributed to a decrease in the growth increment of living stems, an increase in mortality, or both (Xu et al. 2012). In addition, tree species with different physiologies possess different AGB dynamics over time (Schuster et al. 2008, Yuan et al. 2021). For example, Schuster et al. (2008) found that stands at the Black Rock Experimental Forest, a scientific field station in Cornwall, New York, with canopies dominated by highly productive tree species, such as red oak (*Quercus rubra*), accumulated AGB at twice the rate of other stand types. Finally, climate change can also influence aboveground biomass dynamics by potentially increasing or decreasing the living stem increment, mortality, and recruitment (Urbanski et al. 2007). At the HF EMS Site, a study conducted by Urbanski et al. (2007) found that only 40-50% of the variation in annual net ecosystem exchange (NEE), or the exchange of carbon between the atmosphere and canopy, at the EMS site could be explained by climate and seasonality and conclude that changes to NEE depend on differences in underlying stand physiologies. This is supported by additional research conducted at the Harvard Forest by Bassow and Bazzaz (1998), who found that differing tree species respond differently to inter-annual variations in environmental variables. Understanding how these factors influence carbon storage in AGB is essential to understanding the long-term dynamics of carbon sequestration in forests.

Mortality can decrease annual AGB increment through the removal of biomass due to stem death, in addition to potential damage to neighboring trees resulting in the slowed growth of damaged trees (Xu et al. 2012). Previous studies have found that the mortality of large, dominant trees is the primary factor driving the decline of AGB accumulation in ageing forest stands (Xu et al. 2012) and has been found to periodically have a greater influence than living biomass increment in some old-growth forests (Schuster et al. 2008). However, mortality is often noted to be sporadic due to abiotic and biotic stressors (Schuster et al. 2008, Berger et al. 2004, Urbanski et al. 2007). Penderson et al. (2020) found that large trees are most susceptible to the effects of extreme climate events and biotic influences, including pest outbreaks, and therefore have a high potential to determine forest AGB dynamics (see also Bond 2000).

Another factor contributing to the peak and decline of forest AGB accumulation is reductions in forest net primary production (NPP), or the decline in growth rates of individual trees (Xu et al. 2012). Berger et al. (2004) state that the age-related decline in AGB production is a result of the logistical growth curves of individual trees, which arises from physiological constraints. These constraints include imbalances to the photosynthesis-respiration ratio, nutrient limitations, hydraulic resistance, and reduced energy allocation to stem production (Xu et al.

2012, Berger et al. 2004, Gower et al. 1996). It is important to note that these physiological constraints arise from an increase in the size of the tree and not necessarily the tree's age, although the two are tightly correlated (Bond 2000, Forrester 2021). Studies examining the impact of age-related decreases in stem growth on AGB dynamics have yielded mixed results. Some studies have found that decreasing stem production is the primary factor driving AGB decline (Thompson et al. 2011) while others state that decreased tree production has a negligible effect on forest ecosystem dynamics (Xu et al. 2012, Forrester 2021). In addition, different tree species have varying rates of photosynthesis, resulting in different growth rates. For example, Bassow and Bazzaz found that under light saturated conditions, red maple has significantly lower rates of photosynthesis than red oak or birch species (1998).

While there is a wide variety of factors that can influence stand-level AGB accumulation, these factors can be separated into two broad categories: intrinsic and extrinsic factors. Intrinsic factors are species-specific factors that have the potential to influence AGB accumulation and include canopy structure and leaf biochemical composition. Extrinsic factors can be defined as environmental conditions which can also influence AGB accumulation and vary interannually. Extrinsic factors include temperature and precipitation, in addition to their interactive effects, and the introduction of pests and pathogens. Below, I describe how both intrinsic and extrinsic factors influence rates of AGB accumulation among stand types.

Intrinsic Factors

In addition to changes in AGWI, decreases in the NPP of living trees can be investigated through changes to both leaf nitrogen contents (percent N) and leaf area index (LAI), where LAI is defined as the amount of leaf cover per unit of ground area (m^2/m^2). Over time, the photosynthetic capacity of trees decreases because of 1) the lowered photosynthetic capacity of individual leaves and 2) reductions in foliage (Urbanski et al. 2007). Foliar N content is the primary determinant of individual leaf photosynthetic capacity (Reich et al. 1995, Bartlett et al. 2011). In C3 plants, the relationship between photosynthesis (or A_{max}) and foliar N is linear, and the slope varies based on the leaf area of individual tree species (Reich et al. 1995). As trees age, leaf N content begins to decline, which could be the result of physiological constraints or decreased nitrogen availability due to nitrogen immobilization in coarse and standing woody debris (Bond 2000, Flaxa-Raymond et al. 2012).

In addition to foliar N content, LAI is an important determinant of overall productivity is because leaf area is associated with photosynthesis, respiration, and transpiration (Nunes et al. 2013, Binkley et al. 2002). Once LAI reaches a maximum, it is postulated that net productivity in a forest is also reached (Urbanski et al. 2007). At the forest level, LAI has been shown to have a strong correlation with total biomass (Cavender-Bares et al. 2000). In addition, the timing of peak annual LAI is closely related to phenology and rates of annual carbon accumulation. (Savoy and McKay 2015). However, LAI is sensitive to mortality, since tree death removes the leaf area of the dead tree and could potentially damage neighboring trees (Xu et al. 2012). LAI can also respond to extrinsic factors, as LAI has been found to be influenced by both soil nutrient availability and environmental stressors (Cramer et al. 2000).

Extrinsic Factors

Environmental factors have the potential to influence patterns of growth in forest ecosystems (Urbanski et al. 2007). Individual trees will acclimate to environmental conditions at the leaf level by adjusting stomatal conductance and rates of photosynthesis, which has impacts for tree-level growth (Levesque et al. 2017). Global environmental change is predicted to alter previous patterns in environmental factors—most notably patterns of temperature and precipitation. The interactive effects of changing temperature and precipitation patterns have resulted in emergent properties including changes to yearly growing seasons, winter snowpack depth, and drought stress. In addition, climate change has significant implications for the spread of invasive pests and pathogens. Due to the complexity of these changes to environmental variables, the magnitude of change in AGB accumulation due to global environmental change is poorly described (Penderson et al. 2020, McGregor et al. 2020). Part of this uncertainty stems from differences in the sensitivities and responses of different tree species in various geographical locations to changing climate conditions (Penderson et al. 2020, Bassow and Bazzaz 1998). Therefore, my study aims to decouple the direct and interactive effects of climate change on stand-level AGB accumulation, which will allow for better understanding of future trends of AGB accumulation under climate warming scenarios.

Interannual variations in environmental variables can influence AGB accumulation by inducing stressful or beneficial conditions to facilitate tree growth and survival. One such variable is precipitation, as roughly 40% of all terrestrial plants are limited by access to water (Liu et al. 2013). In the Northeastern United States, precipitation events have increased in frequency and intensity due to reductions in the intensity of the jet stream, a result of increased ocean temperatures (Guilbert et al. 2015). This has resulted in an increase of 10 mm of precipitation per decade in the Northeastern United States (Guilbert et al. 2015). Wetter growing season conditions are positively correlated with stomatal conductance and photosynthetic activity, which increases the growth of individual trees (Levesque et al. 2017). Levesque et al. (2017) found that moisture was the primary determinant of the radial growth of various broadleaf species in Northeastern temperate forests. This observation was supported by Heilman et al. (2021), who found that since the 19th century, tree ring growth has been positively related to the amount of water year precipitation. Additionally, Turnbull et al. (2002) found that trees of the same species in stands with varying soil water availabilities had significantly different A_{max} and photosynthetic nitrogen use efficiency (PNUE) values, with trees in drier environments having lower photosynthetic rates.

Temperature trends in the Northeast are predicted to increase, with the potential to either facilitate plant growth in regions constrained by cold temperatures or induce heat stress. Data from the Hubbard Brook Experimental Forest, a temperate Northeastern forest in central New Hampshire, shows an increase in air temperature of 1°C over the past 50 years (Camel et al. 2010). This temperature increase during the growing season is predicted to increase rates of AGB accumulation by 13.5% (Thompson et al. 2011). In climate scenarios where temperature was elevated but water was not limiting, forest productivity has been found to increase (Boisvenue and Running 2006). At the Harvard Forest Long-Term Ecological Research Site (HF LTER), studies have failed to correlate air temperature changes to ecosystem responses (Urbanski et al. 2007). However, this research did not decouple productivity responses to air temperature by forest stand type, and therefore doesn't account for different responses among tree types (Urbanski et al. 2007). For example, cool temperatures have been found to constrain conifers, but this effect is specific to the northern end of their ranges (Penderson et al. 2020). Thompson et al. (2011) found that increased air temperatures reinforced the productivity and dominance of *Pinus strobus* and *Acer rubrum* in forests across Western Massachusetts.

Changes to precipitation and temperature patterns in the Northeastern United States are predicted to alter the intensity and duration of drought stress during the spring, summer, and fall seasons (van Kampen et al. 2022). In conditions where temperatures are elevated and water is limiting, drought stress arises and negatively impacts tree growth (Penderson et al. 2020).

Despite annual increases in precipitation, rising temperatures are anticipated to increase the prevalence of moderate drought stress in these temperate forests (van Kampen et al. 2022). While the magnitude of drought stress experienced in the Northeastern US is less severe than Western droughts, many trees in the Northeast are not well adapted to any levels of drought (van Kampen et al. 2022). Therefore, the increasing prevalence of drought stress is predicted to negatively impact the AGB accumulation of forest stands in the Northeastern USA (van Kampen et al. 2022, D'Orangeville et al 2018). However, the large variety in drought-related changes to forest ecosystems makes the magnitude of change difficult to quantify (McGregor et al. 2020). Drought stress has the potential to impact annual AGB increments and rates of mortality (Schuster et al. 2008). Studies conducted at the Black Rock Forest found that abnormally dry years led to high mortality (Schuster et al. 2008, Xu et al. 2012). While rates of carbon accumulation have been shown to decrease due to drought stress, the timing of drought influences reductions in AGWI. Van Kampen et al. (2022) found that species were most sensitive to seasonal droughts that occurred around the time of their heaviest growth rates. For example, white pines were found to respond most negatively to spring droughts, which is when the majority of their diameter and height growth occurs (Van Kampen et al. 2022).

Differences in the physiologies of tree species can result in drought stress responses of various magnitudes (Levesque et al. 2017, McGregor et al. 2020). McGregor et al. (2020) found that drought tolerant species were those that resist wilting until leaf water content reaches comparatively low levels. In addition, broadleaf trees in temperate forests have been found to be more sensitive to drought stress due to high leaf area and large crown area (Levesque et al. 2017). Older, larger trees in forest ecosystems will be more susceptible to drought stress due to increased canopy exposure and height (McGregor et al. 2020). However, this effect could be counteracted by the increased size of root systems in larger trees, which allows access to deeper water reservoirs (McGregor et al. 2020).

Climate change is predicted to alter winter climate dynamics by increasing air temperatures and increasing the proportion of precipitation falling as rainfall instead of snow (Campbell and Laudon 2019, Boisvenue and Running 2006). In temperate regions which are characterized by cold winters with freezing air temperatures and snow cover, the effects of changing winter climates have the potential to influence forest dynamics (Campbell and Laudon 2019). These climate changes have caused a decline in snowpack depth and snow cover period (Campbell and Laudon 2019). These trends were observed at the Hubbard Brook Experimental Forest, where maximum snow depth, snow-water equivalent, and snow cover duration declined over the 50-year period (Camel et al. 2010). However, in Northern temperate forests, the mechanisms by which winter climate impacts forest productivity are widely understudied (Campbell and Laudon 2019).

This reduction in snow cover and decrease in snowpack depth is predicted to increase soil freezing as snowpacks have been found to insulate soils at a snowpack depth of 20-40 cm (Campbell and Laudon 2019, Camel et al. 2010). Increased soil freezing damages roots, as studies have found that removing snow cover in forests doubled fine root mortality (Camel et al. 2010, Campbell et al. 2019). Shallow snowpack depths have been found to increase the number of freeze-thaw cycles in forest soils that occur during the winter, causing nutrient leaching in the spring (Campbell et al. 2019). Temperate forests are some of the world’s most carbon rich ecosystems, and therefore the negative effects of changing winter climate can have serious implications for regional carbon storage rates (Campbell and Laudon 2019, Penderson et al. 2004). The effects of changing winter climates are likely to differ between tree species due to variations in physiological characteristics. For example, conifer species can perform photosynthesis during the winter when their leaves are not frozen, while deciduous trees are unable to photosynthesize (Penderson et al. 2004). However, maintaining foliage in conifers makes them more sensitive to winter-time damage (Penderson et al. 2004).

As global temperatures have increased, growing season lengths have also expanded (Urbanski et al. 2007). Therefore, the growing season should not be defined as fixed dates, but instead use biologically relevant markers, such as snow cover, NPP thresholds, and plant phenological phases to indicate the start and end of the growing season (Campbell and Laudon 2019). NPP thresholds are defined as the point during the year when NPP reaches a specified percent of the maximum NPP value for that year (Finzi et al. 2020). Applying this method of defining the start and end of the growing season reveals that growing season lengths in the Northeast have increased by 3-6 days every decade over the past 30 years (Campbell and Laudon 2019). An increase in growing season length has been shown to drastically increase plant productivity, as maximum NPP rates are often constrained by growing season length (Campbell and Laudon 2019). However, Swidrak et al. (2013) found that different tree species exhibit divergent phenological patterns under the same growth conditions, indicating that growing season length will differ by tree species. Understanding the magnitude of change to AGB accumulation caused by increased growing seasons is necessary in order to predict how carbon storage in forests will change in coming years (Urbanski et al. 2007).

Both anthropogenic climate change and increased global connectivity can facilitate the spread of invasive pests and pathogens through range shifts and international exchanges. The primary forest pests impacting the Harvard Forest are the Hemlock Wooly Adelgid and the Southern Pine Beetle. Hemlock Wooly Adelgid was introduced to the United States in 1951 and induces mortality in Hemlock trees in 4 to 11 years by inserting their mouthparts into the xylem and feeding on the trees' sap (Dukes et al. 2009). The Southern Pine Beetle moved into the Northeast in 2018, although it was previously constrained to Southern regions due to temperature limitations. These beetles burrow into the cambium of trees, forming galleries which disrupts nutrient flow in trees, killing them in 2 to 4 months (Aoki et al. 2022). Pests impact AGB accumulation differently based on stand composition. Mates-Munchin et al. (2006) found that in stands dominated by tree species impacted by a pest, total AGB declined. However, in mixed stands, other non-affected trees were able to increase their growth increment due to reduced resource competition (Mates-Munchin et al. 2006).

Given the potential influences of intrinsic and extrinsic factors on AGB accumulation, I designed a study to further my understanding of forest AGB. To gain a comprehensive understanding of AGB dynamics at the HF EMS Site, the following questions drive my study: 1) How does carbon storage in AGB at the HF EMS Site change over time, and how does this differ between stand types? 2) What are the relative contributions of mortality and living stem growth to AGB across stand types? 3) How does leaf biochemical composition and canopy structure differ between stand types? And 4) How does interannual variability in environmental variables affect the relative contributions of living stem growth and mortality to AGB between stand types?

METHODS

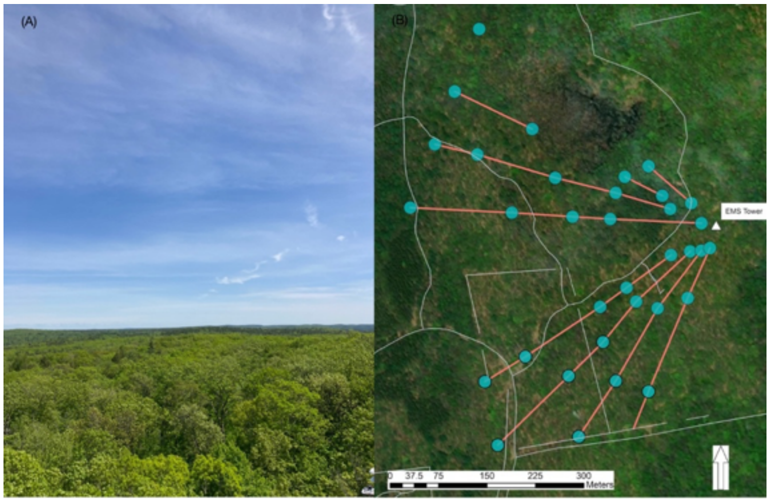


Figure 1: a) View from atop the HF EMS Site b) Aerial view of the HF EMS fetch, with blue circles designating each of the 34 HF EMS plots.

Study area and field work

The Environmental Monitoring Systems (HF EMS) Site at Harvard Forest is a 1.04-ha forest plot dominated by Red Oak (*Quercus rubra*) and Red Maple (*Acer rubrum*) stands, with scattered White Pine (*Pinus strobus*), Hemlock (*Tsuga canadensis*), and Red Pine (*Pinus resinosa*) stands (Urbanski et al. 2007). The forest is 75-110 years old, as most of the forest was destroyed by the hurricane blowdown of 1938 (Urbanski et al. 2007). In 1989, a central eddy-flux covariance tower was installed, and in 1993, 40 plots, each with a 10-meter radius were established surrounding the eddy-flux tower. Each plot is randomly placed along one of eight transects that fall along prevailing wind directions. At the HF EMS Site, net CO_2 exchange, fluxes of latent and sensible heat, and other meteorological variables have been measured at the central eddy-flux tower. Plot-level measurements include dendrometer surveys, leaf litter input, leaf area index, mortality, recruitment, and coarse woody debris inputs. Together, these atmospheric and ground-based measurements build an understanding of carbon cycling at the HF

EMS site. Since 1993, 6 HF EMS plots have been removed due to the expansion of a nearby beaver swamp.

Partition around mediods (PAM) Clustering

The 34 HF EMS plots were classified into one of five different stand types—Red Oak dominated stands, Red Maple dominated stands, Red Pine dominated stands, Red Oak and Red Maple mixed stands and White Pine and Hemlock mixed stands—based on a cluster analysis (PAM function) of the species biomass for each plot at the start of the study period (1993). Dominant stands were identified as stands where the biomass of one species is greater than 70% of total biomass. Mixed stands were identified as stands where the biomass of two or more species is greater than 70% of total biomass, and each tree species is greater than 25% of total biomass.

Dendrometer Surveys

In each of the 34 plots, dendrometer surveys are conducted multiple times each growing season. Dendrometer surveys are performed from April to October, and have been conducted since 1993, with a break from 1994 to 1997. Each individual tree in the ground-plots over 10 cm in DBH is fitted with a flexible stainless steel dendrometer band that expands to accommodate bole expansion. Digital calipers are used to measure the distance between two points on the dendrometer band, which is then converted to diameter at breast height (DBH, cm) using an iterative process (Fatemi et al. 2011, McMahon and Parker 2014). Species and regional-specific allometric equations are used to convert DBH into total tree biomass (kg of carbon) (Jenkins and Chojnacky 2004, Smith and Brand 1983). These allometric equations do not account for stumps, roots, and understory vegetation. Trees that recruit into the minimum size class (10 cm DBH) are fitted with a new stainless steel dendrometer band and the initial DBH is recorded using DBH tape. Dead trees are identified as trees with no or only dead foliage for two consecutive measurements, and have their dendrometer band removed. Trees that have survived for the entire duration of the study period (1993 to present) are labelled as living stems.

Standing Woody Debris and Coarse Woody Debris

Mortality loss from the AGB carbon pool includes all trees that died during the observation period. This includes two classes of dead wood: standing woody debris (SWD) and coarse woody debris (CWD). SWD is defined as dead wood with a DBH greater than 10 cm that has a vertical leaning angle of less than 45 degrees, and includes whole trees, snags, and stumps. To compute the biomass of SWD, stump diameter, DBH, top diameter, and decay class are assessed. Decay class is assessed on a 1-5 scale and is determined using tactile factors including friability and texture (Liu et al. 2006). In each ground-level plot, all occurrences of SWD are recorded. CWD includes fallen woody debris with a diameter greater than 7.5 cm. Two perpendicular diameter measurements are recorded using manual calipers, in addition to decay class. Decay class is assigned through visual and tactile observations to determine relative wood density as the wood decays. The decay class is factored into species-specific allometric equations to calculate the biomass of dead logs.

Foliar N Content

Canopy leaves were collected during the summers of 1998-2000 and 2006-2022 at the HF EMS plots. Canopy leaf samples were collected using a shotgun until 2017 and are now collected using a traditional arborist line launcher. Samples were dried at 65 degrees C for three days, ground to a fine powder using a ball mill, and loaded into tin capsules to be analyzed. Samples from 1998-2000 were analyzed using a Fison Nitrogen Analyzer NA 1500 and samples from 2006-2014 and 2018-2019 were analyzed using an Elementar Vario Micro CHNS analyzer at Harvard Forest. Samples from 2014-2017 were analyzed at the Laboratory of Jennifer Bhatnager at Boston University. Leaf samples were analyzed for percent carbon, percent nitrogen, and C/N ratio. Samples were referenced against acetanilide standards.

Leaf Area Index (LAI)

Leaf area index (LAI) data was collected in HF EMS ground plots in 1998-1999, and every year since 2005. LAI describes the ratio of one-sided leaf area in one unit of ground area (m^2/m^2). These measurements are taken bi-weekly in the spring and fall and monthly during the summer. Five LAI measurements were taken using a LiCOR LAI2000 sensor: once at the plot center and four additional measurements 2 meters from the center in each of the four cardinal directions. Plot-level LAI is calculated by taking the average of these 5 measurements. Each measurement was made under diffuse light conditions.

Environmental Monitoring

Air temperature and precipitation were recorded at the Shaler meteorological station from 1964 to 2000, and at the Fisher Meteorological station from 2001 to 2022. The Shaler meteorological station recorded daily minimum temperature, maximum temperature, and total precipitation. Instruments, including thermometers and rain gages, were supplied and maintained by NOAA. The Fisher Station records air temperature, relative humidity, precipitation, the water equivalent of snow (SWE), and soil temperature (at a 10 cm depth. Each instrument scans once per second. 15 minute and daily values are calculated and stored using datalogger.

Snowpack data was recorded 50 m north of the Nelson Brook Big Wier, about 1.5 miles North of the HF EMS Site (Boose 2022). Trees were removed to create a 15 m opening in the canopy, and leaf litter and organic soil were removed and replaced with sand to create a level surface. A snow pillow (rubber, 3 m diameter) is installed on the level surface. A pressure transducer provides continuous measurements of the mass of snow on the snow pillow. This sensor is scanned every 10 seconds and 15-minute average values are stored. During the start of the 2014-2015 snow season, the snow pillow was damaged and therefore snow records were determined by measuring snowpack depth with snow stakes at the HF EMS tower.

The growing season length was calculated using similar methods to Finzi et al. (2020). Annual net ecosystem productivity (NEP) values, defined as the difference between gross ecosystem photosynthesis and respiration, were collected as the 12-minute averages of measurements taken every 4.8-minutes from the central eddy-flux covariance tower at the HF EMS Site. The start of the growing season was identified as the first day where NEP exceeded 30% of the maximum NEP value for that year, and the end of the growing season was identified as the first day where NEP dropped below 30% of the maximum NEP value. The growing season is defined as the length of time, in days, between these two dates.

Drought levels at the Harvard Forest were evaluated using two different indexes a self-calibrated Palmer Drought Severity Index (scPDSI) and the U.S. Drought Monitor for Worchester County. The PDSI scale ranges from –10 to +10, with negative values representing abnormally dry to severely dry conditions and positive values representing abnormally wet to severely wet conditions. PDSI is calculated relative to historical precipitation and temperature data. Therefore, this scPDSI is calculated relative to precipitation and temperature data from the past 30 years at the Fisher Meteorological station. Using the Thornthwaite method via the climdex.pcic R package (v1.1.11; Bronaugh 2020) monthly average temperatures were used to calculate potential evapotranspiration values (PET). PET and cumulative monthly precipitation (mm) were used to calculate the monthly water balance and soil moisture index (SMI) at Harvard

Forest. Both monthly water balance and SMI are used to calculate monthly PDSI values (Palmer 1965).

The U.S. Drought Monitor evaluates levels of drought, as opposed to dry and wet conditions. This index ranges from None (no drought) to D0-D4 (abnormally dry to exceptional drought) and is calculated based on current temperature, soil moisture, and water availability (NOAA, NIDIS). Data from the U.S. Drought Monitor are presented as the percent area of Worchester County experiencing the five different levels of drought. Weekly drought values at Harvard Forest were estimated as the drought index value that the greatest percentage of the county experienced that week. For example, if 25% of the county experienced D0 conditions and another 25% of the county experienced D1 conditions, but 50% of the county experienced D2 conditions, the drought index value for that week would be D2.

Statistical Analyses

Calculations and analyses were performed in R version 4.0.2. All error bars are representative of one standard deviation of the mean. Linear models were used to analyze trends of AGB accumulation, mortality, and living stem growth over time. ANCOVAs were used to determine whether carbon storage and flux trends were significantly different between different forest stand types. Significance thresholds were set at $p < 0.05$. ANCOVAs were used to analyze the linear relationship between both AGWI and mortality and variables related to forest structure and environmental variables. Stand type was analyzed as a predictor variable.

RESULTS

AGB, Living Stem Growth, and Mortality Trends Over Time

i. Site-Wide Trends in AGB Accumulation

Above-ground biomass accumulation (Mg C / ha) at the HF EMS site showed a steady increase from 1993 to 2022 (Fig. 1a, linear model, $R^2 = 0.94$, $p < 0.001$). However, in 2018, a sharp decline appears in AGB. AGB accumulation differs significantly among the stand types present at the HF EMS Site (Fig. 1b). Red Oak/Red Maple, Red Oak, Red Maple, and White Pine and Hemlock stands are significantly fitted to linear models (Table 1, $p < 0.001$) and followed a constant rate of increase in AGB from 1993 to 2022 (Table 1, $R^2 = 0.68\text{-}0.99$). Red Pine dominated stands increased steadily from 1993 to 2017 (linear model, $R^2 = 0.94$) but experienced a sharp decline in biomass in 2018. This sudden decline was the primary driver of the rapid AGB decline at the HF EMS Site in 2018 (Fig. 1a) and has been attributed to the introduction of the Southern Pine Beetle, a pest that causes rapid red pine mortality (Lesk et al. 2017). Prior to 2018, rates of AGB accumulation among all five stand types were significantly different (Table 2, ANCOVA, $p < 0.001$). Therefore, forest stand type is a significant predictor of rates of AGB accumulation at the HF EMS site.

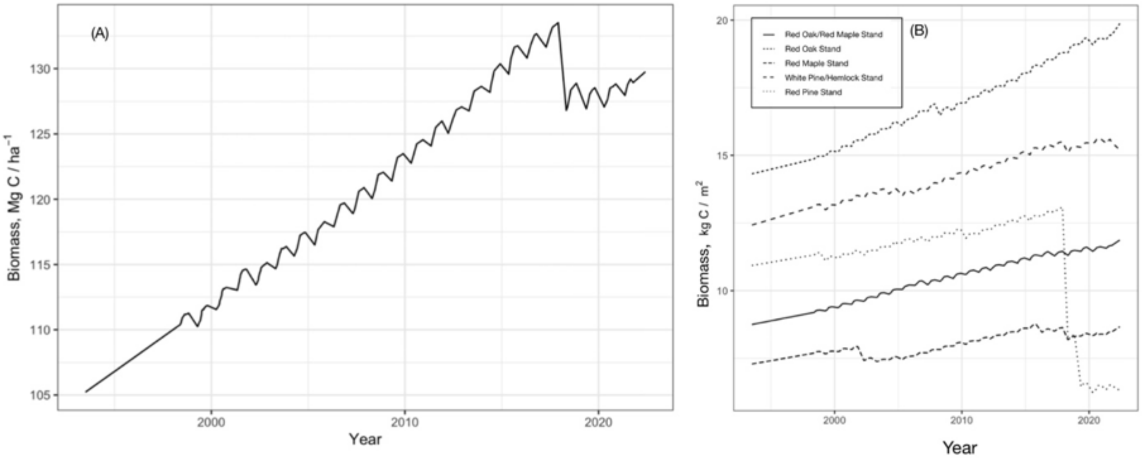


Figure 2: a) Aboveground biomass (AGB) in at the HF EMS Site from 1993-2022. b) AGB of the five forest stand types present at the HF EMS Site. AGB accumulation over the duration of the study period is significantly different between stand types (ANCOVA, $p < 0.001$)

Table 1: Linear Regressions for HF EMS Site and different Stand Types

Linear Regression	**Slope**	**R^2 value**	**p-value**
HF EMS AGB	0.0026x	0.94	< 0.001
Red Oak/Red Maple Stand	3 x 10^{-4x}	0.99	< 0.001
Red Oak Stand	5.4 x 10^{-4x}	0.99	< 0.001
Red Maple Stand	1.1 x 10^{-4x}	0.68	< 0.001
Hemlock/White Pine Stand	3.1 x 10^{-4x}	0.98	< 0.001
Red Pine Stand (1993-2017)	2 x 10^{-4x}	0.94	< 0.001
Red Pine Stand (2018-present)	-0.0014x	0.58	0.544

Table 2: ANCOVA

ANCOVA	**Model**	**p-value**
AGB over time	Model 1	**< 0.001**
	Model 2	< 0.001

ii. Long-Term Trends of Living Stem Growth and Mortality

The growth of surviving trees at the HF EMS site exhibited steady linear increases over time in all stand types (linear model, Fig. 3b). The total carbon stored in the AGB of living stems was significantly correlated with time in a linear model (Fig 3b, $p < 0.001$), in all stand types at the HF EMS site except for Red Pine dominated stands ($p = 0.21$). Stand type was identified as a significant predictor of living stem growth over time (ANCOVA, $p < 0.001$). Mortality across all stand types at the HF EMS Site tended to be sporadic and inconsistent, with no clear trends over time (Fig. 3c). Mortality was not correlated with time in a linear model across all stand types (Table 3, linear regression). One significant pattern that emerged is the sudden spike of red pine tree mortality in Red Pine dominated plots as described above.

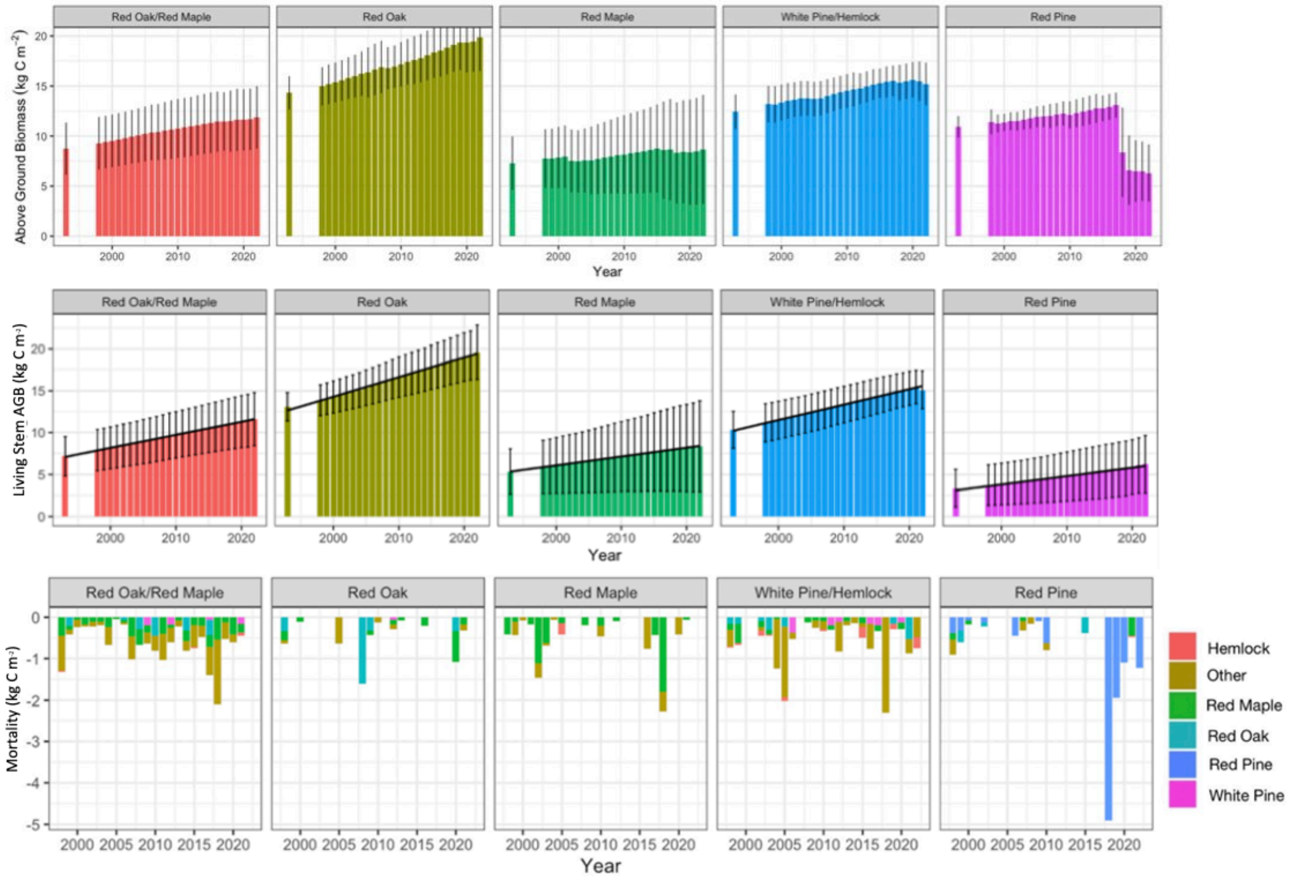


Figure 3: a) Cumulative above-ground biomass (kg C/m^2/year) for each forest stand type b) Carbon stored in the AGB of surviving trees (kg C/m^2) among forest stand types. Rates of AGB accumulation in surviving trees differ significantly between stand type (Table 3, ANCOVA, $p < 0.001$) c) Stand mortality (kg C/m^2) from 1998 to 2022 in each forest stand type.

Table 2: Linear Regressions for Living Stem Growth and Mortality in each stand type over time

Linear Regression	Type	Slope	R^2	p-value
Red Oak/Red Maple Stand	**Living Stem Growth**	0.16	1	**< 0.001 *****
Red Oak Stand		0.23	1	**< 0.001 *****
Red Maple Stand		0.10	1	**< 0.001 *****
White Pine/Hemlock Stand		0.18	0.99	**< 0.001 *****
Red Pine Stand		0.097	0.99	0.210
Red Oak/Red Maple Stand	**Mortality**	0.0047	0.053	0.278
Red Oak Stand		0.0037	0.0037	0.853
Red Maple Stand		0.0054	0.0013	0.673
White Pine/Hemlock Stand		0.0069	0.048	0.325

Red Pine Stand (1993-present)	0.073	0.24	0.061
Red Pine Stand (1993-2017)	0.002	0.0047	0.852

Table 3: ANCOVA

ANCOVA	**Model**	**p-value**
Living Stem Growth Increment over time	Model 1	**< 0.001*****
	Model 2	**< 0.001*****

Relative Contributions of Living Stem Growth and Mortality to stand AGB

i. Living Stem Growth Increments and Mortality Contribute to Variations in Stand-Level AGWI

To understand how both living stem growth increments and yearly mortality contributed to variations in plot-level AGWI, I plotted yearly living stem growth increments and mortality by AGWI for each HF EMS plot. Plot-level AGWI and living stem AGWI for Red Oak/Red Maple, Red Oak, Red Maple, and White Pine/Hemlock stands show a positive linear relationship across all stand types (Table 4, linear regression, $p < 0.001$), although the relationship between plot-level AGWI and living stem AGWI does not explain the large variances in data (Figure 4a). There was no significant linear relationship between plot-level AGWI and living stem AGWI in Red Pine stands (Table 4, linear regression, $p = 0.672$). The relationship between plot-level AGWI and living stem AGWI was significantly different among stand types (Table 5, ANCOVA, $p < 0.001$).

Plot-level AGWI and annual mortality show a negative linear relationship across stand types (Fig. 4b, Table 4, linear model, $p < 0.001$) with a strong correlation (Fig. 4b). Mortality values from 2018 in Red Pine dominated stands were excluded for visual clarity. The relationship between mortality and AGWI is not significantly different among stand types (Table 5, ANCOVA, p = 0.396).

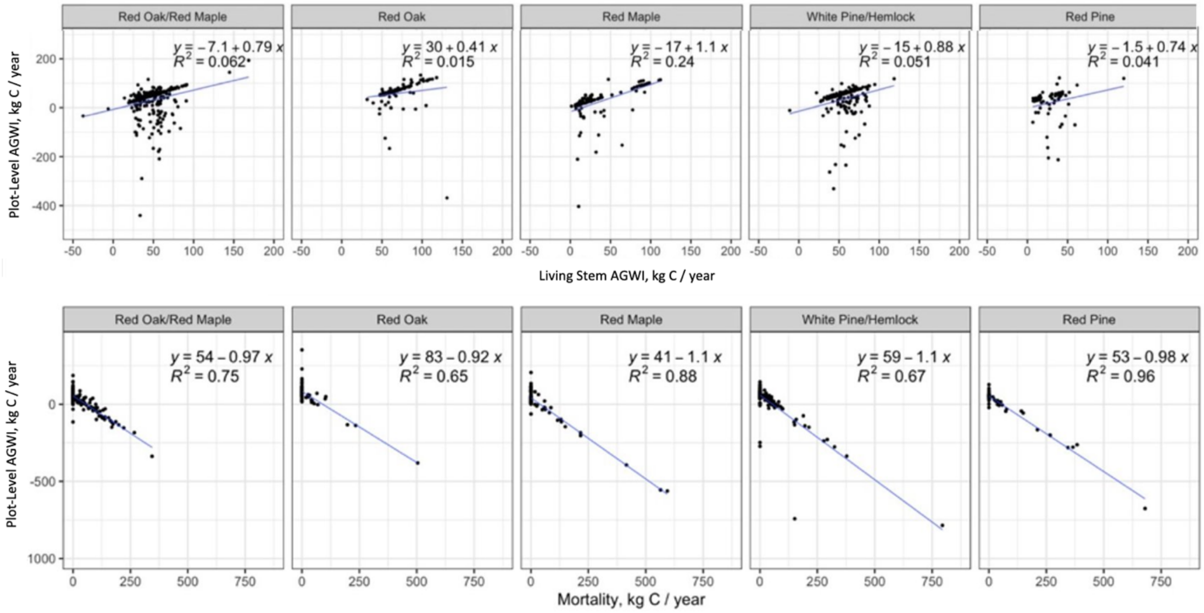


Figure 4: A) Relationship between the AGWI of living stems and AGWI. The relationship between living stem AGWI and plot-level AGWI differs significantly between stand types ($p < 0.001$) b) Relationship between plot-level mortality loss and AGB increment. The relationship between mortality and plot-level AGWI does not differ significantly between stand types ($p = 0.264$). Slopes and R^2 values are shown for each forest stand type, and p-values are included in Table 4.

Table 4: Linear Regressions for Living Stem Growth and Mortality versus AGWI

Linear Regression	Type	p-value
Red Oak/Red Maple Stands	**Living Stem Growth**	**< 0.001 *****
Red Oak Stands		**< 0.001 *****
Red Maple Stands		**< 0.001 *****
White Pine/Hemlock Stands		**< 0.001 *****
Red Pine Stands		0.672
Red Oak/Red Maple Stands	**Mortality**	**< 0.001 *****
Red Oak Stands		**< 0.001 *****
Red Maple Stands		**< 0.001 *****
White Pine/Hemlock Stands		**< 0.001 *****
Red Pine Stands		**< 0.001 *****

Table 5: ANCOVA

ANCOVA	**Model**	**p-value**
Living Stem Growth Increment v AGWI	Model 1	**< 0.001 *****
	Model 2	0.109
Mortality v AGWI	Model 1	0.264
	Model 2	**< 0.001 *****

ii. Living Stem Growth Increments and Mortality Versus Cumulative AGB

To understand how living stem AGB and annual mortality impact total AGB across stand types, I performed a similar analysis comparing the relationship between the AGB of living stems/mortality and total AGB in each HF EMS plot (Fig. 5a-b). While there is natural autocorrelation between total AGB and living stem growth/mortality, it is important to understand the magnitude of each factor on both AGWI and cumulative AGB. This will aid in anticipating how changes to living stem growth and mortality will affect carbon stored in forest AGB.

Living Stem AGB and total AGB have a strong positive linear relationship across Red Oak/Red Maple, Red Oak, Red Maple, and White Pine/Hemlock stands (Table 6, linear regression, $p < 0.001$). However, Red Pine stands have a negative correlation between living stem and total AGB in each plot (Table 6, linear regression, $p = 0.012$). The relationship between living stem and total AGB differs significantly between stand types (Table 7, ANCOVA, $p < 0.001$), indicating that stand type is a significant predictor of this relationship. Therefore, the AGB of living stems is a primary predictor of total AGB and varies across stand types present at the HF EMS Site.

However, a similar analysis comparing the relationship between annual mortality and plot-level AGB showed no linear correlation across stand types (Fig. 5b, Table 6, linear regression, p > 0.147). This lack of linear relationship between the two variables indicates that while mortality has a significant impact on rates of annual AGB gains (AGWI), mortality has little effect on overall stand AGB accumulation.

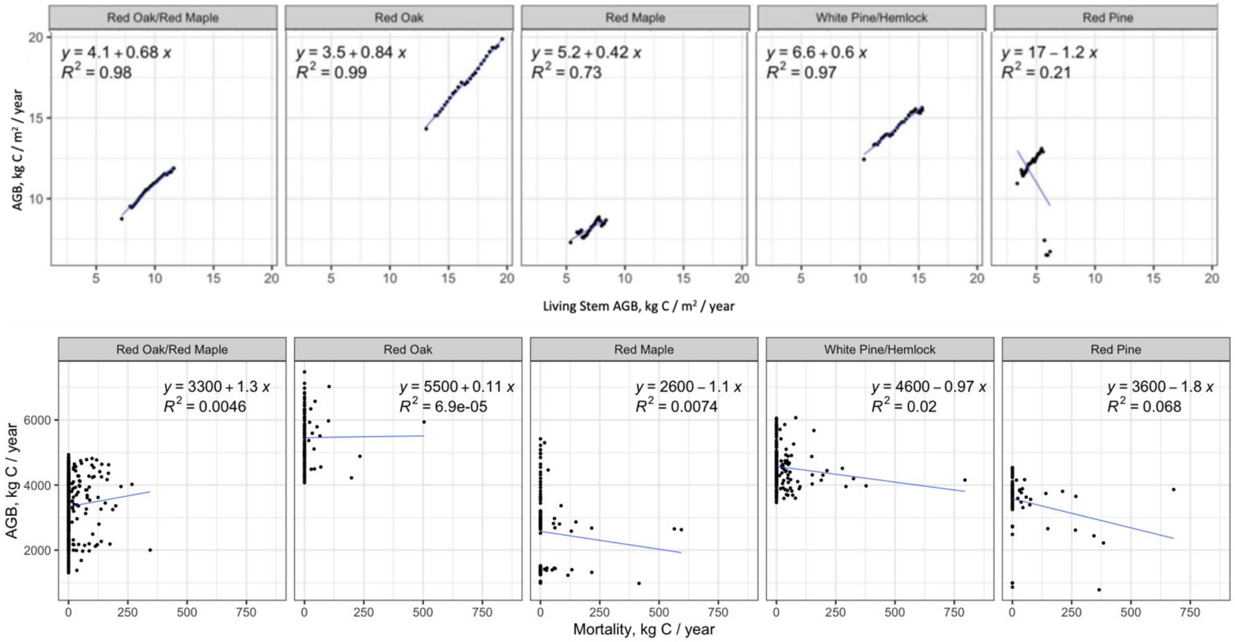


Figure 5: a) Relationship between the AGB of living stems and total AGB. The relationship between the AGB of living stems and total AGB differs significantly between stand types (ANCOVA, p < 0.001) b) Relationship between yearly plot mortality and total AGB. The relationship between mortality and total AGB does not differ significantly between stand types (ANCOVA, p = 0.319). Slopes and R^2 values are shown for each stand type, and p-values are found in Table 6.

Table 6: Linear Regressions for Living Stem Growth and Mortality versus Cumulative AGB

Linear Regression	**Type**	**p-value**
Red Oak/Red Maple Stands	**Living Stem Growth**	**< 0.001 *****
Red Oak Stands		**< 0.001 *****
Red Maple Stands		**< 0.001 *****
White Pine/Hemlock Stands		**< 0.001 *****
Red Pine Stands		**0.018***
Red Oak/Red Maple Stands	**Mortality**	0.966
Red Oak Stands		0.936
Red Maple Stands		0.989
White Pine/Hemlock Stands		0.893

Red Pine Stands	0.147

Table 7: ANCOVA

ANCOVA	Model	p-value
Living Stem Growth Increment v AGWI	Model 1	**< 0.001 *****
	Model 2	**< 0.001 *****

Canopy Structure and Leaf Biochemical Composition

i. Leaf Area Index

Leaf area index (LAI) values have been recorded in each plot at the HF EMS Site from 1997 to 1998 and 2004 to 2020 (Fig. 6). To understand the relationship between canopy structure (LAI) and yearly growth I analyzed the relationship between LAI and the AGWI of living stems using a linear model (Fig. 7a). Red Oak/Red Maple, Red Oak, and Red Maple stands show no linear correlation between LAI and living stem AGWI (Table 8, linear regression, $p > 0.153$). White Pine/Hemlock stands show a significant negative linear relationship between LAI and living stem AGWI (Table 8, linear regression, $p < 0.001$), and Red Pine stands show a significant positive linear relationship between LAI and living stem AGWI (Table 8, linear regression, $p = 0.026$).

To better understand how mortality events might be impacting LAI values through the removal of live leaf tissue, I analyzed the relationship between annual mortality and LAI for each EMS plot using linear regressions (Fig 7b.). None of the stand types present at the HF EMS Site show significant linear relationships between mortality and LAI (Table 8, linear regression, $p > 0.222$).

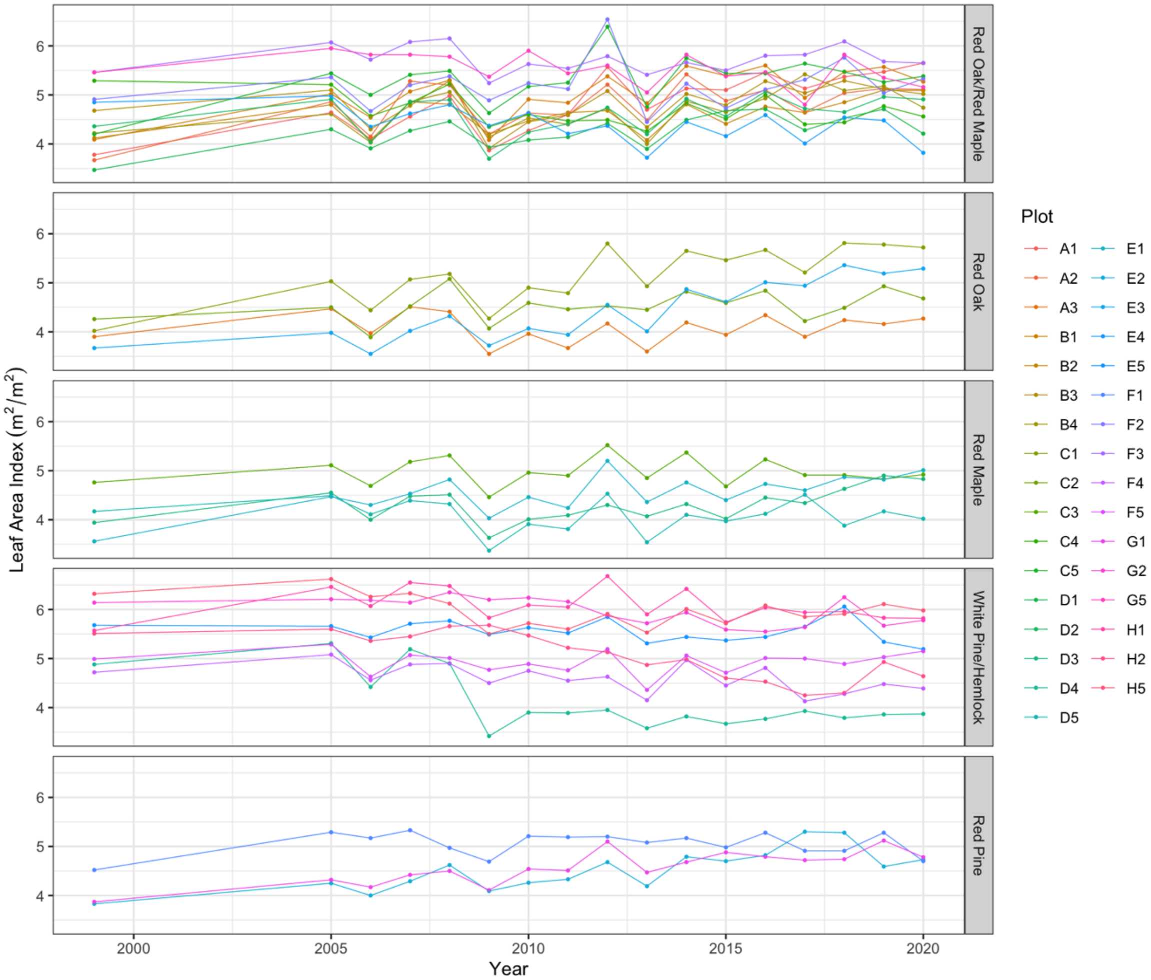
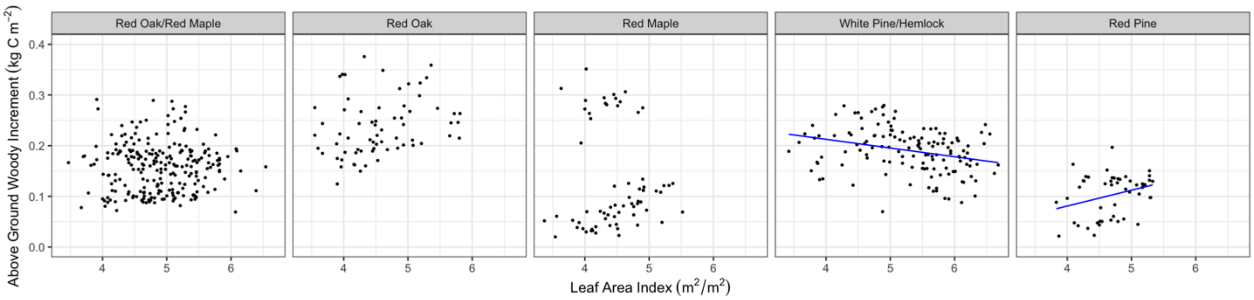


Figure 6: Peak plot-level LAI values from 1998, 1999, and 2005 to 2020.



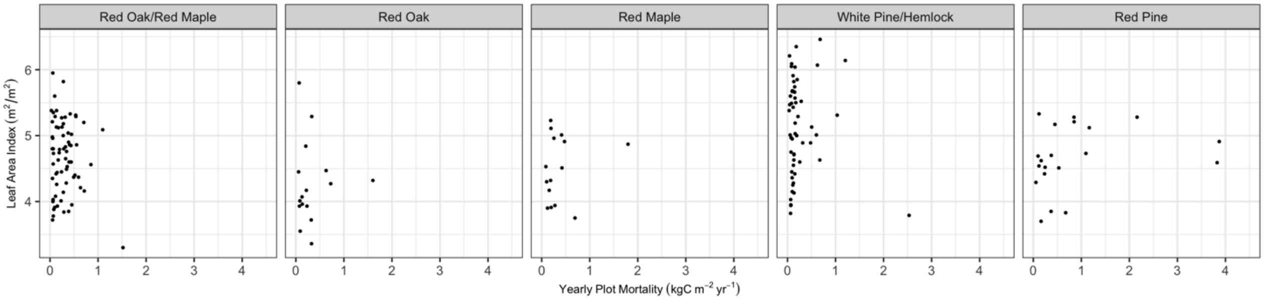


Figure 7: a) Relationship between Leaf Area Index (LAI) and the plot-level AGWI of living stems. B) Relationship between yearly plot mortality and LAI. R^2 and p-values for each stand type are found in Table 7.

Table 8: Linear Regressions for the relationship between LAI and living stem AGWI, and mortality and LAI

Linear Regression	**Type**	**R^2**	**p-value**
Red Oak/Red Maple Stands	**Living Stem Growth**	$1.3e^{-6}$	0.986
Red Oak Stands		0.031	0.153
Red Maple Stands		0.002	0.746
White Pine/Hemlock Stands		0.090	**< 0.001 *****
Red Pine Stands		0.097	**0.026***
Red Oak/Red Maple Stands	**Mortality**	0.022	0.222
Red Oak Stands		$5e^{-4}$	0.934
Red Maple Stands		0.029	0.541
White Pine/Hemlock Stands		0.004	0.649
Red Pine Stands		0.063	0.471

ii. Leaf Nitrogen Content

Over time, leaf nitrogen content in all major tree species at the HF EMS Site decreases (Fig 8, Table 9). Red maple and red oak tree species in Red Oak/Red Maple, Red Oak, and Red Maple stands have a significant quadratic relationship between foliar nitrogen content over time with a vertex around 2005 (Table 9, quadratic regression, $p < 0.001$). The foliar N content of white pine, hemlock, and red pine tree species decreases over time, but is not significantly correlated with a linear model (Table 9, linear regression, $p > 0.154$).

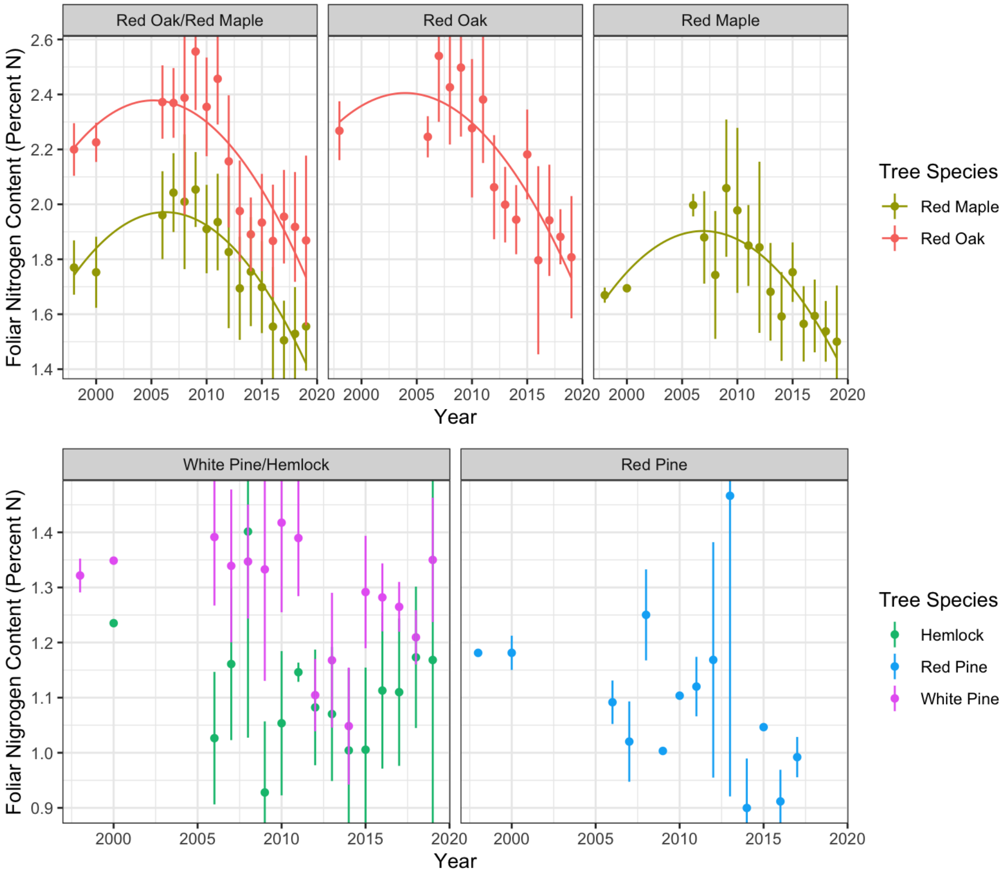


Figure 8: Foliar Nitrogen (percent N) contents of dominant tree species in each stand type present at the HF EMS site over time. Top row represents deciduous tree species, bottom row represents coniferous tree species. Equations, R^2, and p-values are found in Table 9.

Table 9: Quadratic and Linear Regressions of Foliar N content over time for major tree species at the HF EMS Site

Linear Regression	**Species**	**Regression Type**	**R^2**	**p-value**
Red Oak/Red Maple Stands	Red Oak	**Quadratic**	0.849	**< 0.001** ***
Red Oak/Red Maple Stands	Red Maple		0.712	**< 0.001** ***
Red Oak Stands	Red Oak		0.731	**< 0.001** ***
Red Maple Stands	Red Maple		0.720	**< 0.001** ***
White Pine/Hemlock Stands	White Pine	**Linear**	0.036	0.498
White Pine/Hemlock Stands	Hemlock		0.140	0.154
Red Pine Stands	Red Pine		0.100	0.270

Environmental Variables

i. Precipitation

Since 2001, yearly precipitation at the Harvard Forest (measured in mm of water) has averaged 1,235 mm each water year, with a standard deviation of 216 mm and a range of 907 to 1,830 mm (Fig. 9). To understand how water year precipitation affects AGB among different stand types, I analyzed the relationship of both living stem AGWI and mortality to cumulative water-year precipitation.

Across all stand types, there is no significant response of living stem AGWI to cumulative water-year precipitation (Fig. 10a, Table 10, linear regression, $p > 0.107$). Additionally, the relationship between precipitation and living stem AGWI is not significantly different across stand types (Table 11, ANCOVA, $p = 0.919$).

There is no significant response of annual mortality to water-year precipitation in Red Oak/Red Maple, Red Oak, or Red Maple stands (Fig. 10b, Table 10, linear regression, $p > 0.076$). However, in White Pine/Hemlock and Red Pine stands, there is a positive linear relationship between mortality and water year precipitation (Fig. 10b, Table 10, linear regression, $p < 0.017$). The relationship between mortality and water-year precipitation does vary significantly by stand type (Table 11, ANCOVA, $p < 0.001$).

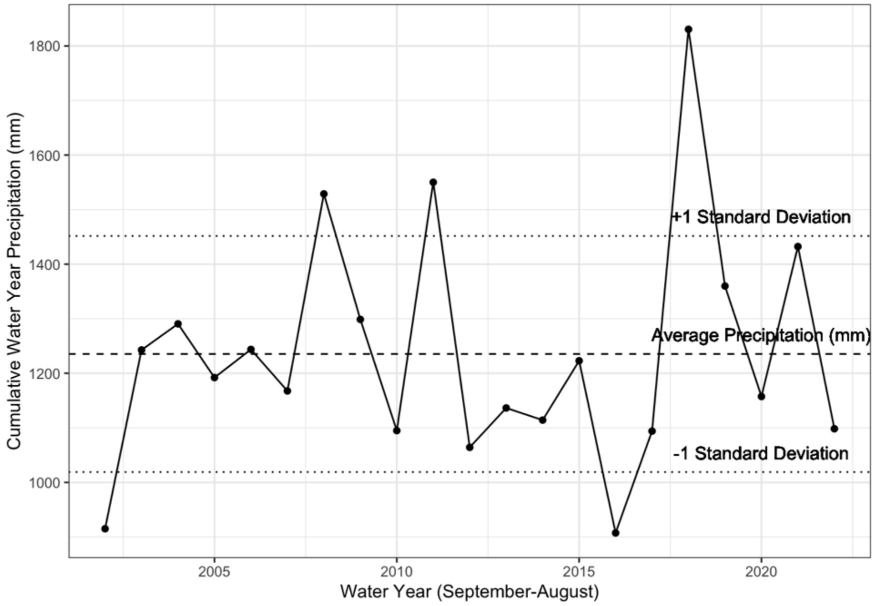


Figure 9: Cumulative water year precipitation (in mm) from 2001 to 2022. Average precipitation (1,235 mm), and ± 1 standard deviation (216 mm) are shown.

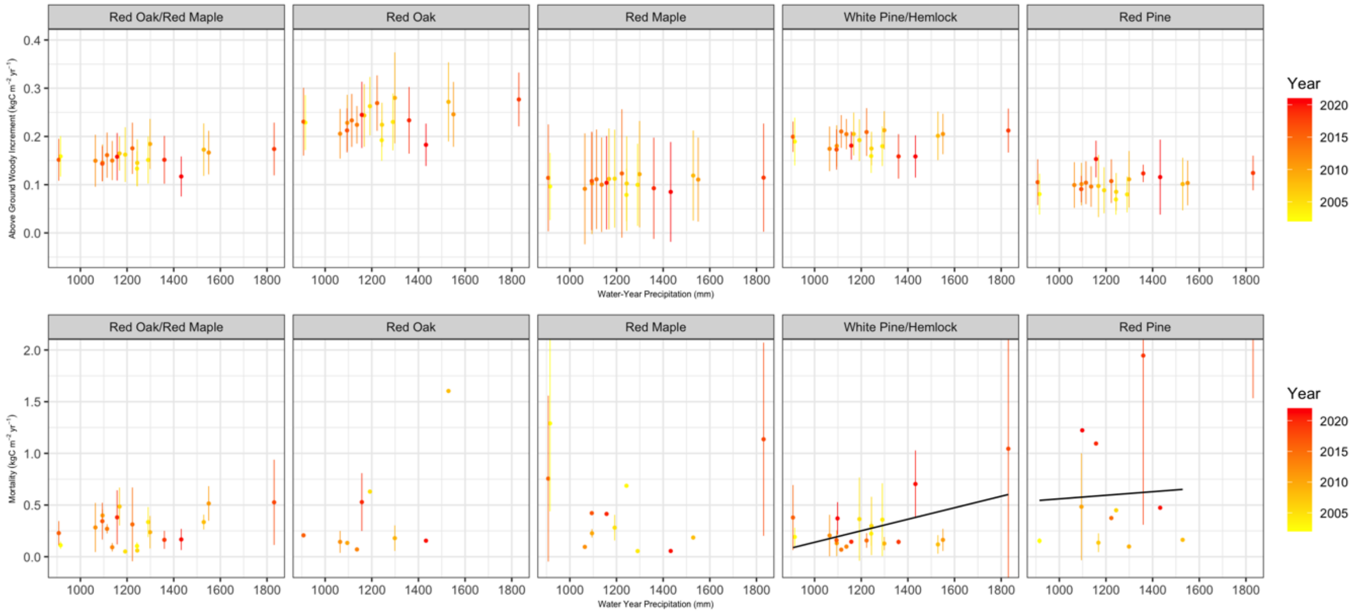


Figure 10: a) Relationship between cumulative water-year precipitation (mm) and the AGWI of living stems. Relationship between precipitation and AGWI does not differ significantly between stand types (ANCOVA, p = 0.919) b) Relationship between cumulative water-year precipitation and annual mortality. Relationship between precipitation and mortality does differ significantly between stand types (ANCOVA, p = 0.003). Error bars represent ± 1 standard deviation of the mean. R^2 and p-values are shown below in Table 9.

Table 10: Linear Regressions of Living Stem Growth and Mortality versus Water Year Precipitation

Linear Regression	**Type**	**R^2**	**p-value**
Red Oak/Red Maple Stands	**Living Stem Growth**	0.058	0.308
Red Oak Stands		0.14	0.107
Red Maple Stands		0.023	0.526
White Pine/Hemlock Stands		0.019	0.556
Red Pine Stands		0.089	0.202
Red Oak/Red Maple Stands	**Mortality**	0.16	0.076
Red Oak Stands		0.36	0.086
Red Maple Stands		0.00056	0.942
White Pine/Hemlock Stands		**0.28**	**0.017***
Red Pine Stands		**0.0026**	**0.016***

Table 11: ANCOVA

ANCOVA	**Model**	**p-value**
Water-year precipitation v AGWI	Model 1	0.913
	Model 2	**< 0.001 *****
Water-year precipitation v AGWI	Model 1	**< 0.003 ****
	Model 2	0.048

ii. Maximum June Temperature

Since 2001, maximum June temperatures have averaged 24.1 °C with a standard deviation of 1.7 °C and a range of 20.3 to 26.9 °C (Figure 11). To better understand the relationship of both living stem AGWI and annual mortality to maximum June temperatures, I analyzed the correlation between both groups using linear regressions.

Red Oak/Red Maple, Red Maple, and White Pine/Hemlock stands all show a significant negative linear correlation between living stem AGWI and maximum June temperature (Fig. 12a, Table 12, linear regressions, $p < 0.044$). On the other hand, Red Oak and Red Pine stands do not have significant linear relationships between living stem AGWI and maximum June temperature

(Fig. 12a, Table 12, linear regressions, p > 0.052). There is no significant difference in the linear relationships across stand types (Table 13, ANCOVA, p = 0.728).

There is no significant relationship between mortality and maximum June temperature across all stand types (Fig. 12b, Table 12, linear regression, p > 0.261). There is no significant difference in the relationship between mortality and maximum June temperature among stand types (Table 13, ANCOVA, p = 0.795).

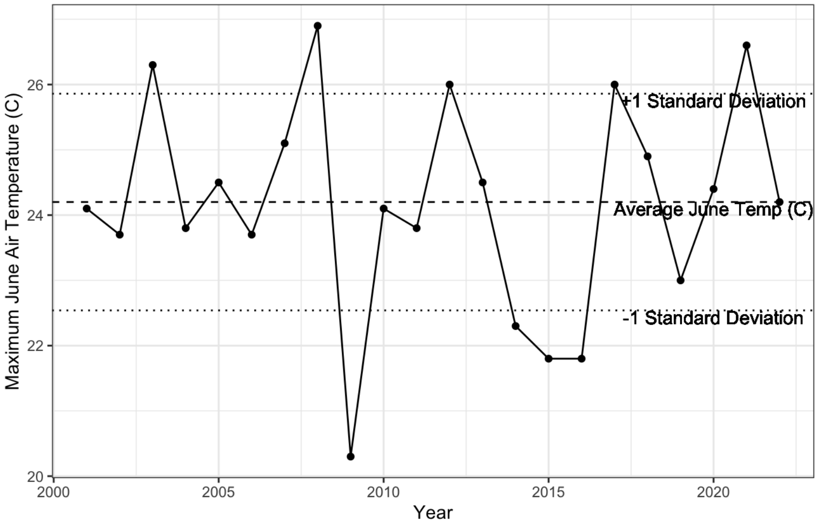


Figure 11: Maximum June temperature (in °C) from 2001 to 2022. Average temperature (24.1 °C) and ± 1 standard deviation (1.7 °C) are shown.

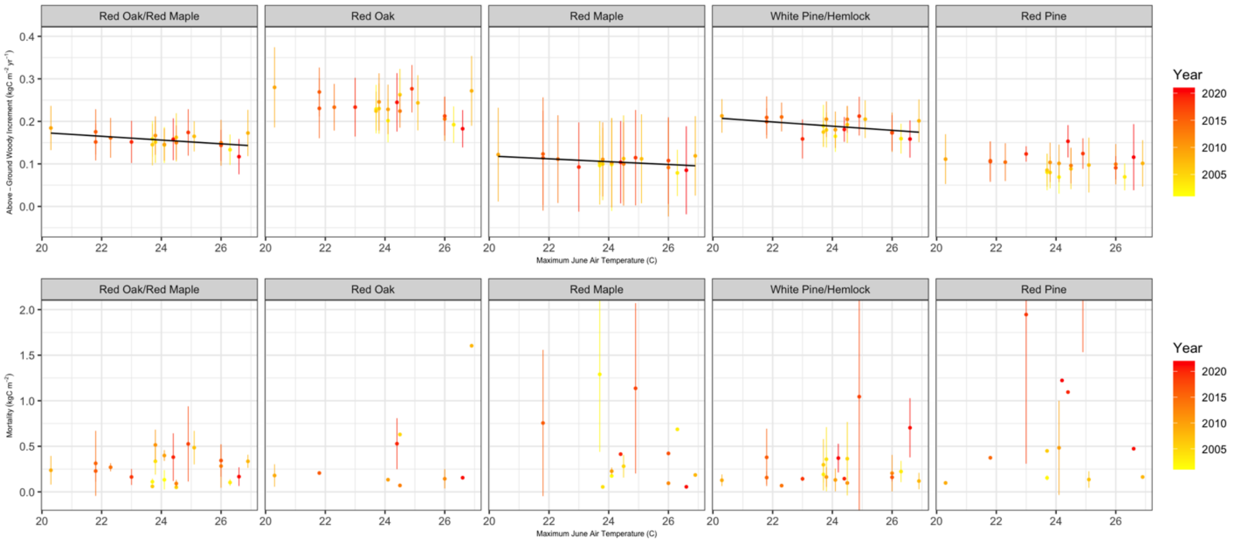


Figure 12: a) Relationship between yearly maximum June temperature (°C) and AGWI of living stems. Relationship between temperature and AGWI does not differ significantly between stand types (ANCOVA, p = 0.728). b) Relationship between yearly maximum June temperature and annual mortality. The relationship between temperature and mortality does not differ significantly between stand types (ANCOVA, p = 0.795). Error bars represent ± 1 standard deviation of the mean. R^2 and p-values are shown below in Table 10.

Table 12: Linear Regressions of living stem growth and mortality versus maximum June temperature.

Linear Regression	Type	R^2	p-value
Red Oak/Red Maple Stands	**Living Stem Growth**	**0.24**	**0.024***
Red Oak Stands		0.18	0.052
Red Maple Stands		**0.23**	**0.027***
White Pine/Hemlock Stands		**0.20**	**0.044***
Red Pine Stands		0.024	0.501
Red Oak/Red Maple Stands	**Mortality**	0.0041	0.784
Red Oak Stands		0.18	0.261
Red Maple Stands		0.11	0.272
White Pine/Hemlock Stands		0.058	0.305
Red Pine Stands		0.003	0.735

Table 13: ANCOVA

ANCOVA	Model	P-value
Max June Air Temperature versus Living Stem AGWI	Model 1	0.728

	Model 2	< 0.001***
Max June Air Temperature versus Mortality	Model 1	0.795
	Model 2	0.037*

iii. Snowpack

Since 2004, snowpack at the Harvard Forest has been measured as snow water equivalent, or SWE (in mm) (Fig. 13). During this period, snowpack has averaged an SWE of 5,076 mm (about 16.65 ft) with a standard deviation of 2,853 mm and a range from 1,162 to 10,818 mm. I analyzed the relationship of both living stem AGWI and annual mortality to water-year SWE to understand how snowpack depth impacts rates of AGB accumulation.

There is no significant linear relationship between living stem AGWI and snowpack depth (Fig. 14a, Table 14, linear regressions, p > 0.347) across all stand types (Table 13, ANCOVA, p = 0.808). In addition, there is no significant linear relationship between annual mortality and snowpack depth (Fig 14b, Table 14, linear regressions, p > 0.349) across all stand types (Table 15, ANCOVA, p = 0.415).

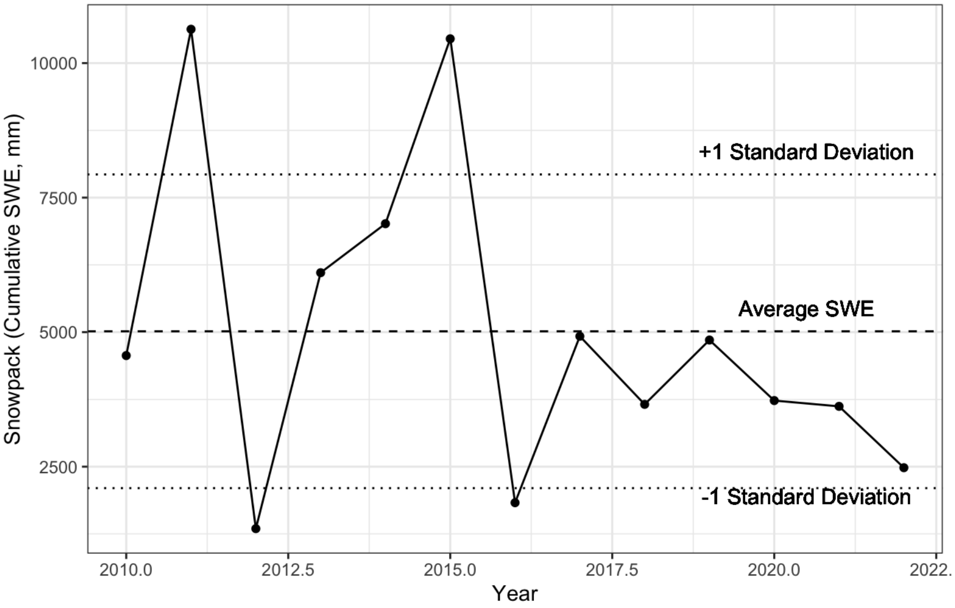


Figure 13: Cumulative wintertime snowpack (in Snow Water Equivalent, SWE) from 2010 to 2021. Average SWE (5,067 mm) and ± 1 standard deviation (2,853 mm) are shown.

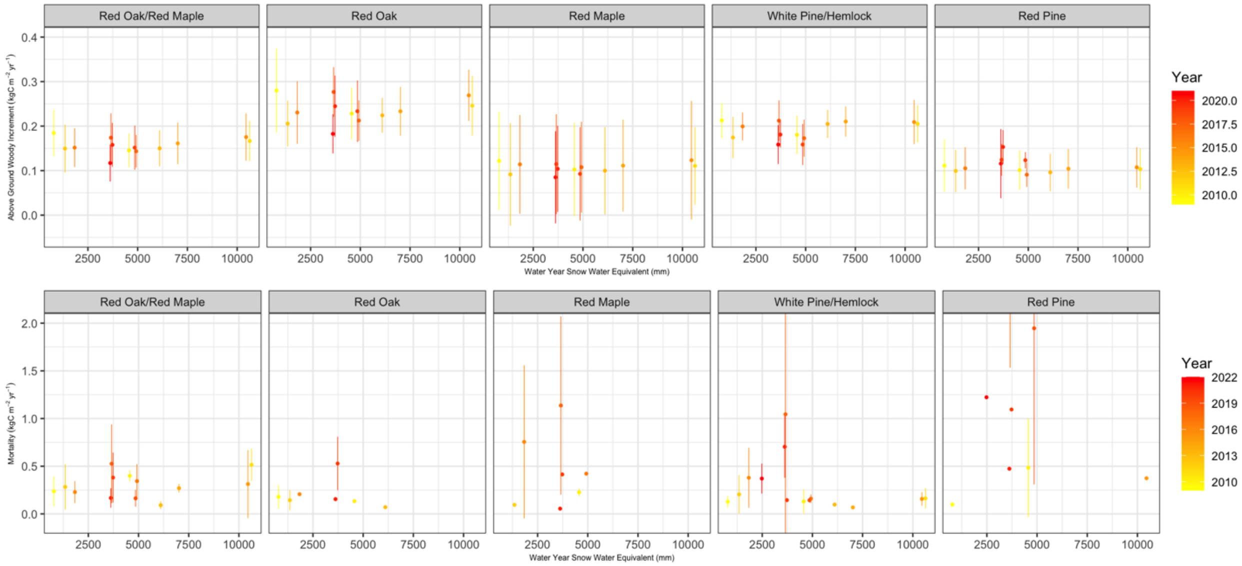


Figure 14: a) Relationship between cumulative water-year snowpack (SWE) and AGWI of living stems. The relationship between SWE and AGWI does not differ significantly between stand types (ANCOVA, p = 0.808). b) Relationship between SWE and annual mortality. The relationship between SWE and mortality does not differ significantly between stand types (ANCOVA, p = 0.415). Error bars represent ± 1 standard deviation of the mean. R^2 and p-values are shown below in Table 14.

Table 14: Linear Regressions for the relationship between Living Stem Growth/Mortality and SWE

Linear Regression	**Type**	**R^2**	**p-value**
Red Oak/Red Maple Stands	**Living Stem Growth**	0.036	0.535
Red Oak Stands		0.028	0.584
Red Maple Stands		0.063	0.406
White Pine/Hemlock Stands		0.081	0.347
Red Pine Stands		0.032	0.561
Red Oak/Red Maple Stands	**Mortality**	0.072	0.375
Red Oak Stands		0.0095	0.836
Red Maple Stands		$5.5e^{-5}$	0.987
White Pine/Hemlock Stands		0.073	0.349
Red Pine Stands		0.00078	0.829

Table 15: ANCOVA

ANCOVA	Model	p-value
SWE versus Living Stem AGWI	Model 1	0.808
	Model 2	0.003**
SWE versus Mortality	Model 1	0.415
	Model 2	0.023*

iv. Growing Season Length

Growing season length has been calculated as the length of days where daily NEP values, or the difference between gross ecosystem photosynthesis and respiration, are greater than 30% of the annual mean daily NEP. Mean growing season length at Harvard Forest is 154 days (about 5 months), with a standard deviation of 17.7 days and a range of 128 to 197 days (Fig. 15). I analyzed the relationship of growing season length to the living stem AGWI and annual mortality of the following year.

In Red Oak/Red Maple, Red Oak, Red Maple, and White Pine/Hemlock stands, living stem AGWI in the following year increased significantly with growing season length (Fig. 16a, Table 16, linear regression, $p < 0.08$). Red Pine stands did not have a significant linear relationship between living stem AGWI and growing season length (Fig 16a, Table 16, linear regression, $p = 0.087$). In addition, the relationship between AGWI and growing season length does not differ significantly between stand type (Table 17, ANCOVA, $p = 0.818$).

In all stand types present at the HF EMS Site, there is no significant linear relationship between growing season length and mortality in the following year (Fig. 16b, Table 16, linear regression, $p > 0.194$). The relationship between growing season length and the following year's mortality is not significant between stand types (Table 17, ANCOVA, $p = 0.615$).

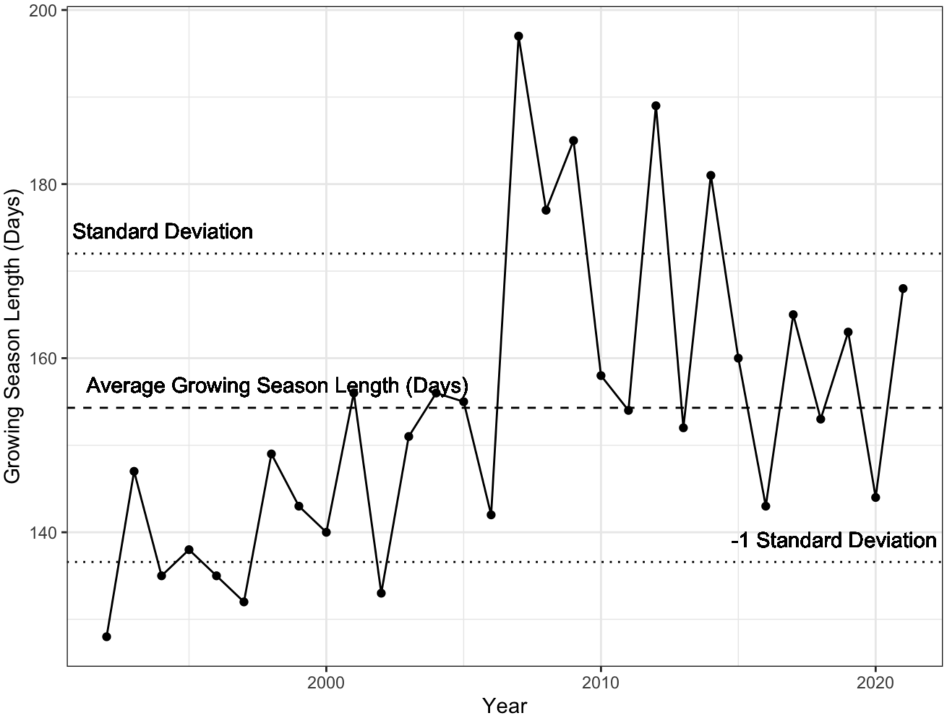


Figure 15: Growing season length (in days) from 1992 to 2022. Growing season length is calculated as the Julian Day where daily NEP values drop below 30% of mean yearly NEP, minus the Julian Day where daily NEP values increase above 30% of mean yearly NEP. Average growing season length (154 days) and ± 1 standard deviation (17.7 days) are shown.

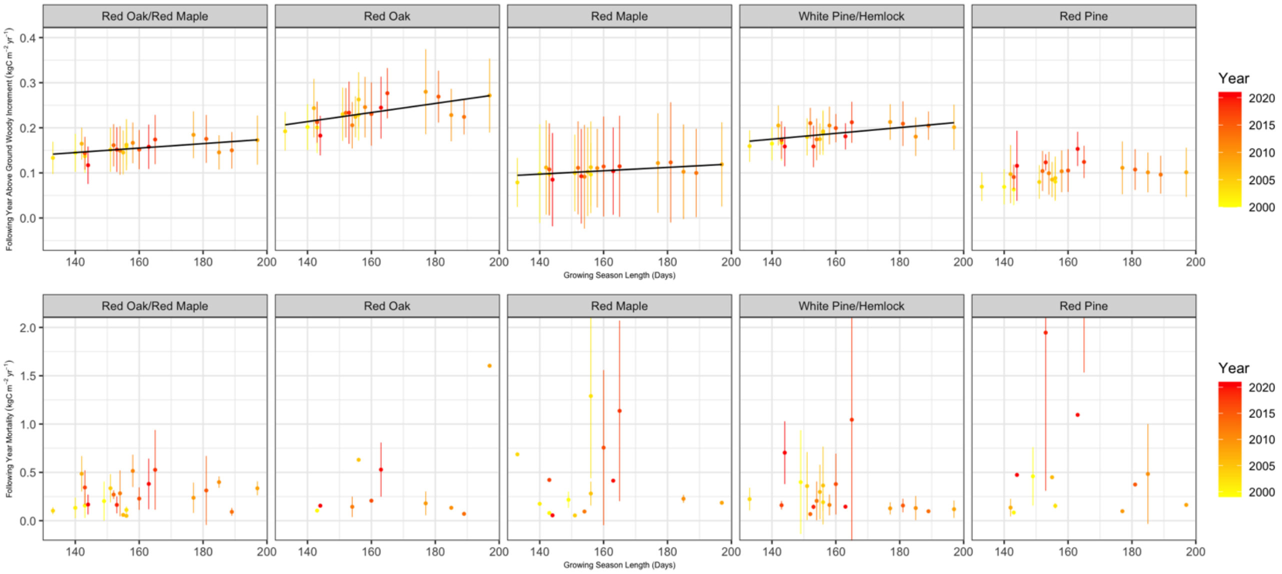


Figure 16: a) Relationship between growing season length (in days) and the AGWI of living stems in the following year. The relationship between growing season length and AGWI does not differ significantly based on stand type (Table 14, ANCOVA, p = 0.818). b) Relationship between growing season length and annual mortality in the

following year. The relationship between growing season length and mortality does not differ significantly between stand types (Table 14, ANCOVA, p = 0.615).

Table 16: Linear Regressions for the relationship between Living Stem Growth/Mortality and Growing Season Length

Linear Regression	**Type**	**R^2**	**p-value**
Red Oak/Red Maple Stands	**Living Stem Growth**	**0.3**	**0.009***
Red Oak Stands		**0.4**	**0.002****
Red Maple Stands		**0.3**	**0.008****
White Pine/Hemlock Stands		**0.33**	**0.005****
Red Pine Stands		0.14	0.087
Red Oak/Red Maple Stands	**Mortality**	0.039	0.364
Red Oak Stands		0.2	0.194
Red Maple Stands		0.001	0.909
White Pine/Hemlock Stands		0.063	0.288
Red Pine Stands		0.017	0.977

Table 17: ANCOVA

ANCOVA	**Model**	**p-value**
Growing Season Length versus Living Stem AGWI	Model 1	0.818
	Model 2	< 0.001 ***
Growing Season Length versus Mortality	Model 1	0.615
	Model 2	0.056

v. Drought

Drought Index has been calculated as a percentage of Worchester County experiencing each drought index value, according to data from the U.S. Drought Monitor. ScPDSI is calculated using precipitation and temperature data from the Fisher Meteorological Station (Palmer 1965). I analyzed the relationship of seasonal drought index and scPDSI values to the living stem AGWI and annual mortality of each stand type.

Spring and fall drought indexes had no effect on the AGWI of living stems across all stands (Fig. 18, Table 18, $p > 0.603$). However, summer drought indexes had a significant effect on the AGWI of living stems in Red Oak/Red Maple and White Pine/Hemlock stands (Fig. 18, Table 18, $p < 0.040$). In the remaining Red Oak, Red Maple, and Red Pine stands, summer drought indexes had no effect on living stem AGWI (Fig. 18, Table 18, $p > 0.060$). Using scPDSI values, I found that spring, summer, and fall droughts have no effect on the AGWI of living stems (Fig. 20, Table 19, $p > 0.220$).

Spring, summer, and fall drought indexes had no effect on mortality across all stand types (Fig. 19, Table 18, $p > 0.377$). However, springtime scPDSI values had a significant positive effect on mortality in Red Oak stands (Table 19, $p < 0.001$), and fall scPDSI values had a significant effect on the following year's mortality in White Pine/Hemlock and Red Pine stands (Table 19, $p < 0.013$).

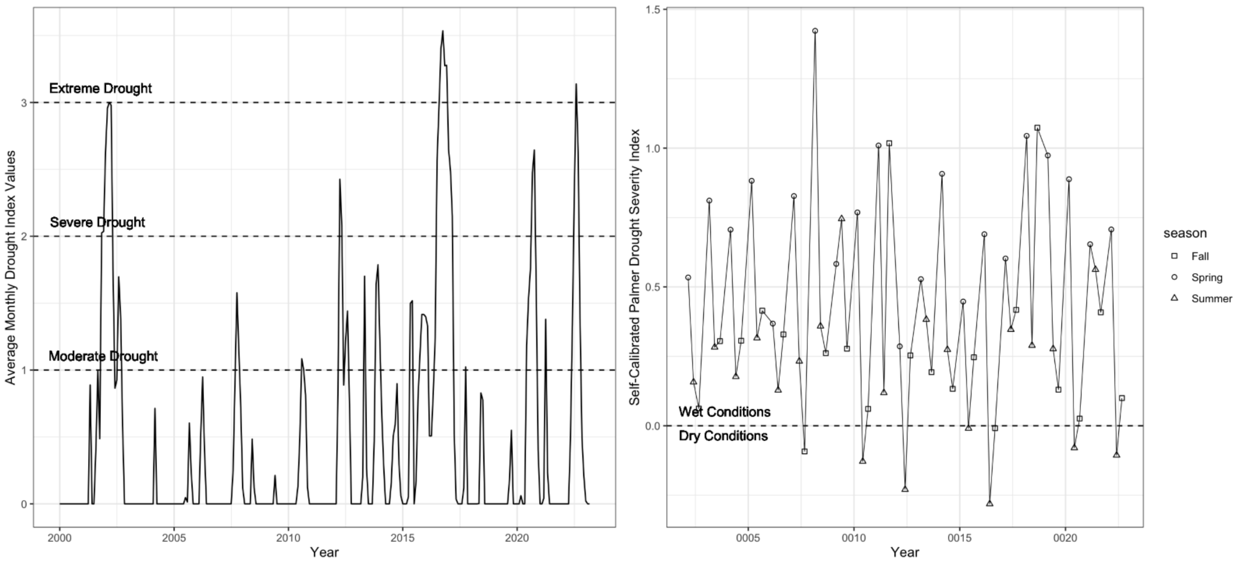


Figure 17: a) Monthly drought index, calculated as a percentage of Worchester County experiencing each drought index value (ranging from None to D4) from 2001 to 2022. B) Seasonal self-calibrated Palmer Drought Severity Index (scPDSI) for Spring, Summer, and Fall seasons. Calculated using precipitation and temperature data from the Fisher Meteorological Station.

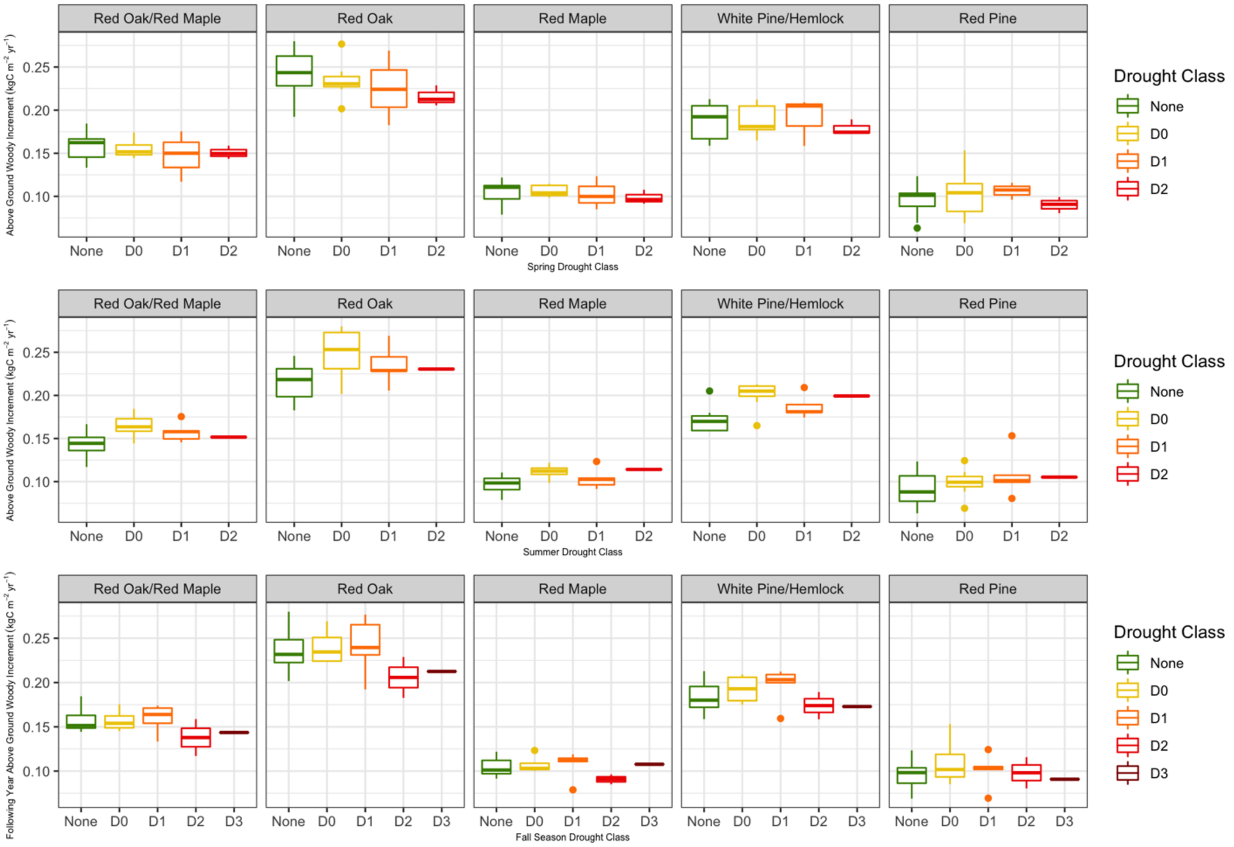


Figure 18: Boxplots of annual living stem AGWI for each drought class for spring (top), summer (middle), and fall (bottom) seasons. The effects of fall season drought are evaluated for the AGWI of the following year. Spring and fall-season droughts have no significant effect on AGWI (Table 18). Summer season droughts significantly affect Red Oak/Red Maple and White Pine/Hemlock stand types (Table 18).

Figure 19: Boxplots of mortality for each drought class for spring (top), summer (middle), and fall (bottom) seasons. The effects of fall season drought are evaluated using mortality from the following year. Spring, summer, and fall droughts have no significant effect on mortality (Table 18).

Table 18: ANOVA p-values for the relationship of living stem AGWI/mortality and seasonal drought index values

			ANOVA p-values	
Living Stem	**Stand Type**	**Spring**	**Summer**	**Fall**
	Red Oak/Red Maple	0.788	**0.040***	0.995
	Red Oak	0.603	0.091	0.980
	Red Maple	0.805	0.060	0.891
	White Pine/Hemlock	0.882	**0.012***	0.717
	Red Pine	0.722	0.565	0.901
Mortality	Red Oak/Red Maple	0.858	0.888	0.529
	Red Oak	0.777	0.671	0.514
	Red Maple	0.591	0.693	0.392
	White Pine/Hemlock	0.405	0.847	0.678
	Red Pine	0.349	0.875	0.377

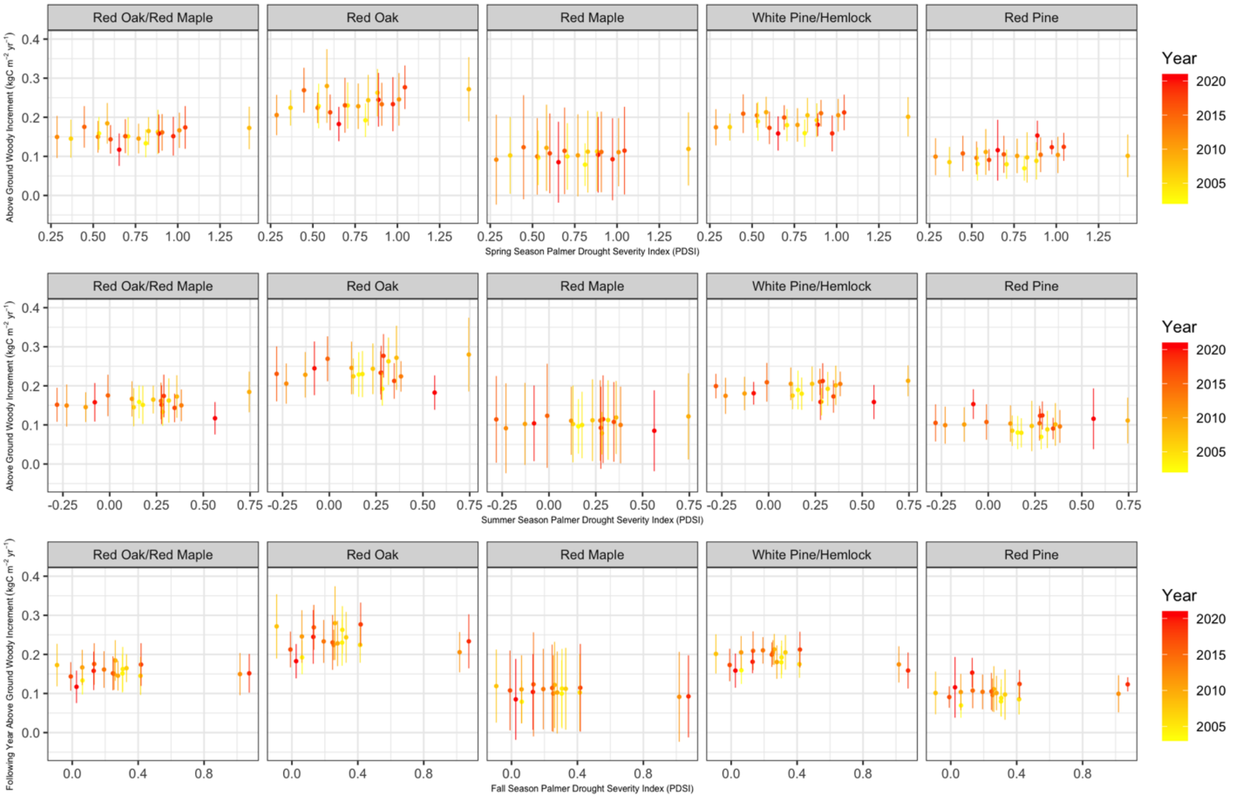


Figure 20: Relationship between spring, summer, and fall scPDSI values and the AGWI of living stems. The relationship between fall scPDSI values and living stem AGWI is determined using the following year's AGWI values. Seasonal scPDSI values have no significant effect on the AGWI of living stems (Table 19, $p > 0.05$). Error bars represent ± 1 standard deviation of the mean.

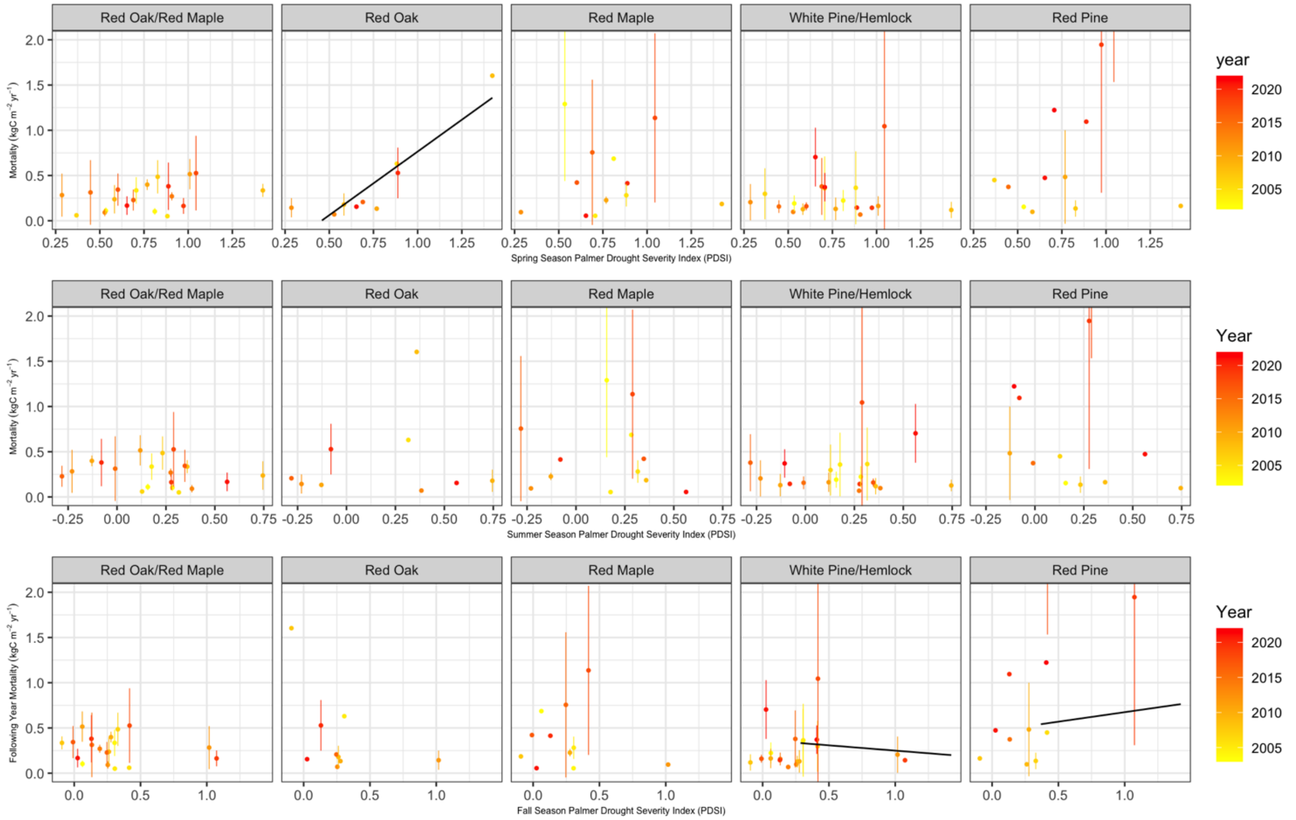


Figure 21: Relationship between spring, summer, and fall scPDSI values and mortality. The relationship between fall scPDSI values and mortality is determined using the following year's mortality values. Error bars represent ± 1 standard deviation of the mean.

Table 19: Linear Regressions for seasonal drought versus living stem AGWI/mortality

			Linear Model p-values	
Type	**Stand Type**	**Spring**	**Summer**	**Fall**
Living Stem	Red Oak/Red Maple	0.220	0.757	0.506
	Red Oak	0.770	0.579	0.372
	Red Maple	0.301	0.896	0.621
	White Pine/Hemlock	0.418	0.769	0.488
	Red Pine	0.235	0.760	0.852
Mortality	Red Oak/Red Maple	0.088	0.367	0.152
	Red Oak	**<0.001*** **	0.718	0.678
	Red Maple	0.949	0.889	0.542
	White Pine/Hemlock	0.666	0.671	**0.013***
	Red Pine	0.268	0.914	**0.004****

DISCUSSION

Ultimately, the goal of this thesis was to understand how AGB carbon stocks in temperate forests are changing over time. Many studies originating at the Harvard Forest aggregate data for the entire HF EMS fetch as opposed to parsing out AGB dynamics by stand type. This study indicates that different forest stand types do not contribute equally to cumulative forest AGB, further supporting the idea that forest carbon modelling must include stand type as a predictor (Bassow and Bazaz 1998). In addition, I sought to understand how the relative contributions of mortality and living stem growth impact both above ground woody increments (AGWI) and cumulative AGB. I found that while both sporadic mortality and living stem growth influenced AGWI values, mortality had little correlation to cumulative AGB values. This indicates that overall, AGB accumulation is driven by the growth of living stems with no significant influence from sporadic mortality events.

Better understanding how stand type, mortality, and living stem growth contributed to AGB trends allowed me to investigate a variety of intrinsic and extrinsic factors that influenced each of these variables. For intrinsic variables, I investigated how structural characteristics of each forest stand, including LAI and foliar nitrogen content, interacted with living stem growth and mortality. I found no correlation between LAI values and both living stem growth and mortality. However, my future research will be directed towards understanding the interactive effects of leaf nitrogen content and LAI values.

Finally, I sought to understand how AGB trends might be influenced by extrinsic factors, most notably widespread climactic changes. As climate change is predicted to primarily alter trends of precipitation and temperature, I began my analysis with those two primary variables before investigating their interactive effect on winter snowpack, growing season length, and drought. I found that living stem growth is unaffected by precipitation levels, while mortality in White Pine/Hemlock and Red Pine stands increased with rising yearly precipitation. On the other hand, maximum June temperatures had a significant relationship with living stem growth, as the AGWI of living stems decreased as June temperatures rose in Red Oak/Red Maple, Red Maple, and White Pine/Hemlock stands. Maximum June temperatures had no significant effect on rates of mortality.

Understanding how the interactive effects of precipitation and temperature can influence trends of AGB is vital under our rapidly changing climate. We found that snowpack depths have no significant effect on both living stem growth or mortality. However, increased growing season lengths are positively correlated to living stem growth across all stand types except for Red Pine. Mortality rates were unaffected. Drought has no effect on living stem growth or mortality. These contrasting effects of climate on the growth and mortality of forest stands should be kept in mind when considering future trends of AGB.

AGB trends among stand types

Overall, AGB at the HF EMS fetch was found to increase linearly over time, as the data was fit to a linear model with high R^2 values. This supports observations from Finzi et al. (2020) And Urbanski et al., (2007) who concluded that the growth of above-ground biomass at Harvard Forest was the machine that drove the majority of forest carbon sequestration. Various literature has discussed the effect of age on forest AGB accumulation, with mixed results. Xu et al. (2012) found that at the Black Rock Forest, stands over 150 years old began to experience mortality-related declines in AGB, while Pregitzer and Eushirken (2004) found that generally forest AGB increases with age in temperate forests. While our results support the findings of Pregitzer and

Eushirken (2004), it is necessary to continue the monitoring of AGB at Harvard Forest to understand how current trends in AGB change as the forest surpasses the 120 year mark.

My results show that Red Oak/Red Maple, Red Oak, Red Maple, and White Pine/Hemlock stands also increase linearly over time, with consistently high R^2 values. However, the rates of AGB accumulation, or AGWI are significantly different between these four stand types. This result highlights how interspecific differences in the physiologies of tree species can result in differing rates of AGB accumulation (Turnbull et al. 2002, Hadley et al. 2008, Bassow and Bazaz 1998). For example, Turnbull et al. (2002) found that Red Maple (*Acer rubrum*) has low water use efficiency (WUE) under both wet and dry soil conditions, slowing rates of photosynthesis. In addition, Bassow and Bazzaz (1998) found that red oak (*Quercus rubra*) had higher photosynthetic rates under light-saturated conditions than Red Maples. Both of these studies supplement my results, as Red Oak stands showed the highest rates of AGB accumulation while Red Maple-dominated stands had the lowest rates.

White Pine and Hemlock stands also showed steady rates of AGB accumulation ($R^2 = 0.98$), despite the introduction of Hemlock Wooly Adelgid (HWA, *Adelges tsugae*) to Massachusetts in the early 2000s (Hadley et al. 2008). This result contrasts the conclusions of several hemlock-centered studies, which found that the introduction of HWA to forests resulted in the widespread growth declines and mortality of hemlock trees (*Tsuga canadensis*) due to widespread crown defoliation (Hadley et al. 2008, Dukes et al. 2009). However, Mates-Munchin et al. (2006) found that the composition of forests impacted the overall AGB response to HWA invasion. In Hemlock-dominated stands, productivity decreased—but in mixed Hemlock stands, the decline in hemlock growth rates was compensated for by an increase in growth of co-habituating species (Mates-Munchin et al. 2006). However, a more thorough species-level analysis is needed to understand if this phenomenon is occurring in mixed White Pine and Hemlock stands at the HF EMS Site.

The case of Red Pine stands in particular emphasizes the importance of breaking a forest down into its respective stand types. Red Pine stands exhibited steady linear growth until 2018, when the introduction of the Southern Pine Beetle resulted in dramatic increases of Red Pine mortality. This period of heavy mortality caused a decline in cumulative AGB at the HF EMS fetch. This example highlights the importance of decoupling forest-wide AGB by different stand types, as each stand's tree species will respond to extrinsic factors in varying ways.

Relative contributions of living stem growth and mortality to AGWI and total AGB

To understand how living stem growth and mortality influence the growth trajectories of the stands present at the HF EMS Site, I evaluated the relationship between both living stem growth and mortality, and how each influences AGWI and total AGB accumulation. While there is an auto-correlation present due to the simple nature of the AGB equation, understanding the driving factors of AGB accumulation is essential in evaluating carbon storage potential and future growth trajectories.

Across all stand types, there was a significant relationship between both living stem increment and mortality when compared to AGWI. Living stem increments positively influence AGWI, while mortality negatively affects AGWI. However, the R^2 values of the relationship between living stem growth and AGWI are much lower than that of mortality and AGWI, indicating that mortality accounts for the majority of variation in AGWI. Therefore, living stem growth increments account for the variation in AGWI in years where there are no instances of mortality.

While the AGB of living stems was found to have a positive relationship with total AGB across all stand types mortality had no relationship with AGB. This indicates that while total AGB accumulation is dependent on the accrual of carbon in the AGB of living stems, sporadic mortality has little overall effect on total AGB accumulation. This further supports the conclusion that Harvard Forest is in the aggregation phase of development (Finzi et al. 2020, Urbanski et al. 2007), although changes to living stem AGB and mortality rates should be monitored as the forest ages (Xu et al. 2012).

Intrinsic Factors

I first sought to understand how the intrinsic properties of different tree species influenced rates of mortality and living stem growth, starting with Leaf Area Index (LAI). LAI is a necessary component of forest ecosystems which determines how energy is exchanged with the atmosphere through photosynthesis and respiration (Vose et al. 1994). Studies examining changes to LAI in a forest ecosystem have shown that increases in LAI correlates strongly to increases in biomass (Cavender-Bares et al. 2000). However, LAI is sensitive to both climate and nutrient stressors, which subsequently have the potential to impact rates of living stem growth in forests (Vose et al. 1994). For example, Vose et al. (1994) have found that severe defoliation events due to pests, fires, desiccation, and other stressors reduce stem growth due to limited carbohydrate production and carbon allocation to new leaf growth (Vose et al. 1994).

Despite these conclusions from a wide variety of literature, I found that LAI has no effect on the woody increment (AGWI) of living stems in Red Oak/Red Maple, Red Oak, and Red Maple stands at the HF EMS Site. There are several possible explanations for why trends of AGWI at these stand types contradict patterns observed in literature. One possible explanation is that it is not the magnitude of LAI that determines yearly growth, but instead the timing of when peak yearly LAI is reached. Savoy and McKay (2015) found that the yearly timing of peak LAI values was strongly correlated to yearly biomass increments at the forest scale. Another possible explanation is that severe defoliation events are not occurring at a large enough magnitude or at a time during the growing season to significantly affect growth increments (Vose et al. 1994).

While LAI values had no relationship with AGWI of living stems in deciduous-dominated plots, I found that in White Pine/Hemlock stands have a negative linear relationship between LAI and AGWI while Red Pine stands have a positive linear relationship between LAI and AGWI. In White Pine and Hemlock stands, it is possible that as hemlocks have declined in crown area due to HWA infestation, white pines and hardwood trees have expanded their leaf area due to reduced competition (Mates-Munchin et al. 2006). In Red Pine stands, the introduction of the Southern Pine Beetle likely caused such a severe and rapid defoliation event, dramatically decreasing rates of living stem growth.

In addition, there is no evidence that sporadic mortality at the HF EMS Site influences LAI (Fig. 7b). Xu et al. (2012) found that at the Black Rock Forest, sporadic mortality decreased LAI values by 1) removing leaf area from the system and 2) damaging nearby trees, further reducing leaf area. Since there is no correlation between mortality and LAI, this could indicate that mortality is primarily occurring in non-canopy dominant trees, and at a fairly low rate. However, this logic cannot be applied to Red Pine stands, where the majority of large canopy trees died. In these instances, it is possible that there is an offset in major defoliation and records of complete tree death, which contributes to the lack of correlation between mortality and LAI in Red Pine stands.

While LAI is used as a proxy for plot-wide productivity, foliar nitrogen content can be used a proxy for the photosynthetic capacity of individuals tree, as it is necessary in the photosynthetic pathway (Cramer et al. 2000, Bartlett et al. 2011). Therefore, observations of foliar N percentages have the potential to explain trends in productivity at the HF EMS Site. I found that over time, the foliar N content of red oak and red maple trees decreased exponentially, while hemlock, white pine, and red pine trees were not significantly correlated with a linear model. Trends of woody stem growth, or productivity, do not appear to follow trends of foliar N contents across species. However, these trends could be explained by the immobilization of N in dead wood stocks. As dead wood accumulates due to sporadic mortality, soil N stocks are immobilized in dead wood (Cramer et al. 2000). This phenomenon has the potential to limit N obtained through the soil (Cramer et al. 2000).

One potential direction is exploring how the relationship between foliar N and leaf area influences photosynthetic capacity, or A_{max}. Multiple studies have found that leaf area influences the slope of the linear foliar N-A_{max} relationship (Reich et al. 2002, Reich et al. 1995, Bartlett et al. 2011), with Turnbull et al. (2002) concluding that tree species with high specific leaf areas (SLA) have steeper slopes of the foliar N-A_{max} relationship. Therefore, interannual variations in AGWI could be partially due to the interaction of LAI and foliar N content.

Extrinsic Factors

In addition to intrinsic differences between stand types, extrinsic environmental variables have the potential to influence the growth and mortality between different forest stands. One such environmental variable is precipitation, which limits growth in roughly 40% of Earth's vegetated surface (Nemani et al. 2003). In the Northeast, precipitation is predicted to increase over time, although both extremely wet and dry conditions are anticipated to increase in frequency (Guilbert et al. 2015). My results indicate that there is no effect of precipitation on the AGWI of living stems across all stand types. It is possible that in the Northeast, precipitation levels have not reached sufficiently low levels to reduce stand productivity. In addition, CO2 fertilization could be confounding this result. Heilman et al. (2021) explain that as levels of CO2 increase due to anthropogenic climate change, water use efficiency increases (iWUE), offsetting the effects of low precipitation and dry conditions on radial growth. Cavender-Bares et al. (2000) corroborate this result, concluding that increased CO2 levels increases radial growth in red oak trees under all precipitation conditions. In addition, Jump et al. (2017) claim that as precipitation conditions continue to reach both wet and dry extremes, forests will accumulate more biomass during heavy precipitation years, leaving them overbuilt during dry years. Therefore, the HF EMS fetch should be continually monitored for responses to precipitation.

While precipitation had no effect on the AGWI of living stems, I found that mortality in both White Pine/Hemlock and Red Pine stands increased with precipitation. This result is partially supported by analyses of the effect of scPDSI on mortality, which found that the mortality of Red Pine stands increases under wetter conditions, while mortality decreases in White Pine/Hemlock stands under wetter conditions. Since each species favors moist soils, I investigated the effect of rainfall on the spread of both Hemlock Woody Adelgid (HWA) and the Southern Pine Beetle. While increased rainfall events had a negative effect on HWA survival in the following year (Chandler et al. 2021), moderate precipitation events have been shown to facilitate the spread of the Southern Pine Beetle, increasing Red Pine mortality (Aoki et al. 2022).

In addition to precipitation, increasing growing season temperatures have the potential to negatively affect radial growth in temperate forests. Heilman et al. (2021) found that iWUE benefits from CO2 fertilization are overwhelmed by heightened temperature stress. Previous research shows that red oak, red maple, and hemlock trees respond negatively to heightened temperatures. Bassow and Bazzaz (1998) found that red oak and red maple were both sensitive to extremely high temperatures, although red oak was deemed to be more temperature sensitive. Additionally, at the Black Rock Forest, hemlocks were found to reduce radial growth rates in response to high summer temperatures (D'Arrigio et al. 2001). However, only Red Oak/Red Maple, Red Maple, and White Pine/Hemlock stands had living stem AGWIs which were negatively correlated to maximum June temperatures. This discrepancy in my results is likely because my study does not encompass all possible effects of temperature on radial growth. For example, Bassow and Bazzaz (1998) found that red oak specifically was more sensitive to later season temperatures. Therefore, additional temperature analyses are needed to understand the inter-seasonal influences of temperature on radial growth between stands.

Changes to previous temperature and precipitation trends can produce interactive climate effects which have the potential to influence trends of forest productivity and mortality. One of the most commonly studied interactive effects is drought stress, which arises under high temperature and low precipitation conditions. As climate change accelerates, drought stress is anticipated to increase in frequency and intensity (Cook et al. 2015), which has the potential to reduce radial tree growth by inducing evapotranspiration stress (Heilman et al. 2017). Specifically in the Northeast, tree species are not well adapted to even moderate drought stress, leading to declines in growth (van Kampen et al. 2022). Declines in radial growth under drought stress occur due to reductions in the size of xylem cells produced during drought periods (van Kampen et al. 2022).

However, I found that seasonal drought conditions at the HF EMS Site do not influence yearly radial growth increments. This result is corroborated by Urbanski et al. (2008) who found that drought stress has little effect on the HF EMS Site, except in late summer.

This result further emphasizes the need for inter-seasonal studies of radial growth increments. Using the example of drought stress, van Kampen et al. (2022) found that the timing of drought in relation to the phenology of certain tree species drove patterns of radial growth. For example, paper birch and white pine were most sensitive to springtime droughts, while summer droughts affected the growth of most other tree species and fall droughts affected growth increments in the following year (van Kampen et al. 2022, D'Orangeville et al. 2022). However, since radial growth can occur for most of the year, the majority of temperate tree species have the ability to recover radial growth rates following a period of drought stress, except for white pines (van Kampen et al. 2022). My study primarily explains how yearly radial growth increments are impacted by drought stress, but the usage of dendrometer bands can allow for various inter-seasonal analyses to better understand the effect of seasonal drought and recovery trajectories between stand types.

As air temperatures in the Northeast increase, the length of the annual growing season will increase, as the ecosystem traditionally experiences winter-time temperature limitations (Cavender-Bares et al. 2000, Nemani et al. 2013). Increases in growing season length due to changes in springtime phenology (Savoy and McKay 2015) can allow for additional carbon storage in yearly radial growth (Nemani et al. 2013). In Red Oak/Red Maple, Red Oak, Red Maple, and White Pine/Hemlock Stands, increases in growing season length are positively correlated with AGWI. There is no correlation in Red Pine stands- however, this could be because the living stem growth increment mostly excludes dead Red Pines, leaving only non-dominant tree species whose growth rates are likely determined by neighborhood competition. This significant correlation between AGWI and growing season length necessitates further investigation of the relationship between LAI and AGWI. Savoy and McKay (2015) found that growing season index is closely related to LAI—however, their study examined the correlation between the timing of peak LAI, as opposed to peak LAI values. Therefore, it is possible that additional analyses surrounding the timing of LAI could influence radial growth increments.

The combination of increased wintertime air temperatures, a higher percentage of precipitation falling as rain, and increased precipitation rates are anticipated to reduce the amount and duration of snow cover during winter months (Cambell and Laudon 2019, Camel et al. 2010). This poses a threat to overwintering tree species, as snow cover insulates soil, preventing soil and root freezing (Camel et al. 2010). Under low snow cover conditions, freeze thaw cycles are predicted to increase, inducing root damage which can reduce the growth increment of the following year (Camel et al. 2010). However, snowpack has no influence on AGWI across all stand types. This result indicates that snow cover in the Northeast has not yet reached low extremes which are causing sufficient root damage to influence the yearly growth increment of trees.

Maximum June temperature, drought, growing season length, and snowpack depth each have no significant effect on instances of sporadic mortality across stand types. However, this study does not account for the interactive effects of environmental stress on both patterns of self-thinning and declining health (due to nutrient stress, pest or pathogen infestations, etc.). Using the example of drought stress, Jump et al. (2017) found that as drought stress increases, trees with a greater competitive ability are favored to survive. This reduces the survival rate of newer recruits and unhealthy trees which are already prone to mortality (Jump et al. 2017). Therefore, the combined effects of environmental stress and intrinsic factors should be examined in greater detail.

CONCLUSION

This study serves as a stepping stone for future research investigating the effects of different intrinsic and extrinsic variables on AGB accumulation in Northeastern forests. While all five stand types accumulate carbon consistently, I found that their rates of accumulation differ significantly. Deviations from the consistent rates of accumulation were explained by sporadic mortality events, while long-term biomass accumulation was driven primarily by the growth of living stems. I found that intrinsic factors have little effect on AGWI among stand types. However, the wealth of data available at the HF EMS Site allows for additional studies of these variables, including the interaction between LAI and foliar N content and the timing of peak LAI. In addition, my research shows that several extrinsic environmental variables do significantly affect living stem growth and mortality; precipitation, temperature, and growing season. The data presented here paves the way for more detailed analyses of seasonal stressors and their effect on stand types. Overall, this paper highlights that forest AGB is ultimately the sum of its parts, and understanding how intrinsic and extrinsic variables influence each stand is vital in the modeling and forecasting of forest carbon dynamics.

Acknowledgements

I would like to thank my advisors, Barry Logan and Bill Munger, for their mentorship, advice, and perspective throughout this project. I would also like to thank Tim Whitby, Greta Van Scoy, and Audrey Barker-Plotkin for assisting with field data collection and R Studio analyses, in addition to my dear field partner, Ellie Kerns. I am also grateful to the Harvard Forest SRPE for providing me with the necessary funding to pursue this project. Finally, I would like to thank the Bowdoin Biology Department for an incredibly transformative four years of academic study.

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