Graduate College Dissertations and Theses

Dissertations and Theses

2017

Quantifying tree response to alterations in pollution deposition and climate change in the northeastern US

Alexandra M. Kosiba
University of Vermont

Follow this and additional works at: https://scholarworks.uvm.edu/graddis

Part of the Climate Commons, Ecology and Evolutionary Biology Commons, and the Forest Sciences Commons

QUANTIFYING TREE RESPONSE TO ALTERATIONS IN POLLUTION
DEPOSITION AND CLIMATE CHANGE IN THE NORTHEASTERN US

A Dissertation Presented

by

Alexandra Maya Kosiba

to

The Faculty of the Graduate College

of

The University of Vermont

In Partial Fulfillment of the Requirements
for the Degree of Doctor of Philosophy
Specializing in Natural Resources

May, 2017

ABSTRACT

Understanding tree physiological responses to climate change is critical for quantifying forest carbon, predicting species' range change, and forecasting growth trajectories. Continued increases in temperature could push trees into conditions to which they are ill adapted – such as decreased depth of winter snow cover, altered water regimes, and a lengthened effective growing season. A complicating factor is that in the northeastern United States, climate change is occurring on a backdrop of acid deposition and land-use change. In this dissertation, I used three studies to investigate the spatiotemporal nuances of resultant tree and sapling physiology to environmental change.

First, I compared annual growth of co-occurring tree species (sugar maple, red spruce, red maple, yellow birch, and balsam fir) along an elevational gradient on Vermont's tallest peak: Mt. Mansfield. I found baseline differences in growth among species, and many annual variations were associated with species-specific events. Yet, protracted growth patterns, such as recent increases for red spruce and red maple, were correlated with increased temperature and cooling degree days (a heat index). For most species, temperature was positively associated with current growth, but negatively associated with growth the following year. This work demonstrated species' differences in response to change and the complex relationships between growth and temperature.

Next, I analyzed how climate, environmental parameters, and site and tree factors related to recent, regional increases in red spruce growth. While there was variability in response to climate and acid deposition by elevation and location, site and tree factors did not adequately explain growth. Higher temperatures outside the traditional growing season were positively related to growth, while nitrogen deposition was strongly negative. However, if nitrogen inputs decline as projected then the strength of this relationship may decrease over time. These results suggest continued favorable conditions for red spruce in the near term as acid deposition declines and temperatures increase, provided precipitation remains adequate to support growth.

Lastly, I used a replicated micro-catchment study to examine how four species of tree saplings (paper birch, quaking aspen, American chestnut and black cherry) responded to experimentally elevated temperature (2-4°C above control) and reduced early winter snow (first six weeks of winter), depending on soil type. Soil and species characteristics strongly influenced sapling response. However, natural weather patterns during the treatment period were highly variable and muted or exacerbated results. Heating increased the potential photosynthetic period in the fall, causing an overall increase in leaf area. Many two- and three-way interactions of treatment factors were also detected. These outcomes demonstrate the variability in sapling response to a changing climate, as well as the complex interactions that occur among soil, species, and weather parameters.

CITATIONS

Material from this dissertation was accepted for publication in Canadian Journal of Forest Research on 02/08/2017 in the following form:

Kosiba, A.M., Schaberg, P.G., Rayback, S.A., and Hawley, G.J.. (2017). Comparative growth trends of five northern hardwood and montane tree species reveal divergent trajectories and response to climate. Canadian Journal of Forest Research.

ACKNOWLEDGEMENTS

I am thankful for the love and encouragement from my family, especially my dad, Peter, and partner, Luke, and Eliza, Kathy, and Steve.

TABLE OF CONTENTS

viii

LIST OF TABLES

LIST OF FIGURES

xviii

CHAPTER 1: COMPREHENSIVE LITERATURE REVIEW

1.1. Introduction

It is well known that trees respond in measurable ways to fluctuations in the environment. Trees can respond by altering their physiology, especially if changes fall within the historical range that populations have encountered. However, persistence of a tree or population does not guarantee the continuation of optimal function or associated ecosystem services. Furthermore, anthropogenic-induced climate change may be occurring faster than relatively long-lived trees can feasibly adapt, especially if rapid or dramatic changes occur. Perceivable changes to the climate have already occurred and will persist regardless of near-term mitigation efforts. The response of trees to these changes remains unclear: we may see species reductions or improvements in vigor and growth, constriction or expansion of current range limits, or even widespread mortality. Such changes could have dramatic impacts on forest ecology, species distributions, ecosystem health and services, and both regional and national economies.

Complicating the matter is that forests will likely respond differently to changes in climate depending on site characteristic, land-use history, individual tree status, forest species composition, and the specific magnitude and directionality of the environmental change. In addition, complex interactions among environmental variables are possible; for example, elevated temperatures may increase the rate of some biological functions, including photosynthesis, but also may increase evapotranspiration, which then could

lead to stomatal closure and a reduced net photosynthetic gain Added to this uncertainty is the fact that the forests in the northeastern US were nearly completely cleared in the 1800s and early 1900s for agriculture and forestry (Foster 1992), have suffered outbreaks of invasive pests and pathogens (Lovett et al. 2006), and been subjected to decades of acidic deposition (Driscoll et al. 2001). Thus, that most present-day forests in the region have been impacted by humans is evident in altered species, age- and size-class composition, the presence of non-native flora, and the homogenization of soil material. Moreover, these forests are and will continue to face unrelenting changes in the form of elevated CO_2 concentrations, composition of atmospheric deposition, and temperature and precipitation regimes. The combination of these human-induced impacts could have a broad range of effects for the forests of the northeastern US.

1.2 Ecosystem services of mid-latitude temperate forests

Annual exchange of CO_2 between terrestrial ecosystems and the atmosphere (~120-125 Gt) is much greater than those attributable to anthropogenic sources (~6-7 Gt); therefore, changes in the terrestrial fluxes have the potential to either exacerbate or ameliorate human inputs (Bonan 2008; Field et al. 1998). Within terrestrial C, forests are a critical component of the global C budget, due in part to the large quantities of C stored in living biomass (Fahey et al. 2010); therefore, changes in tree growth rates and mortality can have a substantial impact on global C pools (Melillo et al. 2011). In particular, mid-latitude temperate forests have large C uptake potential (Dixon et al.

2

1994; Pan et al. 2011; Wofsy et al. 1993) and in these forests, the aboveground biomass of living trees is often the most dynamic C pool (Fahey et al. 2010). According to Pan et al. (2011), established mid-latitude temperate forests (comprising ~800 Mha) contributed 0.7-0.8 Pg C year^{-1} to global C sinks (1990-2007), or approximately 30% of the total global C.

In addition to C budgets, changes in tree growth and physiology can have broad-ranging impacts to hydrological cycles (Foley et al. 2005) and forest nutrient budgets (Aber et al. 1989) through alterations in root uptake and photosynthetic rates. Further, these changes can cause both negative and positive feedbacks to subsequent ecosystem alterations (Bonan 2008). For example, rapid changes in tree mortality can provoke fungal and insect outbreaks (Carnicer et al. 2011) and the increase the frequency and intensity of forest fires (Flannigan et al. 2000).

Therefore, estimating C sequestration by vegetation, of which mid-latitude temperate forests comprise over a quarter of annual global C uptake (Pan et al. 2011), is essential for C model simulation (Foley et al. 1998) – including estimating the impact of stresses to our forests and how they affect tree growth, competition, and vitality. Complicating the matter is that many mid-latitude temperate forests are operating on a legacy of human disturbance (Foster 1992). In the Northeastern US, other than deforestation, two of the largest contemporary influences on forest growth and C storage are acid deposition and climate change.

1.3 Anthropogenic acid deposition

Acid deposition was proposed as a serious environmental threat to forests of the northeast in the early 1970s following marked increases in precipitation acidity (Likens and Bormann 1974) that occur when human-driven emissions of sulfur dioxide (SO_2) and nitrogen oxides (NO_x), as well as ammonia (NH_3), form various acidic compounds (Driscoll et al. 2001). Prevailing winds can transport these compounds hundreds of miles until they are deposited either in either wet (rain, snow, and fog) or dry (gases, aerosols) form (NAPAP 2005). Through the atmospheric conversions to acids and the release of hydrogen ions, sulfur- (S) and nitrogen- (N) based pollutants acidify forest systems (Driscoll et al. 2001).

Among other impacts, the deposition of acidic compounds on forests increases the leaching of base cations, such as calcium (Ca), from plant tissues (Likens et al. 1996) and mobilizes soil-bound Ca, magnesium (Mg), and aluminum (Al), which initially may enhance growth due to increased Ca and Mg availability, but eventually leads to Al toxicity and the leaching loss of Ca and Mg from soils (Johnson and Fernandez 1992; Shortle et al. 1997). Elevated leaching of Ca induced by acid deposition is particularly problematic for forests in the northeast since Ca is a biologically important cation and decreases in soil exchangeable Ca from other causes in addition to acid deposition have been identified, such as changing internal ecosystem processes (Hamburg et al. 2003), biomass removal (Tritton et al. 1987), reduced particulate deposition (Likens et al. 1996),

N saturation (Aber et al. 1998), and decreases in base cation atmospheric deposition (Hedin et al. 1994).

Research has shown that N- and S- deposition has altered ecosystem function in the northeast (Aber et al. 2003; Driscoll et al. 2001). However, recent pollution controls (e.g., the Clean Air Act and subsequent amendments) have reduced pollution emissions resulting in moderate reductions in S-deposition and more varied change for N-deposition. Deposition of NH_4^+ has declined more precipitously than deposition of nitrate (NO_3^-) (Fig. 1.1) (Driscoll et al. 2001). Temporal changes in deposition loading, as well as the cumulative effect of decades of inputs, could continue to impact tree growth through changes in site nutrition, and could also create complex responses to the effects of climate change.
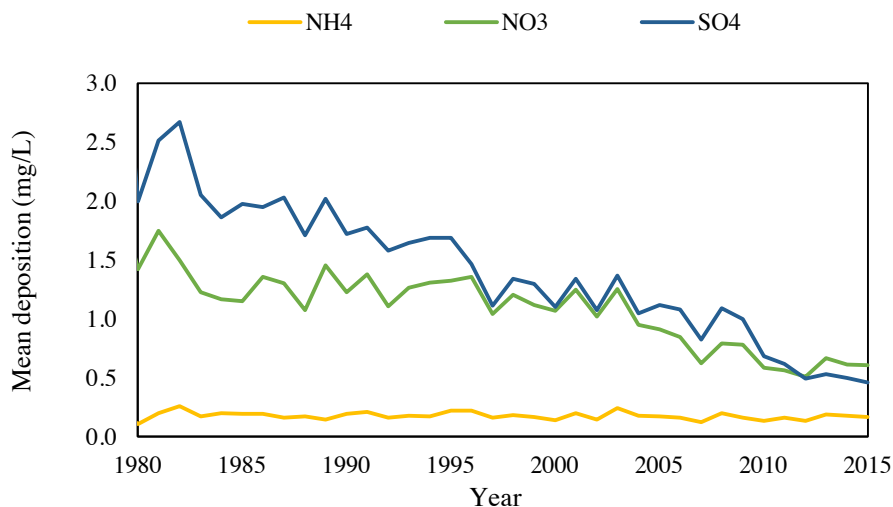
Figure 1.1: Precipitation-weighted mean deposition (mg L^{-1}) by water year (previous October – September) for ammonium (NH$_4^+$), nitrate (NO3$^-$), and sulfate (SO$_4^{2-}$) from NADP sites in Maine, Vermont, New Hampshire, and New York for length of record (1980-2015) (National Atmospheric Deposition Program 2016)

5

1.3.1 Role of Ca in response to environmental cues

Loss of Ca can have innumerable effects on tree physiology. The roles that Ca plays in plant cell function can be divided into two categories: (*i)* structural—maintaining both cell wall architecture and plasma membrane integrity; and (*ii)* regulatory— serving as a messenger in signaling cascades that allow cells to sense and respond to environmental stimuli and integrate C metabolism (Marschner 2002). Both roles that Ca play are important to the structure and function of plant cells; however, regulatory Ca is of particular importance for tree health because it helps cells respond to environmental stress (Webb et al. 1996), such as freeze/thaw events (DeHayes et al. 1999; Schaberg and DeHayes 2000), and trigger compensatory changes in physiology that support stress tolerance (Halman et al. 2008; Schaberg et al. 2000). Ca is also integral in stomatal function (Allen et al. 2001) and losses of Ca can have significant impacts on photosynthesis and internal water pressure (Borer et al. 2005; Eamus et al. 1989).

Thus, depletion of Ca can disrupt fundamental processes in tree function including photosynthesis (McLaughlin et al. 1991), carbohydrate metabolism (McLaughlin and Wimmer 1999), stomatal response (Borer et al. 2005), wood formation (Fromm 2010), wound closure (Huggett et al. 2007), cold tolerance (Halman et al. 2008), and winter injury (DeHayes et al. 2001; Schaberg and DeHayes 2000). Impaired function of these processes can have significant impacts on individual trees, as well as entire populations or species. Because Ca is biologically essential, the leaching of this element has far reaching consequences for forest health and productivity.

1.3.2 Effects of acidification on trees

Sensitivity to reductions in Ca is often species-specific, and some sensitive species have experienced declines in their populations on a regional scale coincident with recent anthropogenic Ca depletion. Perhaps the most noteworthy example of this is red spruce (*Picea rubens* Sarg.) decline in the northeastern US. Considerable experimental evidence has now established that acid deposition exposure and resulting Ca depletion reduces red spruce cold tolerance and significantly increases the risk of winter injury and crown deterioration (DeHayes et al. 2001; Schaberg and DeHayes 2000). The mechanism through which Ca depletion reduces red spruce cold tolerance was first described through controlled exposures of seedlings to simulated acidic deposition which was shown to leach Ca from foliage (DeHayes et al. 1999; Schaberg et al. 2000).

Acidic deposition, similar to levels measured at sites where the decline of red spruce had been observed, can reduce the cold tolerance of red spruce current-year foliage by up to 10°C, depending on the time of year and pH of the deposition load (DeHayes et al. 1990; Fowler et al. 1989; Sheppard 1994; Vann et al. 1992). At the Hubbard Brook Experimental Forest (HBEF), NH, Hawley et al. (2006) found that for all crown classes of red spruce, winter injury was significantly greater for trees growing in a reference watershed with a history of acid deposition-induced Ca depletion than on a watershed where Ca was added to simulate pre-pollution levels. These findings were particularly striking for dominant and co-dominant red spruce: trees on the reference-

7

watershed lost about 75% of their current year foliage due to winter injury, about three times more than the foliar losses for similar trees on the Ca-addition watershed.

Red spruce is not the only tree affected by reductions in soil Ca. Sugar maple (*Acer saccharum* Marsh.) has also suffered declines in growth since the mid-twentieth century (Johnson et al. 1986; Westing 1966) that were coincident with reductions in soil Ca (Bailey et al. 2004; Bishop et al. 2015; Huggett et al. 2007; Schaberg et al. 2006). Research has shown that sugar maple growing in soil with lower Ca content grew less (Bishop et al. 2015), sustained higher incidences of mortality (Bailey et al. 2004), and took longer to heal after wounding (Huggett et al. 2007). Data also suggest that Ca impacts the abundance and vigor of sugar maple seedlings (Juice et al. 2006). In addition, paper birch (*Betula papyrifera* Marsh.) on higher Ca sites showed notable increases in growth after a damaging ice storm relative to birch on Ca-depleted sites (Halman et al. 2011).

Sensitivity to Ca depletion is not uniform across the landscape. While most of New England was subject to elevated acidic loading, high elevation forests in the northeastern US are particularly vulnerable. In late summer and fall, high elevation forests in the northeastern United States are subject to cloud misting approximately 10–40% of the time, depending on altitude, and therefore, receive large amounts of anthropogenic pollutants in the form of acid rain, mist, and ozone (Siccama et al. 1982). Acidic inputs may be three- to four- times higher than at comparable low elevation sites (Johnson and Siccama 1983). Research looking at spatial analysis of patterns of red

spruce winter injury in 2003 in New York, Vermont, New Hampshire, and Massachusetts indicated that winter injury was greatest at high elevations, in western portions of the region, and on west-facing slopes – all areas that received higher atmospheric inputs of H+ and would be prone to Ca depletion (Lazarus et al. 2006). Further, there is high variability in resultant change from acidic loading based on a site's characteristics (e.g., nutrient content, buffering capacity, timber extractions, etc.). Research by Engel (2013) showed that red spruce growing on sites with a low capacity to tolerate acidic inputs (assessed through Critical Load and Exceedence models) displayed reduced growth compared to red spruce growing on high buffering capacity sites .

Given the broad extent to which acid deposition has impacted northeastern forests, it is not surprising that other Ca-sensitive tree species have also experienced health declines in recent years. Evidence now suggests that climate change may also contribute to soil acidification by increasing the frequency of soil freezing events, which damage roots, reduce nitrate uptake, and leach base cations from soils (Comerford et al. 2013). Climate change is occurring on a background of decades of acid deposition and Ca leaching, from which the soils have not fully recovered (Lawrence et al. 2012), as well as the long-term impacts of land use history (e.g., deforestation, agriculture, etc.). Indeed, it is possible that the combined effect of decades of acid deposition and climate change may push trees over a threshold of Ca deficiency that could predispose trees to decline. Therefore, an ecosystem with reduced Ca from acid deposition may have a diminished ability to respond to environmental changes as successfully or rapidly as one

with adequate Ca stores. Understanding the response of trees on varied sites (e.g., a range of soil-Ca status, elevation, land use history, and aspect) could help us predict how trees may cope with the combined impact of these stressors.

1.4 Anthropogenic climate change

1.4.1 Observed regional changes

Added to the stress of anthropogenic pollutants and decades of soil cation depletion, the region is also experiencing changes in climate. Since 1895, the annual mean temperature has increased by nearly 2°C (0.16°C per decade), with winter temperature having risen more steeply (Hayhoe et al. 2007; Kunkel et al. 2013; USGCRP et al. 2014). This warming has resulted in a lengthened growing season (increase of 3.7 (±1.1) days per decade), more winter precipitation falling as rain rather than snow, reduced snowpack in some winters, earlier spring snowmelt (freeze period has decreased 3.9 (±1.1) days per decade), and more days with temperatures above 32.2°C (Betts 2011; Kunkel et al. 2013; Northeast Climate Impacts Assessment Synthesis Team 2007). Precipitation has increased more than 10% since 1895 (0.8 cm per decade) (Kunkel et al. 2013), with a 70% increase in the amount falling during very heavy precipitation events (Groisman et al. 2013; Kunkel et al. 2013; Northeast Climate Impacts Assessment Synthesis Team 2007; USGCRP et al. 2014).
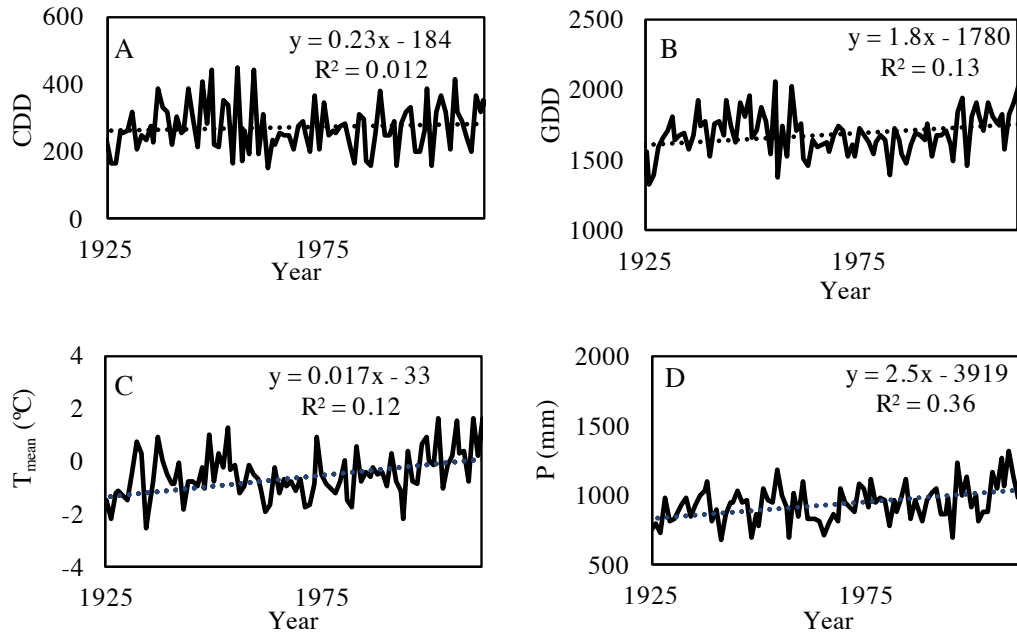
Figure 1.2: Examples of climate trends for the northeastern US (shown with dashed trend line) from 1925-2016: (a) total cooling degree days (CDD, degree days >18.3°C), (b) total growing degree days (GDD, degree days >5°C), (c) mean water year (previous Oct-current Sept) temperature (Tmean; °C), and (d) total water year precipitation (P; mm). See methods for data sources and descriptions (Climatic Research Unit 2016; NOAA National Centers for Environmental Information 2016; NOAA Regional Climate Centers 2016)

These changes are also coupled with increased atmospheric CO_2 concentrations and alterations to other anthropogenic atmospheric inputs (e.g., S- and N- deposition). Through the burning of fossil fuels, atmospheric CO_2 concentration rose from 311.3 ppm in 1950 to over 400 ppm in 2016 (NOAA Earth System Research Laboratory Global Monitoring Division 2016; Peters et al. 2013) (Figure 1.3). Elevated atmospheric CO_2 concentration, compared to pre-industrial levels, combined with other anthropogenic gasses, such as methane and nitrous oxide, have led to changes in the global energy balance, causing observable changes in the global climate.

11
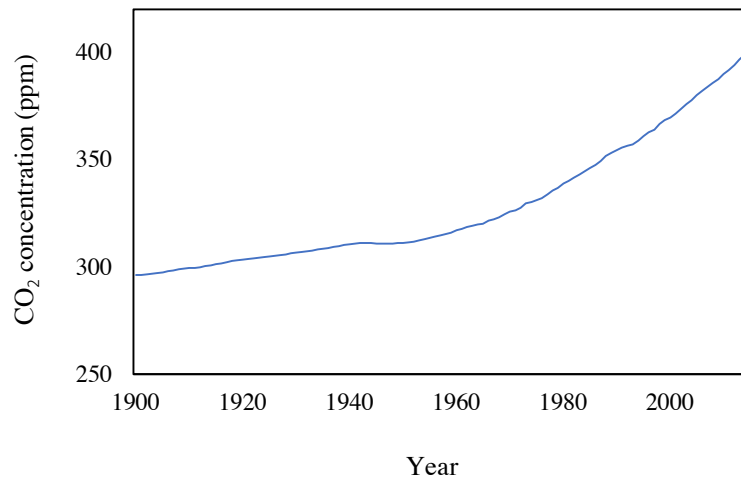
Figure 1.3: Atmospheric CO$_2$ concentration (in parts per million, ppm) measured from Law Dome ice cores (1900-2004) and atmospherically at Mauna Loa, Hawaii (1950-2016) (NOAA Earth System Research Laboratory Global Monitoring Division 2016; World Data Center for Paleoclimatology and NOAA Paleoclimatology Program).

1.4.2 Regional climate projections

Climate projections for the future include continued rising global temperatures, changes in precipitation patterns (including increased severity and duration of precipitation events), more frequent extreme weather events, biogeophysical changes (e.g., changes to albedo), and higher sea levels (IPCC 2014; USGCRP et al. 2014). In the northeastern US, climate models predict an increase in temperature of 2-10°C by 2050 under continued high greenhouse gas emissions scenarios and about 2-6°C under low emission conditions (Kunkel et al. 2013; Northeast Climate Impacts Assessment Synthesis Team 2007). A climate model developed for the Lake Champlain Basin (VT) projects mean annual temperatures to be nearly 5.0°C above the base temperature (1970-1999) by the end of the 21st century, with mean winter temperatures possibly rising to

12

6.0°C above the baseline (Guilbert et al. 2014). The length of the growing season is also projected to increase concurrent with spring temperatures from approximately 141 days (1970-1999) to over 180 days by the end of the 21st century (Guilbert et al. 2014).

Although precipitation patterns are difficult to predict, according to Betts (2011), by the end of the century seasonal precipitation in the Northeast is projected to increase approximately 15% in winter, 10% in spring, and 5% in fall, but exhibit no change in summer (high emission scenario); however, a model for the Lake Champlain Basin suggests that mean annual precipitation will increase 0.3 mm per day by 2099 compared to the base period (1970-99), with increases likely for all seasons (Guilbert et al. 2014). In addition, many climate models also indicate larger inter-annual variation in both temperature and precipitation (Hayhoe et al. 2007) and higher variability in resulting weather patterns may become the norm. According to the IPCC (2014), global warming of approximately 2°C above the pre-industrial baseline will very likely lead to more frequent heat and precipitation extremes over most areas of North America, though most precipitation will fall as rain rather than snow. An earlier timing of spring snowmelt due to elevated temperatures and increased runoff from heavier rainfall events, possibly coupled with increased evapotranspiration with co-occurring elevated temperatures, could increase the frequency of summer droughts (Northeast Climate Impacts Assessment Synthesis Team 2007).

1.4.3 Possible effects of changes in temperature on forests

Anthropogenically driven temperature increases could have broad impacts on the health and distribution of trees. Temperature is critical to all metabolic processes involved in the uptake, release, and storage of C (Pallardy 2010). Elevated temperatures, especially if coinciding with sufficient water and nutrient availability, can increase tree metabolic processes leading to higher biomass accumulation (Luo 2007). Research has reported myriad changes that may result, including changes to the timing of spring phenology (Chmielewski and Rötzer 2001), geographical habitat range (Doak and Morris 2010), productivity (Way and Oren 2010), and habitats (Kelly and Goulden 2008).

Temperate forests, like those in the northeastern US, have been shown to have a broader temperature range for growth than forests in areas with more consistent temperature, such as tropical forests (Cunningham and Read 2002), and as a result, may be able to more quickly respond to increased temperatures. Observational studies correlating temperature to diameter growth across forest types have shown both increases and decreases with higher temperatures (Way and Oren 2010). Research has found conifers to grow both more (Saxe et al. 1998) and less (Way and Oren 2010) than deciduous trees under elevated temperatures. Additionally, some temperate conifers, such as red spruce and white pine (*Pinus strobus* L.), are capable of photosynthesis when fall, winter, and spring temperatures are mild (Schaberg and DeHayes 2000; Schaberg et al. 1995) and could benefit from elevated C capture relative to leafless hardwoods as the climate warms.

Changes in tree physiology due to increased temperature are closely tied to the soil community, and the responses of soil microbes and mesofauna to warming may intensify or weaken tree responses. Indeed, studies imposing warming on plants and soil communities have shown short-term losses of soil C, in the form of CO_2, and acceleration of N cycling rates due to increased soil microbial activity (Melillo et al. 2011). In a replicated soil warming study, Melillo et al. (2011) showed that the acceleration of soil-mediated N cycling enhanced N availability for the vegetation and thus, increased tree growth rates. Others have hypothesized that climate warming may lead to decreased N supplies in a warmer world (Groffman et al. 2009) and some evidence along elevational transects at the HBEF may support this possibility (Durán et al. 2014).

Warming may not only affect soil turnover of nutrients, but also the nutrient quality of plant matter. For example, increases in temperature are expected to cause increases in the ratio of C:N in litter, particularly for conifers (Tjoelker et al. 1999), which in turn, would decreases the rate of decomposition (Pallardy 2010) and retard the return of nutrients to the ecosystem. Thus, understanding how warming may affect plant-soil relations is fundamental to our understanding of forest ecosystem response to widespread temperature change.

Elevated temperatures are also projected to reduce the duration of cold winter conditions, alter the frequency of soil freeze-thaw cycles and reduce both the amount and duration of snow cover (Northeast Climate Impacts Assessment Synthesis Team 2007). Research by Comerford et al. (2013) at HBEF showed that sugar maple trees subjected

to a reduced snowpack and consequent increased soil freezing depth had increased root damage, lessened stem growth, reduced starch stores, and lowered leaf Ca:Al ratios. This is especially striking in the northeastern US where climate change is operating on the backdrop of decades of acid deposition that has leached soil Ca and elevated Ca:Al ratios.

1.4.4 Possible effects of changes in growing season length on forests

A steady lengthening of the growing season concurrent with increases in annual temperature has been documented in Vermont (Betts 2011) and elsewhere in the region (Huntington et al. 2009). Changes in the timing of flowering and spring phenology have been observed (Betts 2011; Richardson et al. 2006; Schwartz and Reiter 2000). Increasing growing degree-days (GDD), a measure of the mean daily temperature deviation from a base temperature (usually 4-5°C for forested ecosystems), correlate with increased plant growth in boreal forests (Peltola et al. 2002). Several studies have demonstrated that early spring growth due to a prolonged growing season and earlier timing of snowmelt increased forest productivity (Goulden et al. 1996; Menzel and Fabian 1999; Myneni et al. 1997).

Extending the growing season may increase plant C and nutrient uptake. However, changes in warming may also create phenological mismatches between plant and soil community activity, resulting in nutrient buildups and leaching when plants are dormant but the soil community is not (Groffman et al. 2012); for example, during prolonged winter thaws, prior to leaf-out, or following leaf senescence. Although climate

change is predicted to generally increase air temperatures, especially in the winter, extreme winter lows may persist and freeze-thaw cycles may increase in number, duration or magnitude (Christensen et al. 2007; Hayhoe et al. 2008; Kunkel et al. 2008). Indeed, for red spruce trees in the northeast, periods of decline have often been temporally aligned with episodes of unfavorable climatic influences, such as drought or unusual climatic events (e.g., winter freeze-thaw episodes) (Johnson et al. 1988), which may become more frequent or intense (Kunkel et al. 2008; Meehl and Tebaldi 2004).

1.4.5 Possible effects of increasing atmospheric CO_2 concentration on forests

Among other factors, elevated atmospheric CO_2 concentrations have been shown to provide a fertilization effect in some plants (Martinez-Vilalta et al. 2008; Soule and Knapp 2006), and when combined with increases in temperatures, growing season length, and precipitation, could promote increased growth for some species or elevations over others (Salzer et al. 2009). The primary effect of the response of plants to rising atmospheric CO_2 is to increase resource use efficiency. Elevated CO_2 has been shown to alter stomatal conductance, transpiration, and water use efficiency (Battipaglia et al. 2013). However, research results are varied on the specific effects of CO_2 fertilization on trees, including both increases (Körner et al. 2005) and decreases (Silva et al. 2010) in radial growth, changes to leaves, including the number, size (Radoglou and Jarvis 1990), life-span, and lignin concentration (Körner et al. 2005), and changes to flowering/fruiting (Körner et al. 2005). However, many of these findings show differences in the magnitude

17

and direction of change depending on the species and genotype (Saxe et al. 1998), as well as site factors, such as latitude, annual water balance, and mean annual temperature (Silva and Anand 2013).

Like changes in temperature, elevated CO_2 concentrations may alter plant nutrient relations. For example, Tjoelker et al. (1999) imposed both increased CO_2 concentration and temperature on five boreal tree species and found that growth under elevated CO_2 concentrations reduced leaf N and increased non-structural carbohydrates compared to the control. Other studies have shown increased C uptake by plants under elevated CO_2 concentrations despite acclimation of photosynthetic capacity (measured as decreased carboxylation rate of Rubisco) (Leakey et al. 2009).

In addition, for some plant species, growth under elevated temperatures and CO_2 levels can reduce resistance and tolerance to freezing temperatures (Repo et al. 1996), which could be problematic for marginally cold tolerant trees such as red spruce (DeHayes 1992). Repo et al. (1996) examined changes in frost hardiness of Scots pine (*Pinus sylvestris* L.) saplings subjected to increased atmospheric CO_2 concentrations and/or elevated air temperatures. They found that elevated temperatures caused needles to harden later and deharden earlier than controlled conditions, and that elevated CO_2 concentrations hastened dehardening in the spring. However, work with other conifer species (e.g., black spruce, *Picea mariana* Mill. BSP) had contrary findings (Bigras and Bertrand 2006).

1.5 Conclusions

While evidence of anthropogenic stresses within forests continues to mount, there is limited indication of clear trends regarding forest response in the northeastern US. Site conditions may buffer or boost the impacts of heat, drought, and storm events, but the impact of regional changes, such as increased annual temperatures and rising CO_2 concentrations, may be more widespread. Continued changes in temperature, precipitation, and depth, duration, and extent of snow cover could push trees beyond historic environmental thresholds to which they are adapted and result in reduced competitive capacity, growth, and survival. In the northeast, forests have been heavily logged for farms and timber (Foster 1992), and have been impacted by pollution and acid deposition (Likens and Bormann 1974; Schaberg et al. 2001).

Currently, there are mixed reports of how forests are reacting to observable changes in the environment and how they may react in the future. Indeed, one would expect that some species might benefit from climatic perturbations, while others would not. In some forest stands, biomass accumulation over the past 50 years have increased more than predicted (Johnson and Abrams 2009; McMahon et al. 2010; Pan et al. 2011). Johnson and Abrams (2009) hypothesized that the recent observed increases in growth across all age classes, including the oldest age classes, and several genera, is due to anthropogenic causes.

Changes in tree growth rate and/or mortality could have profound impacts to the ecology of forests in the region, including alterations to C pools and other

biogeochemical cycles, hydrological cycles, and species composition, among other outcomes. Increased growth rates have been shown to be inversely related to tree longevity (Johnson and Abrams 2009); therefore, changes could decrease tree survival. Indeed, in several other locales, tree mortality has been higher than expected based on historical data (Allen et al. 2010; van der Maaten-Theunissen and Bouriaud 2012).

The complex interactions between plants and soil, coupled with the range of weather/climate patterns that may occur and the varied response of species to these, highlight a need to better understand the possible changes we may see in regional forest systems. Several researchers are using climate and biomass modeling to project how net primary productivity (NPP) of forests may change in the future; however, understanding how trees and saplings across the northeast have responded to past changes and continue to respond to change will allow us to better calibrate models.

To this end, in this dissertation I have investigated tree response to environmental parameters to assess how trees (1) have responded to past environmental perturbations and (2) may respond to continued and accelerated changes. The longevity of trees is an asset to examining change: growth under a variety of conditions can be assessed and the relationship between environmental change and productivity investigated. In the northeastern US, we have already observed changing abiotic factors that forests are responding to in both negative and positive ways; important questions to ask are, how will tree species in the northeast respond to changes in local temperature, atmospheric CO_2, growing season length, anthropogenic atmospheric inputs and other perturbations?

Which environmental variables have the largest impact on productivity? How will tree physiological characteristics (such as rooting depth, leaf morphology) affect responses to change? How will changes affect nutrient and water budgets? How do site factors moderate or exacerbate tree response?

While there is considerable uncertainty in how trees in the region will respond to rapid environmental change, the three research projects described in the following pages specifically address issues of tree productivity and vigor in terms of climate change. Through these projects, I help elucidate the changes to our forests that are occurring now, but also provide understanding of how trees may respond in the future. Are some tree species responding positively to changes while others are declining? Have the mechanisms that drive tree growth changed in recent years? This research aims to better understand how trees are or will respond to global climate change – information that can inform policy makers and forest managers who must assess future scenarios for forests in the northeastern US.

1.6 References

Aber, J., McDowell, W., Nadelhoffer, K., Alison, M., Berntson, G., Kamakea, M., McNulty, S., Currie, W., Rustad, L., and Fernandez, I. 1998. Nitrogen saturation in temperate forest ecosystems. BioScience **48**(11): 921-934.

Aber, J.D., Goodale, C.L., Ollinger, S.V., Smith, M.-L., Magill, A.H., Martin, M.E., Hallett, R.A., and Stoddard, J.L. 2003. Is nitrogen deposition altering the nitrogen status of northeastern forests? BioScience **53**(4): 375-389. doi: 10.1641/0006-3568(2003)053[0375:indatn]2.0.co;2.

Aber, J.D., Nadelhoffer, K.J., Steudler, P., and Melillo, J.M. 1989. Nitrogen saturation in northern forest ecosystems. BioScience **39**(6): 378-286.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A., and Cobb, N. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for

forests. Forest Ecology and Management **259**(4): 660-684. doi: http://dx.doi.org/10.1016/j.foreco.2009.09.001.

Allen, G.J., Chu, S.P., Harrington, C.L., Schumacher, K., Hoffmann, T., Tang, Y.Y., Grill, E., and Schroeder, J.I. 2001. A defined range of guard cell calcium oscillation parameters encodes stomatal movements. Nature **411**(6841): 1053-1057.

Bailey, S., Horsley, S., Long, R., and Hallett, R. 2004. Influence of edaphic factors on sugar maple nutrition and health on the Allegheny Plateau. Soil Science Society of America Journal **68**(1): 243-252.

Battipaglia, G., Saurer, M., Cherubini, P., Calfapietra, C., McCarthy, H.R., Norby, R.J., and Francesca Cotrufo, M. 2013. Elevated CO2 increases tree-level intrinsic water use efficiency: insights from carbon and oxygen isotope analyses in tree rings across three forest FACE sites. New Phytologist **197**(2): 544-554. doi: 10.1111/nph.12044.

Betts, A.K. 2011. Vermont climat change indicators. Weather, Climate, and Society **3**: 106-115.

Bigras, F., and Bertrand, A. 2006. Responses of Picea mariana to elevated CO2 concentration during growth, cold hardening and dehardening: phenology, cold tolerance, photosynthesis and growth. Tree Physiology **26**(7): 875-888.

Bishop, D.A., Beier, C.M., Pederson, N., Lawrence, G.B., Stella, J.C., and Sullivan, T.J. 2015. Regional growth decline of sugar maple (Acer saccharum) and its potential causes. Ecosphere **6**(10): art179. doi: 10.1890/ES15-00260.1.

Bonan, G.B. 2008. Forests and Climate Change: Forcings, Feedbacks, and the Climate Benefits of Forests. Science **320**(5882): 1444-1449. doi: 10.1126/science.1155121.

Borer, C.H., Schaberg, P.G., and DeHayes, D.H. 2005. Acidic mist reduces foliar membrane-associated calcium and impairs stomatal responsiveness in red spruce. Tree Physiology **25**(6): 673-680. doi: 10.1093/treephys/25.6.673.

Carnicer, J., Coll, M., Ninyerola, M., Pons, X., Sánchez, G., and Peñuelas, J. 2011. Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. Proceedings of the National Academy of Sciences **108**(4): 1474-1478.

Chmielewski, F.-M., and Rötzer, T. 2001. Response of tree phenology to climate change across Europe. Agricultural and Forest Meteorology **108**(2): 101-112.

Christensen, J.H., Hewitson, A., and Busuioc, A. 2007. Regional Climate Projections. Cambridge University Press, Cambridge, United Kingdom.

Climatic Research Unit. 2016. University of East Anglia. Monthly CRU TS3.24 temperature [accessed 4 June 2016]

Comerford, D.P., Schaberg, P.G., Templer, P.H., Socci, A.M., Campbell, J.L., and Wallin, K.F. 2013. Influence of experimental snow removal on root and canopy physiology of sugar maple trees in a northern hardwood forest. Oecologia **171**(1): 261-269. doi: 10.1007/s00442-012-2393-x.

Cunningham, S., and Read, J. 2002. Comparison of temperate and tropical rainforest tree species: photosynthetic responses to growth temperature. Oecologia **133**(2): 112-119.

DeHayes, D.H. 1992. Winter injury and developmental cold tolerance of red spruce. *In* The Ecology and Decline of Red Spruce in the Eastern United States. *Edited by* C. Eagar and M.B. Adams. Springer-Verlag New York Inc., New York, NY, USA. pp. 295-337.

DeHayes, D.H., Schaberg, P.G., Hawley, G.J., and Strimbeck, G.R. 1999. Acid rain impacts on calcium nutrition and forest health. BioScience **49**(10): 789-800.

DeHayes, D.H., Schaberg, P.G., and Strimbeck, G.R. 2001. Red spruce cold hardiness and freezing injury susceptibility. *In* Conifer Cold Hardiness. *Edited by* F. Bigras. Kluwer Academic Publishers, Dordrecht, the Netherlands.

DeHayes, D.H., Waite, C.E., Ingle, M.A., and Williams, M.W. 1990. Winter injury susceptibility and cold tolerance of current and year-old needles of red spruce trees from several provenances. Forest Science **36**: 982-994.

Dixon, R.K., Solomon, A.M., Brown, S., Houghton, R.A., Trexier, M.C., and Wisniewski, J. 1994. Carbon pools and flux of global forest ecosystems. Science **263**(5144): 185-190. doi: 10.1126/science.263.5144.185.

Doak, D.F., and Morris, W.F. 2010. Demographic compensation and tipping points in climate-induced range shifts. Nature **467**(7318): 959-962.

Driscoll, C.T., Lawrence, G.B., Bulger, A.J., Butler, T.J., Cronan, C.S., Eagar, C., Lambert, K.F., Likens, G.E., Stoddard, J.L., and Weathers, K.C. 2001. Acidic deposition in the northeastern United States: sources and inputs, ecosystem effects, and management strategies. BioScience **51**(3): 180-198. doi: 10.1641/0006-3568(2001)051[0180:aditnu]2.0.co;2.

Durán, J., Morse, J.L., Groffman, P.M., Campbell, J.L., Christenson, L.M., Driscoll, C.T., Fahey, T.J., Fisk, M.C., Mitchell, M.J., and Templer, P.H. 2014. Winter climate change affects growing-season soil microbial biomass and activity in northern hardwood forests. Global Change Biology: n/a-n/a. doi: 10.1111/gcb.12624.

Eamus, D., Leith, I., and Fowler, D. 1989. Water relations of red spruce seedlings treated with acid mist. Tree Physiology **5**(3): 387-397. doi: 10.1093/treephys/5.3.387.

Engel, B.J. 2013. Investigating the relationship between modeled calcium depletion and red spruce growth and response to environmental stress. MS Thesis, the University of Vermont. *In* Rubenstein School of Environment and Natural Resources.

Fahey, T.J., Woodbury, P.B., Battles, J.J., Goodale, C.L., Hamburg, S.P., Ollinger, S.V., and Woodall, C.W. 2010. Forest carbon storage: ecology, management, and policy. Frontiers in Ecology and the Environment **8**(5): 245-252.

Field, C.B., Behrenfeld, M.J., Randerson, J.T., and Falkowski, P. 1998. Primary production of the biosphere: integrating terrestrial and oceanic components. Science **281**(5374): 237-240.

Flannigan, M.D., Stocks, B.J., and Wotton, B.M. 2000. Climate change and forest fires. Science of The Total Environment **262**(3): 221-229. doi: http://dx.doi.org/10.1016/S0048-9697(00)00524-6.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., and Snyder, P.K. 2005. Global Consequences of Land Use. Science **309**(5734): 570-574. doi: 10.1126/science.1111772.

Foley, J.A., Levis, S., Prentice, I.C., Pollard, D., and Thompson, S.L. 1998. Coupling dynamic models of climate and vegetation. Global Change Biology **4**(5): 561-579. doi: 10.1046/j.1365-2486.1998.t01-1-00168.x.

Foster, D.R. 1992. Land-Use History (1730-1990) and Vegetation Dynamics in Central New England, USA. Journal of Ecology **80**(4): 753-771.

Fowler, D., Cape, J.N., Deans, J.D., Leith, I.D., Murray, M.B., Smith, R.I., Sheppard, L.J., and Unsworth, M.H. 1989. Effects of acid mist on the frost hardiness of red spruce seedlings. New Phytologist **113**(3): 321-335.

Fromm, J. 2010. Wood formation of trees in relation to potassium and calcium nutrition. Tree Physiology. doi: 10.1093/treephys/tpq024.

Goulden, M.L., Munger, J.W., Fan, S.-M., Daube, B.C., and Wofsy, S.C. 1996. Exchange of carbon dioxide by a deciduous forest: response to interannual climate variability. Science **271**(5255).

Groffman, P., Hardy, J., Fisk, M., Fahey, T., and Driscoll, C. 2009. Climate Variation and Soil Carbon and Nitrogen Cycling Processes in a Northern Hardwood Forest. Ecosystems **12**(6): 927-943. doi: 10.1007/s10021-009-9268-y.

Groffman, P.M., Rustad, L.E., Templer, P.H., Campbell, J.L., Christenson, L.M., Lany, N.K., Socci, A.M., Vadeboncoeur, M.A., Schaberg, P.G., Wilson, G.F., Driscoll, C.T., Fahey, T.J., Fisk, M.C., Goodale, C.L., Green, M.B., Hamburg, S.P., Johnson, C.E., Mitchell, M.J., Morse, J.L., Pardo, L.H., and Rodenhouse, N.L. 2012. Long-term integrated studies show complex and surprising effects of climate change in the northern hardwood forest. Bioscience **62**: 1056-1066.

Groisman, P.Y., Knight, R.W., Zolina, O.G., and Pielke, R. 2013. Recent trends in regional and global intense precipitation patterns. Climate vulnerability **5**: 25-55.

Guilbert, J., Beckage, B., Winter, J.M., Horton, R.M., Perkins, T., and Bomblies, A. 2014. Impacts of projected climate change over the Lake Champlain basin in Vermont. Journal of Applied Meteorology and Climatology **53**(8): 1861-1875. doi: 10.1175/JAMC-D-13-0338.1.

Halman, J.M., Schaberg, P.G., Hawley, G.J., and Eagar, C. 2008. Calcium addition at the Hubbard Brook Experimental Forest increases sugar storage, antioxidant activity and cold tolerance in native red spruce (*Picea rubens*). Tree Physiology **28**(6): 855-862. doi: 10.1093/treephys/28.6.855.

Halman, J.M., Schaberg, P.G., Hawley, G.J., and Hansen, C.F. 2011. Potential role of soil calcium in recovery of paper birch following ice storm injury in Vermont, USA. Forest Ecology and Management **261**: 1539-1545.

Hamburg, S.P., Yanai, R.D., Arthur, M.A., Blum, J.D., and Siccama, T.G. 2003. Biotic control of calcium cycling in northern hardwood forests: acid rain and aging forests. Ecosystems **6**(4): 399-406.

Hayhoe, K., Wake, C., Anderson, B., Liang, X.-Z., Maurer, E., Zhu, J., Bradbury, J., DeGaetano, A., Stoner, A., and Wuebbles, D. 2008. Regional climate change projections for the Northeast USA. Mitigation and Adaptation Strategies for Global Change **13**(5-6): 425-436. doi: 10.1007/s11027-007-9133-2.

Hayhoe, K., Wake, C., Huntington, T., Luo, L., Schwartz, M., Sheffield, J., Wood, E., Anderson, B., Bradbury, J., DeGaetano, A., Troy, T., and Wolfe, D. 2007. Past and future changes in climate and hydrological indicators in the US Northeast. Climate Dynamics **28**: 381-407.

Hedin, L.O., Granat, L., Likens, G.E., Buishan, T.A., Galloway, J.N., Butler, T.J., and Rodhe, H. 1994. Steep declines in atmospheric base cations in regions of Europe and North America. Nature **367**: 351-354.

Huggett, B.A., Schaberg, P.G., Hawley, G.J., and Eagar, C. 2007. Long-term calcium addition increases growth release, wound closure, and health of sugar maple (Acer saccharum) trees at the Hubbard Brook Experimental Forest. Canadian Journal of Forest Research **37**(9): 1692-1700. doi: 10.1139/X07-042.

Huntington, T.G., Richardson, A.D., McGuire, K.J., and Hayhoe, K. 2009. Climate and hydrological changes in the northeastern United States: recent trends and implications for forested and aquatic ecosystemsThis article is one of a selection of papers from NE Forests 2100: A Synthesis of Climate Change Impacts on Forests of the Northeastern US and Eastern Canada. Canadian Journal of Forest Research **39**(2): 199-212. doi: 10.1139/X08-116.

IPCC. 2014. Executive summary of the Intergovernmental Panel on Climate Change.

Johnson, A.H., Friedland, A.J., and Dushoff, J.G. 1986. Recent and historic red spruce mortality: Evidence of climatic influencee. Water, Air, & Soil Pollution **30**(1): 319-330. doi: 10.1007/bf00305203.

Johnson, A.H., and Siccama, T.G. 1983. Acid deposition and forest decline. Environmental Science & Technology **17**(7): 294A-305A. doi: 10.1021/es00113a001.

Johnson, D.W., and Fernandez, I.J. 1992. Soil-mediated effects of atmospheric deposition on eastern U.S. spruce-fir forests. Ecological Studies: Analysis and Synthesis **96**: 235-270.

Johnson, S.E., and Abrams, M.D. 2009. Age class, longevity and growth rate relationships: protracted growth increases in old trees in the eastern United States. Tree Physiology **29**(11): 1317-1328. doi: 10.1093/treephys/tpp068.

Juice, S.M., Fahey, T.J., Siccama, T.G., Driscoll, C.T., Denny, E.G., Eagar, C., Cleavitt, N.L., Minocha, R., and Richardson, A.D. 2006. Response of sugar maple to calcium addition to northern hardwood forest. Ecology **87**(5): 1267-1280.

Kelly, A.E., and Goulden, M.L. 2008. Rapid shifts in plant distribution with recent climate change. Proceedings of the National Academy of Sciences **105**(33): 11823-11826.

Körner, C., Asshoff, R., Bignucolo, O., Hättenschwiler, S., Keel, S.G., Peláez-Riedl, S., Pepin, S., Siegwolf, R.T.W., and Zotz, G. 2005. Carbon flux and growth in mature deciduous forest trees exposed to elevated CO_2. Science **309**(5739): 1360-1362. doi: 10.1126/science.1113977.

Kunkel, K.E., Bromirski, P.D., Brooks, H.E., Cavazos, T., Douglas, A.V., Easterling, D.R., Emanuel, K.A., Groisman, P.Y., Holland, G.J., Knutson, T.R., Kossin, J.P., Komar, P.D., Levinson, D.H., and Smith, R.L. 2008. Observed changes in weather and climate extremes. *In* Weather and Climate Extremes in a Changing Climate: Regions of Focus: North America, Hawaii, Caribbean, and U.S. Pacific Islands. *Edited by* T.R. Karl and G.A. Meehl and C.D. Miller and S.J. Hassol and A.M. Waple and W.L. Murray. Synthesis and Assessment Product 3.3. U.S. Climate Change Science Program Washington, DC. pp. 35-80.

Kunkel, K.E., Stevens, L.E., Stevens, S.E., Sun, L., Janssen, E., Wuebbles, D., Hilberg, S., Timlin, M., Stoecker, L., and Westcott, N. 2013. Regional climate trends and scenarios for the US national climate assessment. Part 1. Climate of the Northeast U.S. NOAA Technical Report NESDIS 142-1.

Lawrence, G.B., Shortle, W.C., David, M.B., Smith, K.T., Warby, R.A.F., and Lapenis, A.G. 2012. Early Indications of Soil Recovery from Acidic Deposition in U.S. Red Spruce Forests. Soil Science Society of America Journal **76**(4): 1407-1417. doi: 10.2136/sssaj2011.0415.

Lazarus, B.E., Schaberg, P.G., Hawley, G.J., and DeHayes, D.H. 2006. Landscape-scale spatial patterns of winter injury to red spruce foliage in a year of heavy region-wide injury. Canadian Journal of Forest Research **36**(1): 142-152. doi: 10.1139/x05-236.

Leakey, A.D.B., Ainsworth, E.A., Bernacchi, C.J., Rogers, A., Long, S.P., and Ort, D.R. 2009. Elevated CO2 effects on plant carbon, nitrogen, and water relations: six important lessons from FACE. Journal of Experimental Botany **60**(10): 2859-2876. doi: 10.1093/jxb/erp096.

Likens, G.E., and Bormann, F.H. 1974. Acid rain: a serious regional environmental problem. Science **184**(4142): 1176-1179. doi: 10.1126/science.184.4142.1176.

Likens, G.E., Driscoll, C.T., and Buso, D.C. 1996. Long-term effects of acid rain: response and recovery of a forest ecosystem. Science **272**(5259): 244-246. doi: 10.1126/science.272.5259.244.

Lovett, G.M., Canham, C.D., Arthur, M.A., Weathers, K.C., and Fitzhugh, R.D. 2006. Forest Ecosystem Responses to Exotic Pests and Pathogens in Eastern North America. BioScience **56**(5): 395-405. doi: 10.1641/0006-3568(2006)056[0395:FERTEP]2.0.CO;2.

Luo, Y. 2007. Terrestrial carbon-cycle feedback to climate warming. Annual Review of Ecology, Evolution, and Systematics **38**: 683-712. doi: 10.2307/30033876.

Marschner, H. 2002. Mineral Nutrition of Higher Plants. 2nd ed. Academic Press, Boston.

Martinez-Vilalta, J., Lopez, B.C., Adell, N., Badiella, L., and Ninyerola, M. 2008. Twentieth century increase of Scots pine radial growth in NE Spain shows strong climate interactions. Global Change Biology **14**(12): 2868-2881. doi: 10.1111/j.1365-2486.2008.01685.x.

McLaughlin, S.B., Andersen, C.P., Hanson, P.J., Tjoelker, M.G., and Roy, W.K. 1991. Increased dark respiration and calcium deficiency of red spruce in relation to acidic deposition at high-elevation southern Appalachian Mountain sites. Canadian Journal of Forest Research **21**(8): 1234-1244. doi: 10.1139/x91-172.

McLaughlin, S.B., and Wimmer, R. 1999. Tansley Review No. 104: Calcium physiology and terrestrial ecosystem processes. New Phytologist **142**(3): 373-417. doi: 10.1046/j.1469-8137.1999.00420.x.

McMahon, S.M., Parker, G.G., and Miller, D.R. 2010. Evidence for a recent increase in forest growth. Proceedings of the National Academy of Sciences **107**(8): 3611-3615.

Meehl, G.A., and Tebaldi, C. 2004. More intense, more frequent, and longer lasting heat waves in the 21st Century. Science **305**(5686): 994-997. doi: 10.1126/science.1098704.

Melillo, J.M., Butler, S., Johnson, J., Mohan, J., Steudler, P., Lux, H., Burrows, E., Bowles, F., Smith, R., Scott, L., Vario, C., Hill, T., Burton, A., Zhou, Y.-M., and Tang, J. 2011. Soil warming, carbon–nitrogen interactions, and forest carbon budgets. Proceedings of the National Academy of Sciences **108**(23): 9508-9512. doi: 10.1073/pnas.1018189108.

Menzel, A., and Fabian, P. 1999. Growing season extended in Europe. Nature **397**(6721): 659-659.

Myneni, R.B., Keeling, C., Tucker, C., Asrar, G., and Nemani, R. 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. Nature **386**(6626): 698-702.

NAPAP. 2005. National Acid Precipitation Assessment Program Report to Congress National Acid Precipitation Assessment Program, Washington, D.C.

National Atmospheric Deposition Program. 2016. NADP/NTN Monitoring. US Geological Survey [accessed 4 May 2016].

NOAA Earth System Research Laboratory Global Monitoring Division. 2016. Monthly Average Mauna Loa CO_2. http://www.esrl.noaa.gov/gmd/ccgg/trends/ [accessed 6 October 2016].

NOAA National Centers for Environmental Information. 2016. Monthly global summaries by station http://www.ncdc.noaa.gov/cdo-web/search [accessed 18 August 2016].

NOAA Regional Climate Centers. 2016. DROUGHT-ACIS: Single station temperature and precipitation data http://drought.rcc-acis.org/ [acessed 14 August 2016].

Northeast Climate Impacts Assessment Synthesis Team. 2007. Confronting climate change in the U.S. Northeast. A report of the Northeast Climate Impacts Assessment.

Pallardy, S.G. 2010. Physiology of woody plants. Academic Press.

Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S., and Hayes, D. 2011. A Large and Persistent Carbon Sink in the World's Forests. Science **333**(6045): 988-993. doi: 10.1126/science.1201609.

Peltola, H., Kilpeläinen, A., and Kellomäki, S. 2002. Diameter growth of Scots pine (Pinus sylvestris) trees grown at elevated temperature and carbon dioxide concentration under boreal conditions. Tree physiology **22**(14): 963-972.

Peters, G.P., Andrew, R.M., Boden, T., Canadell, J.G., Ciais, P., Le Quéré, C., Marland, G., Raupach, M.R., and Wilson, C. 2013. The challenge to keep global warming below 2 C. Nature Climate Change **3**(1): 4-6.

Radoglou, K., and Jarvis, P. 1990. Effects of CO2 enrichment on four poplar clones. I. Growth and leaf anatomy. Annals of Botany **65**(6): 617-626.

Repo, T., Hanninen, H., and Kellomaki, S. 1996. The effects of long-term elevation of air temperature and CO_2 on the frost hardiness of Scots pine. Plant, Cell & Environment **19**(2): 209-216. doi: 10.1111/j.1365-3040.1996.tb00242.x.

Richardson, A.D., Bailey, A.S., Denny, E.G., Martin, C.W., and O'Keefe, J. 2006. Phenology of a northern hardwood forest canopy. Global Change Biology **12**(7): 1174-1188. doi: 10.1111/j.1365-2486.2006.01164.x.

Salzer, M.W., Hughes, M.K., Bunn, A.G., and Kipfmueller, K.F. 2009. Recent unprecedented tree-ring growth in bristlecone pine at the highest elevations and possible causes. Proceedings of the National Academy of Sciences **106**(48): 20348-20353. doi: 10.1073/pnas.0903029106.

Saxe, H., Ellsworth, D.S., and Heath, J. 1998. Tree and forest functioning in an enriched CO2 atmosphere. New Phytologist **139**(3): 395-436.

Schaberg, P.G., and DeHayes, D.H. 2000. Physiological and envrionmental causes of freezing injury to red spruce. *In* Responses of Northern U.S. Forests to Environmental Change. *Edited by* R.A. Mickler and R.A. Birdsey and J.L. Hom. Springer-Verlag, New York. pp. 181-227.

Schaberg, P.G., DeHayes, D.H., and Hawley, G.J. 2001. Anthropogenic Calcium Depletion: A Unique Threat to Forest Ecosystem Health? Ecosystem Health **7**(4): 214-228. doi: 10.1046/j.1526-0992.2001.01046.x.

Schaberg, P.G., DeHayes, D.H., Hawley, G.J., Strimbeck, G.R., Cumming, J., Murakami, P.F., and Borer, C.H. 2000. Acid mist, soil Ca and Al alter the mineral nutrition and physiology of red spruce. Tree Physiology **20**: 73-85.

Schaberg, P.G., Tilley, J.W., Hawley, G.J., DeHayes, D.H., and Bailey, S.W. 2006. Associations of calcium and aluminum with the growth and health of sugar maple trees in Vermont. Forest Ecology and Management **223**(1–3): 159-169. doi: http://dx.doi.org/10.1016/j.foreco.2005.10.067.

Schaberg, P.G., Wilkinson, R.C., Shane, J.B., Donnelly, J.R., and Cali, P.F. 1995. Winter photosynthesis of red spruce from three Vermont seed sources. Tree Physiology **15**: 345-350.

Schwartz, M.D., and Reiter, B.E. 2000. Changes in north American spring. International Journal of climatology **20**(8): 929-932.

Sheppard, L.J. 1994. Causal mechanisms by which sulphate, nitrate and acidity influence frost hardiness in red spruce: review and hypothesis. New Phytologist **127**(1): 69-82.

Shortle, W.C., Smith, K.T., Minocha, R., Lawrence, G.B., and David, M.B. 1997. Acidic deposition, cation mobilization, and biochemical indicators of stress in healthy red spruce. Journal of Envrionmental Quality **26**: 871-876.

Siccama, T.G., Bliss, M., and Vogelmann, H.W. 1982. Decline of Red Spruce in the Green Mountains of Vermont. Bulletin of the Torrey Botanical Club **109**(2): 162-168. doi: 10.2307/2996256.

Silva, L.C.R., and Anand, M. 2013. Probing for the influence of atmospheric CO2 and climate change on forest ecosystems across biomes. Global Ecology and Biogeography **22**(1): 83-92. doi: 10.1111/j.1466-8238.2012.00783.x.

Silva, L.C.R., Anand, M., and Leithead, M.D. 2010. Recent widespread tree growth decline despite increasing atmospheric CO_2. PLoS ONE **5**(7): e11543. doi: 10.1371/journal.pone.0011543.

Soule, P.T., and Knapp, P.A. 2006. Radial growth rate increases in naturally occurring ponderosa pine trees: a late-20th century CO2 fertilization effect? The New phytologist **171**(2): 379-390. doi: 10.1111/j.1469-8137.2006.01746.x.

Tjoelker, M., Reich, P., and Oleksyn, J. 1999. Changes in leaf nitrogen and carbohydrates underlie temperature and CO2 acclimation of dark respiration in five boreal tree species. Plant, Cell & Environment **22**(7): 767-778.

Tritton, L.M., Martin, C.W., Hornbeck, J.W., and Pierce, R.S. 1987. Biomass and nutrient removals from commercial thinning and whole-tree clearcutting of central hardwoods. Environmental Management **11**: 659-666.

USGCRP, Horton, R., Yohe, G., Easterling, W., Kates, R., Ruth, M., Sussman, E., Whelchel, A., Wolfe, D., and Lipschultz, F. 2014. Ch. 16: Northeast. Climate Change Impacts in the United States: The Third National Climate Assessment. *Edited by* J.M. Melillo and T.C. Richmond and G.W. Yohe. U.S. Global Change Research Program.

van der Maaten-Theunissen, M., and Bouriaud, O. 2012. Climate–growth relationships at different stem heights in silver fir and Norway spruce. Canadian Journal of Forest Research **42**(5): 958-969. doi: 10.1139/x2012-046.

Vann, D.R., Strimbeck, G.R., and Johnson, A.H. 1992. Effects of ambient levels of airborne chemicals on freezing resistance of red spruce foliage. Forest Ecology and Management **51**: 69-79.

Way, D.A., and Oren, R. 2010. Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data. Tree Physiology **30**(6): 669-688.

Webb, A.A.R., McAinsh, M.R., Mansfield, T.A., and Hetherington, A.M. 1996. Carbon dioxide induces increases in guard cell cytosolic free calcium. The Plant Journal **9**(3): 297-304. doi: 10.1046/j.1365-313X.1996.09030297.x.

Westing, A.H. 1966. Sugar Maple Decline: An Evaluation. Economic Botany **20**(2): 196-212. doi: 10.2307/4252732.

Wofsy, S.C., Goulden, M.L., Munger, J.W., Fan, S.-M., Bakwin, P.S., Daube, B.C., Bassow, S.L., and Bazzaz, F.A. 1993. Net exchange of CO_2 in a mid-latitude forest. Science **260**(5112): 1314-1317. doi: 10.1126/science.260.5112.1314.

World Data Center for Paleoclimatology and NOAA Paleoclimatology Program. Law Dome ice core data.

CHAPTER 2: COMPARATIVE GROWTH TRENDS OF FIVE NORTHERN HARWOOD AND MONTANE TREE SPECIES REVEAL DIVERGENT TRAJECTORIES AND RESPONSE TO CLIMATE

Alexandra M. Kosiba[a*], Paul G. Schaberg[b], Shelly A. Rayback[c], and Gary J. Hawley[a]

[a] The University of Vermont, Rubenstein School of Environment and Natural Resources, Burlington, VT 05405, USA, p: +1 (802) 656-2911, f: +1 (802) 656-8683, akosiba@uvm.edu, ghawley@uvm.edu

[b] Forest Service, U.S. Department of Agriculture, Northern Research Station, Burlington, VT 05405, USA, p: +1 (802) 656-1715, f: +1 (802) 656-8683, pschaberg@fs.fed.us

[c] The University of Vermont, Department of Geography, Burlington, VT 05405, USA, p: +1 (802) 656-3019, f: +1 (802) 656-3042, srayback@uvm.edu

[*] Corresponding author. *E-mail address*: akosiba@uvm.edu (A.M. Kosiba).

2.1 Abstract

In the northeastern US, tree declines associated with acid deposition-induced calcium depletion have been documented, notably for red spruce (*Picea rubens* Sarg.) and sugar maple (*Acer saccharum* Marsh.). There is conflicting evidence if co-occurring tree species have capitalized on these declines or suffered similar growth reductions; and further, how growth has fluctuated relative to environmental variables. We examined five species along three elevational transects on Mt. Mansfield, Vermont: sugar maple, red spruce, red maple (*Acer rubrum* L.), yellow birch (*Betula alleghaniensis,* Britton), and balsam fir (*Abies balsamea,* [L.] Mill.). We found baseline differences in growth. Red maple and yellow birch had the highest growth, sugar maple and red spruce intermediate, and balsam fir the lowest. While some of year-to-year declines were associated with specific stress events, protracted patterns, such as recent increases in red spruce and red maple growth, were correlated with increased temperature and cooling degree days (a measure of heat index). For most species and elevations, there was a positive association between temperature and growth, but a negative association with growth the following year. Based on our comparisons, for some species growth at Mt. Mansfield aligns with regional trends and suggests that patterns assessed here may be indicative of the broader region.

Key words: *red spruce, sugar maple, yellow birch, red maple, balsam fir*

2.2 Introduction

Regional forests in the northeastern United States (US) reflect temporally and spatially complex land use change in the 19th and 20th centuries that included deforestation, agricultural expansion, and subsequent reforestation (Whitney 1994). Resulting second growth forests were then subjected to novel anthropogenic stress in the 20th century – notably acid deposition-induced nutrient perturbations that altered forest health and productivity (DeHayes et al. 1999; Greaver et al. 2012). In particular, acidic deposition and resulting calcium (Ca) depletion have been associated with health and productivity declines for red spruce (*Picea rubens* Sarg.) (DeHayes et al. 1999) and sugar maple (*Acer saccharum* Marsh.) (Schaberg et al. 2006) – two dominant and economically important tree species in the northeastern US. Added to the stress of pollutants and decades of soil cation depletion, anthropogenic emissions of carbon dioxide (CO_2) and other greenhouse gases have induced changes in the global climate. Greenhouse gas accumulations have led to an increase in the annual mean temperatures in the northeastern US of 0.09°C decade^{-1} (1895-2011), resulting in a lengthening of the freeze-free period and functional growing season (Kunkel et al. 2013). While precipitation has not significantly changed for winter, spring, or summer, fall and annual precipitation totals have increased 0.61 and 0.99 cm decade^{-1}, respectively (Kunkel et al. 2013). Continued changes in temperature and precipitation, alone and in combination with other stressors, could push trees beyond the environmental thresholds to which they are

adapted and result in reduced competitive capacity, growth, and survival for some species compared to others.

Whereas the declines of several tree species associated with acid deposition are well documented in the region, recent research suggests that some of these chronically stressed species are experiencing contemporary growth increases (Kosiba et al. 2013) and possible range expansion (Beckage et al. 2008; Foster and D'Amato 2015). Both of these deviations are hypothesized to be associated with changes in environmental factors, such as elevated atmospheric CO_2 concentrations, fluctuating atmospheric pollution, and rising temperature. Elevated CO_2 has been proposed to cause a fertilization effect in some trees (Salzer et al. 2009; Soule and Knapp 2006), but other findings have not supported this (Bader et al. 2013; Girardin et al. 2016; Körner et al. 2005). While acid deposition initially caused declines in some tree species, the enforcement of the Clean Air Act and subsequent amendments has reduced sulfur (S) and, less dramatically, nitrogen (N) deposition (Burns et al. 2011). Removal of this source of damage could allow for a recovery for chronically stressed species and, further, N deposition can promote growth, particularly in N-limited ecosystems (Aber et al. 1998). Rising temperatures could also extend the functional growing season, especially for temperate conifers that retain foliage year-round (Kosiba et al. 2013).

While anthropogenic stress continues to mount within northeastern forests, there is limited evidence of clear trends in forest response; yet, large alterations in tree growth rates could have profound effects on the ecology of these forests, including changes to

carbon (C) pools, biogeochemical and hydrological cycles, and species composition. These fluctuations could alter important ecosystem services, including ones with direct economic impacts, such as wood products and recreation.

Here, we present growth patterns and trends determined using xylem annual increment measurements for five tree species that characterize the northern hardwood and montane spruce-fir forests: sugar maple, red spruce, red maple (*Acer rubrum* L.), yellow birch (*Betula alleghaniensis,* Britton), and balsam fir (*Abies balsamea,* [L.] Mill.) growing along elevational transects on Vermont's tallest mountain: Mt. Mansfield. We hypothesized that trees would have different growth rates dependent on species, elevation, and year, with some species displaying muted growth rates in recent decades. We expected that sugar maple, a species that has experienced a geographically broad decline since the 1980s (Horsley et al. 2002), and yellow birch, a species with limited reports of decline (van Doorn et al. 2011), would have reduced recent growth. Conversely, we predicted that red spruce would show recent increases in growth at Mt. Mansfield synchronous with a regional growth pattern of unknown origin (Kosiba et al., 2013). We expected that sympatric balsam fir may have experienced competitive reductions in growth concurrent with increases in red spruce growth. Although red maple stocking and growth in the understory has increased regionally (Abrams 1998), growth trends for dominant and co-dominant red maple are unresolved.

By associating the nature and timing of observed growth relative to local weather and pollution data, we assessed how putative environmental drivers may have influenced

32

species growth and productivity over time. Specifically, we anticipated that deposition of S and N would be negatively associated with red spruce and sugar maple growth, particularly in the 1970s-90s when deposition was the greatest. We hypothesized that atmospheric CO_2 concentration, summer temperature, and growing season length would be positively associated with growth and that temperature relationships would strengthen with increasing elevation. We expected that increased fall and spring temperatures would be beneficial to evergreen conifers, as they can photosynthesize outside the traditional growing season when sympatric deciduous trees are leafless. We also predicted that metrics of precipitation would have a variable association with tree growth at Mt. Mansfield considering that these trees persisted through severe droughts in the 1930s and 60s (Dupigny-Giroux 2002) as well as a current pluvial (Pederson et al. 2013).

2.3 Methods

2.3.1 Site description

Mt. Mansfield State Forest, part of the northern Appalachian mountain chain, located in north-central VT (Underhill, VT, USA; 44.5439° N, 72.8143° W), is a 18 000 hectare parcel comprised of multiple forest types across an altitudinal range of approximately 1 000 m, with a summit at 1 339 m. A northern hardwood forest, dominated by sugar and red maple, American beech *(Fagus grandifolia Ehrh.)*, and yellow birch, extends to ~800 m, where it merges in a transition zone with a montane spruce-fir forest, primarily composed of balsam fir and red spruce. Red spruce, a

33

temperate conifer, is frequently found intermixed in the northern hardwood ecotone. The dynamics of the forests are controlled by localized wind events and individual tree mortality; however, historical timber harvest occurred sporadically in the early 20th century through parts of the Mt. Mansfield State Forest (Cogbill 1996). Soils are primarily stony podzols with considerable areas of rock outcrops, particularly approaching the summit (Soil Survey Staff 2015).

The climate of Mt. Mansfield State Forest is continental, encompassing a large temperature range (Fig. S2.1) and is affected by its proximal location to Lake Champlain, a 126 910 hectare lake 24 km west of the study site, which moderates temperature and increases snow fall amounts. The annual mean temperature is 4.2℃ with an average of 154.6 cm of precipitation deposited uniformly throughout the year (Fig. S2.1) (PRISM Climate Group 2004). January is the coldest month and July is the warmest (-10.5°C and 17.6°C average temperature 1925-2012 for study location, respectively) (PRISM Climate Group 2004). Continuous snow cover is the winter norm, persisting over 5 months at higher elevations. Humidity and water availability increase with elevation.

2.3.2 Plot selection

Elevational transects were set up in three of the four watersheds on Mt. Mansfield (Brown's River, Stevensville Brook, and Ranch Brook Watersheds). No transect was established in the fourth watershed because this area has experienced anthropogenic disturbance associated with a commercial ski area. Along each transect, three plots were

selected – one within each of the following elevational zones: low (450-650 m a.s.l.), mid (750-850 m) and high (900-1000 m) (n plots = 9, Fig. 2.1), which align with northern hardwoods, transition, and montane spruce-fir ecotones. No obvious stand mortality or substantial recent disturbance was evident in any of the plots.

Plots contained 10-14 dominant or co-dominant trees of each of the target tree species equally distributed around plot center to avoid differing competition pressures among trees. Trees with obvious bole or crown damage or those growing in anomalous conditions were not selected. We sampled red maple, sugar maple, and red spruce at low elevation; sugar maple, yellow birch, and red spruce at mid elevation; and red spruce and balsam fir at high elevation (Fig. 2.1). Due to differential species densities across the landscape and different number of species sampled per plot, plots were of variable radius (approx. 20-35 m).

We selected species if they were the dominant components of the montane spruce-fir (red spruce and balsam fir) or northern hardwood (sugar maple and yellow birch) forests, or if the species has experienced increased dominance in this latter forest type (red maple; Abrams 1998). A dominant component of the northern hardwood forest, American beech, was not assessed because its growth dynamics have been altered following widespread damage from the beech bark disease complex (Gavin and Peart 1993).
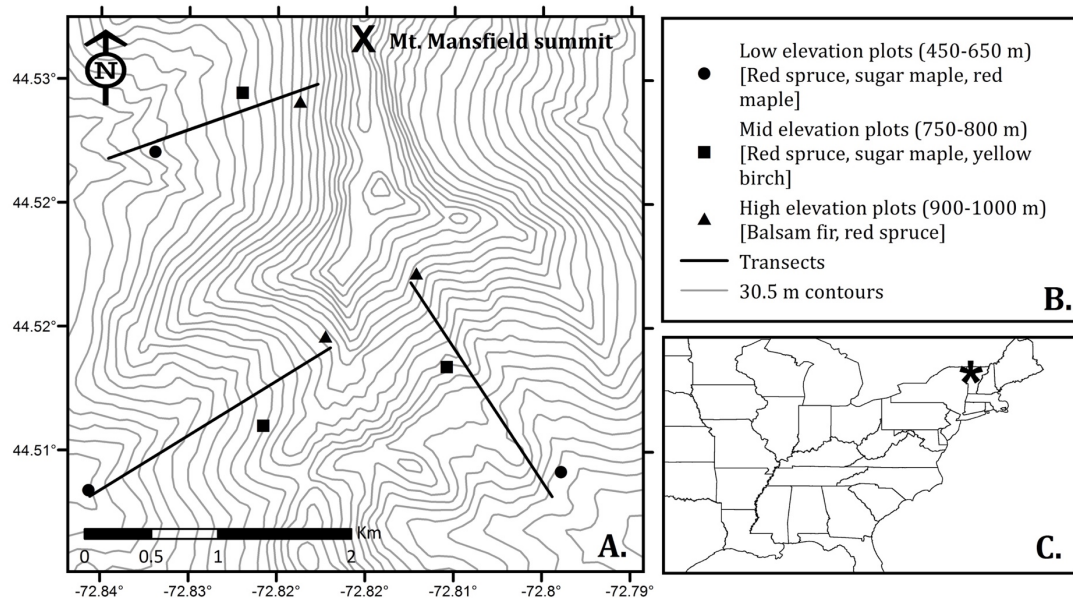
Figure 2.1: Map of plot locations in Mt. Mansfield State Forest, VT, USA, showing (A) three watershed transects, each with three plots located within low, mid, and high elevational zones, (B) species sampled per elevational band, and (C) study site location within the region.

2.3.3 Dendrochronology

We increment cored selected trees ($n = 256$) following standard dendrochronological techniques (Stokes and Smiley 1996) in the fall of 2012. We collected two 5 mm increment cores per tree at stem DBH (diameter at breast height, 1.37 m above ground level) at 180° and perpendicular to the slope. Cores were air-dried, sanded with progressively finer grit sandpaper (ranging from 100-1500 grit dependent on species) and visually crossdated using the list method (Yamaguchi 1991). We microscopically measured rings to 0.001 mm resolution using a Velmex sliding stage unit with MeasureJ2X software (VoorTech Consulting, Holderness, NH) and used the

36

computer program COFECHA to detect and correct for potential crossdating errors in ring series (Holmes 1983). Individual cores were discarded if they were poorly correlated with the master chronology (i.e., below Pearson critical correlation level of 0.328 [99% CL]). For descriptive purposes, tree age (at breast height) was calculated using the maximum number of rings per tree if pith was evident or was estimated per core using a pith indicator (Speer 2010) if pith was not reached. For all trees, we were able to estimate age from at least one core.

For the climate analyses, we detrended, standardized, and prewhitened all raw ring width series and computed biweight robust mean chronologies per species per elevation. Descriptive statistics (sample sizes, R bar, EPS [expressed population signal] and SNR [signal:noise]) of resulting chronologies were calculated using a running 30-year window with 15-year overlap using Spearman correlation coefficients (Table S2.1) and used to select the best detrending and standardization technique. For all series chronologies, a 67%n cubic smoothing spline (CSS) (dplR package in R), using a frequency response cutoff of 0.5 was used. If this spline was a poor fit, a more conservative horizontal line was fit to the data. Traditionally, chronologies are truncated at the year when the EPS value falls below 0.85 (Speer 2010), but this would preclude the use of a portion of both the red maple and sugar maple chronologies at low elevations due to their young age and comparatively small sample size. Because results here were solely used to investigate growth-climate or –deposition relationships rather than for climatic reconstructions, we reduced the threshold to 0.80, allowing for the use of a

common period spanning from 1925-2012. However, lower EPS values indicate that these trees have a weaker stand-wide signal and may be more influenced by micro-site factors, which could mask a cohesive stand-wide signal. Summary statistics and data on the nine plots and resulting chronologies can be found summarized by species and elevational zone in Table S2. Comparisons of growth among species and elevations was done with Kruskal-Wallis rank sums test followed by the Wilcoxon method for pairwise comparisons, as data did not meet the assumptions of equal variance ($P \le 0.05$).

We also averaged raw ring widths by tree and converted measurements into basal area increment (BAI, $cm^2 year^{-1}$) assuming a circular outline of stem cross sections (Cook and Kairiukstis 1990) and accounting for bark thickness. BAI is considered a more meaningful indicator of tree growth from a physiological standpoint because it provides an indication of annual stemwood production while accounting for the effects of stem geometry on radial growth associated with tree-maturation (Hornbeck and Smith 1985; LeBlanc 1992; West 1980). We then computed biweight robust mean BAI chronologies per species per elevation using the dplR package (Bunn et al. 2015) for R (Version 3.1.1)(R Development Core Team 2016) to moderate the effect of large BAI values and/or outliers on the mean chronology.

2.3.4 Growth associated with climate, deposition

Climate data (maximum and minimum monthly temperature [T_{min}, T_{max}] and total monthly precipitation [P]) from 1925-2012 were obtained from the PRISM Climate

Group (PRISM Climate Group 2004). To reduce the number of variables assessed and limit the occurrence of type II errors, we computed seasonal mean (T_{mean}), maximum, and minimum temperatures (Winter: previous December–February, Spring: March–May, Summer: June–August, Fall: September–November), annual water year (previous [p] October to current September) mean temperature, and seasonal and water year precipitation totals. Using monthly data, we also calculated the average temperature for an extended growing season (May–August and June–September) (Fig. S1).

Pollutant S- and N- deposition data by water year were obtained from the Hubbard Brook Experimental Forest (HBEF; Watershed 1), Thorton, NH, USA, spanning 1965-2010 (Likens 2010) (Fig. S1). As this dataset covers more years than the one from Mt. Mansfield (1984-2012) (National Atmospheric Deposition Program 2016) and the datasets were highly correlated (R = 0.94, $P < 0.0001$), we combined them by adjusting HBEF data via regression analysis and then added this to the Mt. Mansfield dataset for continuous coverage from 1965-2012. We gathered data of annual atmospheric CO_2 concentration from Mauna Loa Observatory, HI, USA (NOAA Earth System Research Laboratory Global Monitoring Division 2016) and from Law Dome, Antarctica ice core data (World Data Center for Paleoclimatology and NOAA Paleoclimatology Program); combined for a CO_2 dataset spanning 1925-2012. We also collected the following data: Vermont Palmer Drought Severity Index (PDSI) (National Drought Mitigation Center 2014), and three measures of degree days: growing degree days (GDD, measured as cumulative degrees > 5°C [41°F]), cooling degree days (CDD,

> 18.3°C [65°F]) and heating degree days (HDD, < 18.3°C [65°F])) for Burlington International Airport, VT (NOAA National Weather Service 2014), and monthly Standardized Precipitation-Evapotranspiration Index (SPEI, 1-month sum) for VT, a multi-scalar drought and temperature index that includes the effects of evapotranspiration (National Drought Mitigation Center 2012). These datasets were chosen based on proximity or length of record; these datasets covered 1945-2012 (Fig. S1).

Growth relationships with climate, deposition, and other data were assessed using treeclim (Zang and Biondi 2015) for R. Treeclim uses time-dependent bootstrapped resampling (1000 iterations) to test for linear correlations between the residual ring width data and each subvector of the climate matrix (Zang and Biondi 2015). To investigate the dominant drivers of tree growth, we first examined stationary correlations over the common period (or a limited subset for climate/deposition datasets spanning fewer years), including previous year's climate and deposition on current year's growth, to investigate the dominant drivers of tree growth. Second, to assess the temporal stability of climate-growth relationships, we used the significant variables from the first analysis to evaluate relationships with growth per temporal quartile. Third, we used principal component analysis to examine common modes of growth among species per elevation. Using the first principle component (PC) per elevation, we again examined stationary correlations with our climate and deposition variables. For all analyses, Spearman correlation coefficients were computed with a 99% CI to reduce the number of input variables, type II errors, and covariation among variables.

Lastly, we used the significant climate and pollution deposition variables from the first analysis to model growth per species and elevation. All variables were first standardized ($\mu = 0$, $\sigma = 1$). If multicollinearity was evident among variables, we used forward stepwise linear regression (using AIC criteria) to reduce selected variables. For all species and elevation pairs, we then created linear models to best explain growth; non-significant variables were removed and the model was reassessed. Using the residuals of these models, we then regressed CO_2 data to examine if, after accounting for the dominant climate effects, there was a detectable CO_2 affect (Girardin et al. 2016).

2.3.5 Comparisons with other chronologies and datasets

We used other crossdated (± 0 yrs.) tree ring chronologies collected by the authors or affiliates (Engel et al. 2016; Hansen 2015; Weverka 2012) to compare growth trends on Mt. Mansfield to other locations in the region using Pearson Product-Moment Correlation. All chronologies were collected following similar methods described above and converted into BAI. Due to age limits of the chronologies from the HBEF, we constrained analyses to 1950-2012 for sugar maple and yellow birch (Hansen 2015).

2.4 Results

2.4.1 Absolute growth

We found significant and consistent growth differences among the species ($P < 0.001$) (Fig. 2.2A). Yellow birch and red maple had the largest mean growth (mean BAI

± SD: 15.2 ± 5.1 and 13.0 ± 4.3 cm^2, respectively). Sugar maple and red spruce were intermediate in growth (7.1 ± 2.0 and 7.7 ± 2.9 cm^2, respectively) and balsam fir had the lowest growth (4.7 ± 2.4 cm^2). These patterns were fairly stable over the quartiles of the chronology, excluding the first quartile (1925-1946) and the most recent growth (2002-2012).

Growth was consistently higher at low and mid elevations compared with high elevation (Fig. 2.2B) ($P < 0.001$). For the chronology overall and for the central two quartiles (1947-1968, 1969-1990), growth was greater at mid elevations than low elevation. For all three elevations, overall growth increases in the most recent decade were driven by increases in two species: red spruce and red maple.

For the two species sampled at multiple elevations (sugar maple and red spruce), species-specific growth across elevations showed differing patterns (Fig. 2.3). Sugar maple at low elevation had significantly higher mean growth than at mid elevation (8.1 ± 2.6 and 6.5 ± 1.7 cm^2, respectively; $P < 0.01$), juxtaposing the general patterns that mid elevation plots had higher mean BAI overall. For both elevations, sugar maple maximum growth was only slightly higher than the mean and occurred in the third quartile: 1985-95 for low elevation and 1970-90 for mid elevation trees. Following this peak, both chronologies exhibited slight declines in growth. Mid elevation red spruce had the highest average growth (13.0 ± 4.3 cm^2), with low elevation intermediate (7.8 ± 3.1 cm^2), and high elevation the lowest (4.1 ± 3.2 cm^2) (Fig. 2.3) ($P < 0.01$). For red spruce at all elevations, maximum growth occurred in 2012 (year of sampling), and was considerably

higher than overall chronology means. At both mid and high elevations, four out of five

years of maximum red spruce growth occurred in the years immediately prior to sampling

(2009-12).
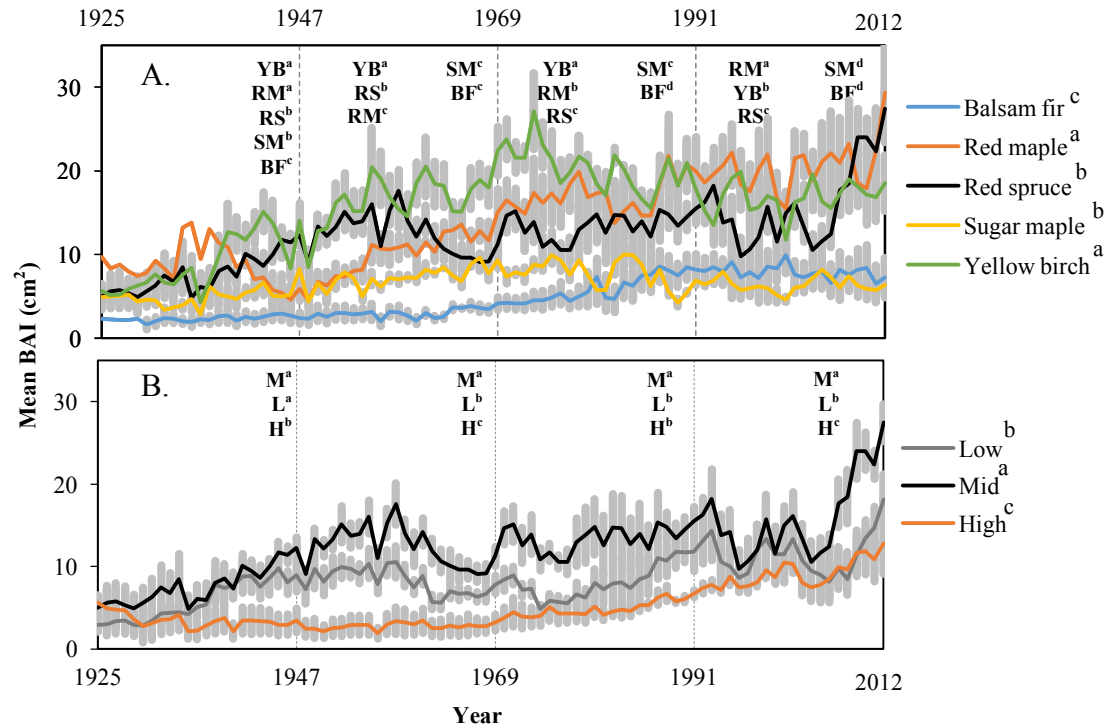
Figure 2.2: Biweight robust mean basal area increment (BAI, cm^2 ± SD shown with grey bars) by (A) species and (B) elevation from 1925-2012. A non-parametric Kruskal-Wallis test, followed by Wilcoxon Each Pair test, using species, elevation, and year as factors was significant for the three factors (P < 0.001). Different letters following species and elevations categories denote significant differences overall (P < 0.001). The model was also significant for each of the four 21-year quartiles (1925-1946, 1947-1986, 1969-1990, 1991-2012; denoted with grey dashed line, P < 0.001), for species and elevation, but year was only significant for the period 1925-1946 (BF: balsam fir, RM: red maple, RS: red spruce, SM: sugar maple, YB: yellow birch, L: low elevation [450-650 m a.s.l.], M: mid [750-800 m], and H: high [900-1000 m]). Bonferonni adjusted P-values were used.

2.4.2 Growth trends

Species-to-species comparisons per elevation (Fig. 2.3) reveal that peak growth varied, but for all species, the highest growth years were in the second half of the chronology (e.g., 1960s to 2012). At low elevation, both red spruce and red maple displayed recent increases in growth, while sugar maple did not. For all three species at low elevation, peak growth roughly coincided; although for both red maple and red spruce, maximum growth persisted longer and was more recent than for sugar maple. At mid elevation, highest growth for yellow birch and sugar maple corresponded (1960s-80s), yet red spruce peak growth occurred when these neighboring species were showing decreases. At high elevation, balsam fir experienced maximum growth at the end of the 1980s through the early 2000s.

The recent growth surge of red spruce was not seen in the other species at mid elevation. While this increase was most pronounced for low and mid elevation red spruce, red spruce growing at high elevation, where growth over the length of the chronology was more stable and constrained compared to lower elevation red spruce, also exhibit this upward trend. At all elevations, red spruce exhibited periods of depressed growth beginning in the mid-twentieth century that align with suspected or known winter injury events (Johnson et al. 1986; Lazarus et al. 2004).
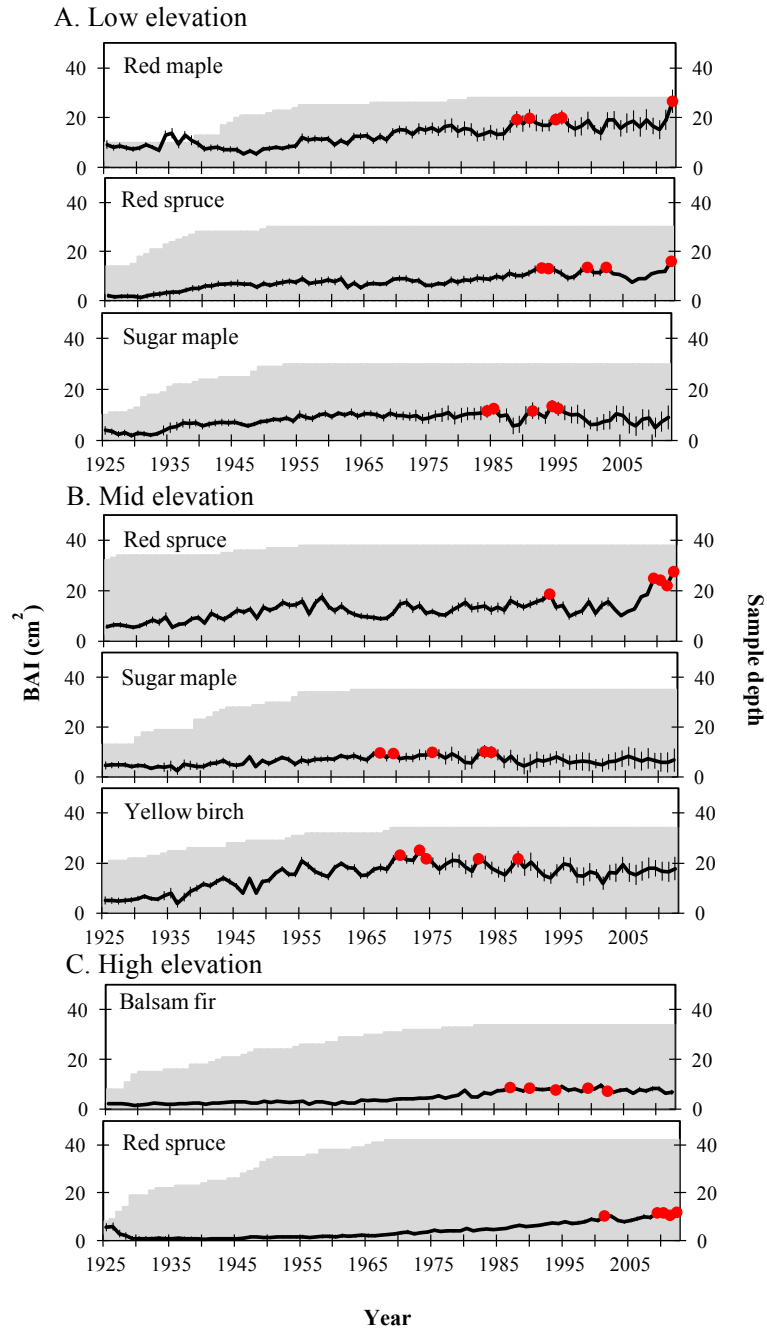
Figure 2.3: Mean basal area increment (BAI, cm^2, solid black line) (± SD) chronologies per species and elevational zone: (A) low 450-650, (B) mid 750-800, and (C) high 900-1000 m a.s.l. elevation from 1925-2012 in Mt. Mansfield State Forest, VT. Number of trees contributing the mean are shown with grey bars. Red circles designate the five highest growth years per chronology.

2.4.3 Climate and deposition relationships with growth

Examining climate-growth relationships using the principal components (PCs) derived from chronologies per elevation, we saw that overall, all three elevations display a positive correlation between growth and growing season temperature ($P < 0.01$, Table 1). At low elevation, Summer T_{mean} was best associated with growth ($\rho = 0.38$), along with NH_4^+ deposition ($\rho = 0.35$). Both mid and high elevations showed positive correlations with CDD and growing season temperatures (e.g., Spring, Summer T_{mean}). However, non-growing season temperatures and PDSI were important to high elevation trees only. A model of growth at both mid and high elevations identified CDD as the best predictor ($R^2_{adj} = 0.13$, $P = 0.001$ and $R^2_{adj} = 0.10$, $P = 0.04$, respectively). At low elevation, the growth model included a positive effect of May-Aug T_{mean} ($R^2_{adj} = 0.08$, $P = 0.005$). Atmospheric CO_2 concentration was not significantly associated with growth for any of the species or elevations using either growth, PCs by elevation, or residuals (not shown).

At high elevation balsam fir growth was positively correlated with temperature ($P < 0.01$; Table 2). The strongest positive correlations occurred with previous year's (p) Fall T_{min} ($\rho = 0.38$) and Spring T_{min} ($\rho = 0.24$), while there was a negative association with pCDD ($\rho = -0.37$) and pGDD ($\rho = -0.31$) (Table 2). Although significant overall ($P < 0.01$), the strength of the relationships between balsam fir growth and other variables declined in the middle of the chronology (1969-1990). The best model to predict balsam

fir growth (R^2_{adj} = 0.19, P = 0.0008) included a negative effect of pCDD (R^2_{adj} = 0.13, P=0.002) and a positive effect of Spring T_{min} (R^2_{adj} = 0.05, P = 0.04).

Red spruce exhibited the strongest positive relationships ($P < 0.01$) with temperature (CDD, GDD, and water year T_{mean}), including a strong correlation with non-growing season temperature was important to red spruce (Table 2). Indeed, water year T_{mean} was positively associated with red spruce growth at all elevations and while not always significant, displayed a consistently positive correlation with growth across quartiles. Like other species, pCDD was strongly, negatively correlated to red spruce growth, and this pattern persisted through time ($P < 0.01$). At both mid and high elevations, there was a positive association between growth and pWinter T_{max} (ρ = 0.27 and 0.23, respectively). This relationship was negative in the third quartile, 1969-1990. Interestingly, pNO$_3$ deposition was negatively associated with growth of red spruce at low elevation ($P < 0.01$, ρ = -0.37), which strengthened through the quartiles of the chronology.

For red spruce at low elevation, we found that the negative effects of both HDD (R^2_{adj} = 0.11, $P<0.0001$) and pCDD (R^2_{adj} = 0.15, $P<0.0001$) were the best predictors of growth in a linear model (R^2_{adj} = 0.40, $P>0.0001$). At mid elevation, the best model (R^2_{adj} =0.31, $P<0.0001$) included a positive effect of water year T_{mean} (R^2_{adj} =0.13, P = 0.0006) and, like low elevation, a negative effect of pCDD (R^2_{adj} = 0.12, P = 0.0002). At high elevation, the best model included a negative effect of both pCDD (R^2_{adj} =0.09 , P =

0.0001) and HDD (R^2_{adj} =0.11 , P = 0.018), and a positive effect of GDD (R^2_{adj} =0.19 , P = 0.017) (overall model R^2_{adj} =0.35, P<0.0001).

Measures of degree-days and temperature were also important for red maple at low elevation (P < 0.01) (Table 2). Growing season temperature (i.e., Summer T_{mean}, June-September T_{mean}, and CDD) was positively correlated with red maple growth (P < 0.01, ρ = 0.30, 0.26, and 0.39, respectively), while preceding year's heat accumulation (pCDD) was negatively associated (ρ = -0.34). For red maple, the best growth model (R^2_{adj} = 0.20, P = 0.0004) included a negative effect of pCDD (R^2_{adj} = 0.11, P = 0.002) and a positive effect of Summer T_{mean} (R^2_{adj} = 0.08, P = 0.006).

At low elevation, sugar maple growth was not correlated (P > 0.01) with the selected variables (Table 2); therefore, we were unable to create a model of growth. For sugar maple at mid elevation, Summer T_{mean} was positively associated with growth (P < 0.01, ρ = 0.26). However, this relationship was not consistent through the quartiles. Like many of the other species in this study, growth for these trees also exhibited a negative correlation (P < 0.01) with pSummer T_{mean} (ρ = -0.25) and pSummer T_{max} (ρ = -0.27), as well as with pCDD (ρ = -0.38). To model growth, we were limited by the number of and high collinearity of input variables. Both pSummer T_{mean} and pSummer T_{max} explained a similar amount of growth variation when fit separately (R^2_{adj} = 0.06, P=0.01 for both).

We did not find any negative correlations between yellow birch growth and the variables selected (Table 2.2). Yellow birch, however, did display positive associations with summer T_{mean} (P < 0.01, ρ = 0.29) and these trends were consistent through the

quartiles of the chronology. However, when we modeled growth using Summer T_{mean}, only a small amount of growth variation was explained ($R^2_{adj} = 0.07$, *P*=0.008).

Table 2.1: Significant correlations from stationary climate-growth assessments for all species combined per elevation for trees from Mt. Mansfield, VT, as evaluated using Principal Component analysis (1925-2012). Significance based on 99% CI.

Elevation[a]	Positive		Negative	
	Variable[b,c]	Cor. Coef.	Variable[b]	Cor. Coef.
High	Water year T_{mean}	0.34	HDD	-0.38
	pWinter T_{max}	0.25		
	pFall T_{min}	0.40		
	Winter T_{mean}	0.26		
	Spring T_{mean}	0.27		
	CDD	0.37		
	GDD	0.39		
	PDSI	0.36		
Mid	Summer T_{mean}	0.33		
	May-June T_{mean}	0.32		
	Jun-Sep T_{mean}	0.36		
	CDD	0.34		
	pFeb SPEI	0.43		
	pDec SPEI	0.38		
Low	pSpring T_{max}	0.25	Mar SPEI	-0.27
	Summer T_{mean}	0.38		
	May-Aug T_{mean}	0.28		
	pMar SPEI	0.28		
	NH_4^+	0.35		

[a] Low = 450-650 m a.s.l., mid = 750-850 m, and high = 900-1000 m
[b] p = previous year, T = temperature, Min = minimum, GDD = growing degree days (cumulative degrees > 5°C [41°F]), HDD = heating degree days (cumulative days < 18.3°C [65°F]), CDD = cooling degree days (cumulative degrees > 18.3°C [65°F]), CDD = cooling degree days (cumulative degrees > 18.3°C [65°F]), SPEI = Standardized Precipitation-Evapotranspiration Index, Winter: previous December–February, Spring: March–May, Summer: June–August, Fall: September–November. For more information on variables see methods.
[c] Not all variables span the entire chronology (1925-2012, 1945-2012, or 1965-2012). See methods.

Table 2.2: Correlations from stationary climate-growth assessments from Mt. Mansfield, VT, shown by species and elevation for the entire chronology (1925-2012) and by chronology quartile. Coefficients in bold text are significant at 99% CI.

Species	Elevation[a]	Variable[b]	Overall 1925-2012[c]	Quartiles 1925-1946	1947-1968	1969-1990	1991-2012
Balsam fir	High	pFall T_{min}	**0.38**	0.29	0.48	0.44	0.30
		Spring T_{min}	**0.24**	0.17	0.59	0.19	0.08
		pCDD	**-0.37**		-0.47	-0.17	**-0.88**
		pGDD	**-0.31**		-0.48	0.03	-0.88
Red maple	Low	CDD	**0.39**		0.24	0.34	**0.65**
		Summer T_{mean}	**0.30**	0.37	0.22	0.31	**0.55**
		Jun-Sep T_{mean}	**0.26**	0.43	0.28	0.26	0.43
		pCDD	**-0.34**		-0.59	-0.27	-0.17
Red spruce	Low	Water year T_{mean}	**0.43**	**0.44**	**0.52**	0.24	0.48
		pFall T_{min}	**0.32**	0.19	0.41	0.23	**0.53**
		Winter T_{mean}	**0.26**	0.14	0.39	-0.04	0.52
		Spring T_{mean}	**0.36**	0.34	0.37	0.26	0.46
		May-Aug T_{mean}	**0.28**	0.27	0.29	0.16	0.37
		Jun-Sep T_{mean}	**0.43**	0.31	**0.48**	0.01	0.13
		pCDD	**-0.35**		-0.40	-0.31	-0.39
		HDD	**-0.37**		-0.46	-0.05	-0.50
		GDD	**0.38**		0.46	0.21	0.37
		PDSI	**0.36**		0.44	-0.56	0.10
		pNO_3^-	**-0.37**		-0.164	-0.17	-0.46
	Mid	Water year T_{mean}	**0.27**	0.35	**0.53**	0.17	0.42
		pWinter T_{max}	**0.27**	0.38	**0.55**	-0.19	0.37
		Jun-Sep T_{mean}	**0.26**	0.29	0.49	0.12	0.17
		pCDD	**-0.41**		-0.38	-0.51	-0.40
		GDD	**0.34**		0.44	0.13	0.39
		May SPEI	**-0.30**		-0.15	-0.29	-0.44
	High	Water year T_{mean}	**0.36**	0.28	**0.47**	0.27	0.41
		pWinter T_{max}	**0.23**	0.36	0.46	-0.07	0.24
		pFall T_{min}	**0.32**	0.05	**0.53**	-0.28	0.52
		Winter T_{mean}	**0.26**	0.16	0.22	0.13	0.41
		Summer T_{max}	**0.27**	-0.03	0.31	0.38	0.45
		Fall T_{mean}	**0.23**	0.39	0.28	0.25	0.11
		Jun-Sep T_{mean}	**0.31**	0.06	**0.55**	0.48	0.41
		May-Aug T_{mean}	**0.33**	0.04	0.39	0.46	0.20
		pCDD	**-0.32**		-0.44	-0.29	-0.37
		CDD	**0.42**		0.36	0.43	0.50
		HDD	**-0.34**		**-0.45**	0.07	-0.44
		GDD	**0.45**		0.50	0.30	-0.49
Sugar maple	Low	N/S					
	Mid	pSummer T_{mean}	**-0.25**	-0.12	-0.40	-0.23	-0.22
		pSummer T_{max}	**-0.27**	-0.25	-0.38	-0.28	-0.09
		Summer T_{mean}	**0.26**	0.19	0.45	0.08	0.33
		pCDD	**-0.38**		**-0.55**	-0.29	-0.23
Yellow birch	Mid	Summer T_{mean}	**0.29**	0.37	0.29	0.29	0.29

[a] Low = 450-650 m a.s.l., mid = 750-850 m, and high = 900-1000 m
[b] p = previous, T = temperature, Max = maximum, Min = minimum, PDSI = Vermont Palmer Drought Severity Index, GDD = growing degree days (cumulative degrees > 5°C [41°F]), HDD = heating degree days (cumulative days < 18.3°C [65°F]), CDD = cooling degree days (cumulative degrees > 18.3°C [65°F]), SPEI = Vermont Standardized Precipitation-Evapotranspiration Index, Winter: previous December–February, Spring: March–May, Summer: June–August, Fall: September–November. For more information on variables see methods.
[c] Not all variables span the entire chronology (1925-2012, 1945-2012, or 1965-2012). See methods.

2.4.4 Comparisons with other chronologies

We compared red spruce growth from this study with red spruce from a wide range of plots in VT, New Hampshire, and Massachusetts (*n* trees = 452) collected in 2010, 2011, and 2012 (Engel et al. 2016; Kosiba et al. 2013; Weverka 2012). The chronologies were significantly correlated (R = 0.92, *P*< 0.0001; Fig. 2.4A). We also compared sugar maple and yellow birch from this study to those species from the HBEF collected in 2012 (Hansen 2015). For sugar maple (*n* trees HBEF = 163; Fig. 2.4B) the chronologies were significantly correlated (R = 0.57, *P* < 0.0001), but for yellow birch (*n* trees HBEF = 170; Fig. 2.4C) they were not (R = -0.19, *P*=0.13).

A. Red spruce

Region (n = 452)   Mt. Mansfield (n = 106)

R = 0.92
$P < 0.0001$

B. Sugar maple

HBEF (n = 163)   Mt. Mansfield (n = 63)

R = 0.57
$P < 0.0001$

Mean BAI (cm^2)

C. Yellow birch

HBEF (n = 170)   Mt. Mansfield (n = 34)

R = -0.19
$P = 0.13$

Year
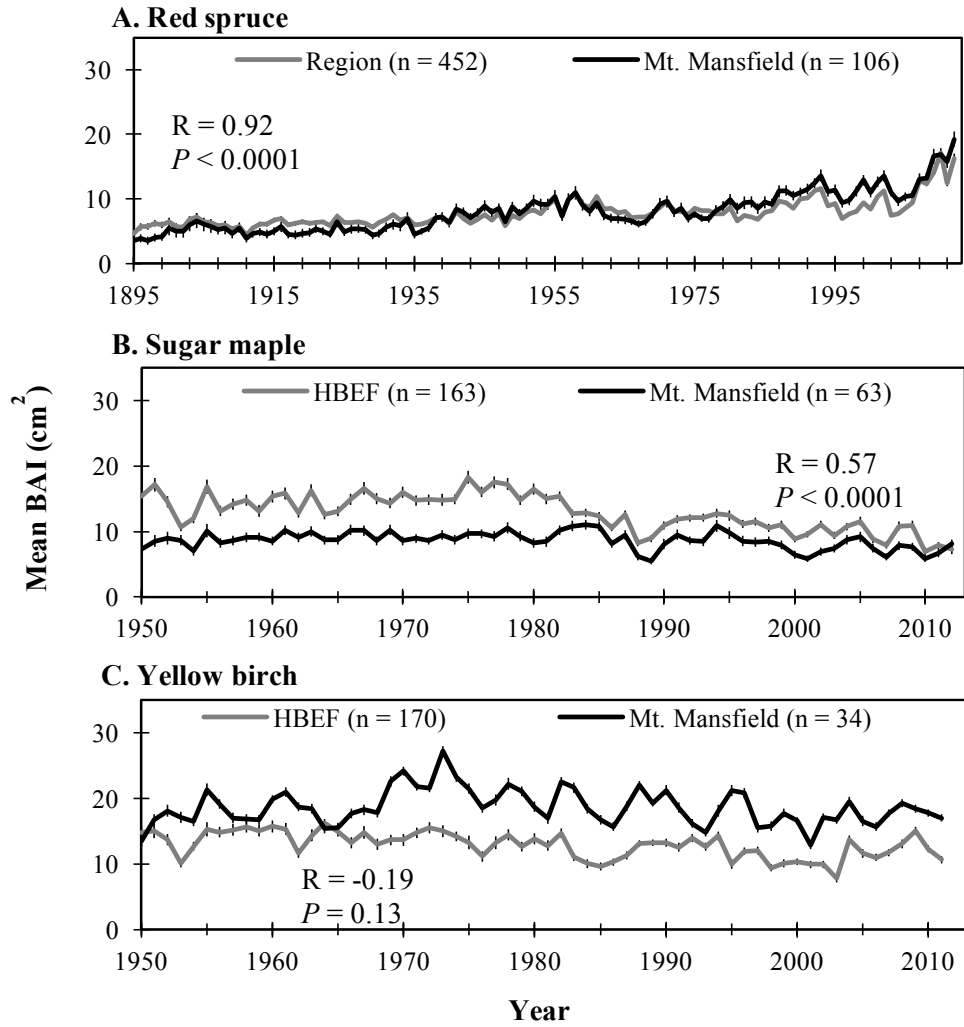
Figure 2.4: Comparisons of mean growth (BAI ± SD) for red spruce, sugar maple, and yellow birch from this study on Mt. Mansfield to (A) sugar maple and (B) yellow birch at Hubbard Brook Experimental Forest (HBEF), NH, and (C) red spruce in the region (34 plots in VT, NH, MA). Spearman correlation coefficients (R) and associated *P*-values are shown in each figure. Chronologies at HBEF were limited to 1950-2012.

2.5 Discussion

2.5.1 Patterns of growth

Significant and consistent growth differences among the species highlight their divergent silvics (Burns and Honkala 1990). Yellow birch and red maple, which are intermediate in shade tolerance with moderately high growth potentials (Burns and Honkala 1990), had the greatest mean growth. Sugar maple and red spruce, which are both shade tolerant with the ability to display higher growth when a mature component of the canopy (Burns and Honkala 1990), were intermediate in growth, while balsam fir, highly shade tolerant and with the potential for constrained growth with elevated stocking (Burns and Honkala 1990), displayed the lowest growth. Species-to-species comparisons per elevation reveal that peak growth varied over time, but for all species, the highest growth years occurred in the second half of the chronology.

Lower growth and more muted disparities among the species in the first quartile of the chronology may signify that competition during stand maturation was a strong constraint on growth. Historical anthropogenic land clearing has left a legacy on the forests of Mt. Mansfield evident in the ages of sample trees (Table S2.1). In the absence of a substantial natural disturbance, it is likely that selective logging has resulted in the age divergence among the species and elevations. Cogbill (1996) outlined several logging events in the Stevensville Brook Watershed on the western flank of Mt. Mansfield, and it is suspected that widespread harvesting occurred in the other

53

watersheds as well. Assessment of stand dynamics (data not shown) confirmed that release events were stochastic and not consistent within or among plots.

Some of the year-to-year variations in growth (Fig. 2.3) can be attributed to known biotic and abiotic stressors. For example, specific low growth years for sugar maple are likely associated with the 1993 infestation of pear thrips (*Taeniothrips inconsequens* [Uzel]) and a late spring frost in 2010 (Hufkens et al. 2012; Vermont Agency of Natural Resources Department of Forest Parks & Recreation 2010). While this late frost event could have affected sugar maple at low elevation, because no coincident downturn in growth was evident at mid elevation (Fig. 2.3), we suspect that mid elevation trees were unaffected due to a later timing of bud break relative to frost exposure. Additionally, a severe ice storm in 1998 that broke the limbs and crowns of many hardwood species (Rhoads et al. 2002), was reported for many mid and high elevation sites (Vermont Agency of Natural Resources Department of Forest Parks & Recreation 2013). Areas of high ice loading align with our mid elevation zone, and when followed by a severe drought in 1999, may have caused the growth declines for yellow birch and sugar maple evident in 1999 through 2000 (Fig. 2.3). Lastly, declines in growth apparent for red spruce at all elevations (Fig. 2.3) correspond with documented winter injury events (Johnson et al. 1986), including in 2003, which was a severe event across the region (Lazarus et al. 2004).

At high elevation, balsam fir experienced maximum growth at the end of the 1980s through the early 2000s (Fig. 2.3), which parallels the documented decline of red

54

spruce (Lazarus et al. 2004) and suggests that balsam fir was able to capitalize on the resulting foliar losses and growth declines of sympatric red spruce. Balsam fir is not affected by winter injury due to its extreme cold tolerance (DeHayes et al. 2001). Since 2003, a substantial winter injury event has not occurred in the region (Vermont Agency of Natural Resources Department of Forest Parks & Recreation 2013), which may in part, explain the increase in red spruce growth relative to balsam fir. However, despite some differences over time, at high elevation plots, both red spruce and balsam fir had relatively low growth due to limitations in growing season length and lower annual temperature.

We detected growth reductions for sugar maple at both low and mid elevations that are temporally consistent with regional declines attributed to acid deposition-induced Ca depletion combined with other stress exposures (Schaberg et al. 2006). In this study, growth declines were more dramatic for sugar maple at mid elevation then at low elevation. As acid deposition is more severe with increasing elevation (Johnson and Siccama 1983), mid elevation sugar maple may have suffered from Ca depletion more extensively and earlier than trees at lower elevation. Indeed, other studies have indicated that sugar maple at mid and high elevations display greater signs of physiological stress from Ca depletion than those at low elevation (Minocha et al. 2010). Although sugar maple growth measurements reported here are low compared to the other sampled species, they are not atypical when compared to other dendrochronological studies in

eastern North America (Bishop et al. 2015; Duchesne et al. 2003; Hansen 2015; Long et al. 2009).

Red spruce on Mt. Mansfield have experienced a recent growth increase consistent with other locations (Fig. 2.2, 2.3) (Kosiba et al. 2013). This increase is especially pronounced at mid elevations, which has been previously demonstrated (Kosiba et al. 2013). However, the other species at mid elevations did not display an analogous increase in growth, discounting stand dynamics for this rapid change.

Regardless of species-specific growth, mid elevation plots displayed significantly higher growth than low and high elevation plots. This could signify that mid elevation sites provide more advantageous conditions for tree growth than either lower or higher elevation (e.g., for red spruce), or it could be confounded by the fact that the fastest growing species for all quartiles (yellow birch) was only sampled at mid elevations.

Red maple also exhibited increased growth recently. However, since this study surveyed a relatively small number of red maple, and comparably few studies have examined red maple growth in the region, it is difficult to assess the extent of this growth surge at this time (see Silva et al. 2010; Zhang et al. 2015). Additionally, because red maple was only sampled at low elevation, we do not to know if elevation influences this apparent growth increase. Limited reports on red maple have revealed that its abundance increased dramatically in the 20th century (Siccama 1971), due in part to its purported niche as a "super-generalist" and large ecological amplitude, which permitted competitive growth advantages at a range of site conditions (Abrams 1998).

56

2.5.2 Relationships with climate and deposition

As expected, growth associations among species and elevations had differing relationships to local climate and deposition. Two general growth associations were evident: (1) a positive correlation with higher temperature in the year of growth (particularly for red maple and red spruce, and to a lesser extent, balsam fir, yellow birch, and sugar maple) and (2) a negative correlation with excessive heat (CDD: cumulative temperatures > 18.3°C) during the previous year (for all species except yellow birch). Positive relationships between temperature and growth imply that low temperature restricted growth. Negative relationships between temperature and growth the following year suggest a legacy effect of higher temperature, conceivably through limitations of C or other compulsory elements. For example, higher temperature could increase contemporary growth if the tree consumes C for immediate needs, such as increased maintenance respiration, growth, or reproductive buds, rather than to store C to support growth the next year (Rennenberg et al. 2006). Similarly, temperature-induced increases in growth could result in the sequestration of other nutrients (e.g., N, Ca) that temporarily become limiting and indirectly suppress growth the following year (Rennenberg et al. 2006).

Using CDD in growth-climate relationships provides a readily available index of integrated heat exposure that was consistently associated with growth for trees at Mt. Mansfield. Measures of growing season temperatures were important for both mid and low elevations, while water year temperature and pFall T_{min} were important at high

elevations. Trees at both high and mid elevations displayed a positive growth correlation with CDD. By quartile, it is clear that climate-growth relationships were not steady through time (Table 2.2). For some species and variables, associations reversed for one or more quartiles, complicating our ability to predict tree responses to these variables.

Non-growing season temperature was important for the two conifers in this study. For both balsam fir and red spruce, mild autumn temperatures can delay cold hardening, which allows the foliage to remain photosynthetically active for a prolonged period. Additionally, because red spruce is a temperate conifer that can photosynthesize in fall, winter, and spring, provided that temperatures are moderate (Schaberg and DeHayes 2000), it has been hypothesized that the notable and recent increase in growth could be due to climatic warming that has lengthened the functional growing season for red spruce (Kosiba et al. 2013).

At mid elevations, there was a positive association between red spruce growth and previous Winter T_{max}, suggesting that warmer winter temperatures could provide increased growth opportunities for this species. This finding has been reported by others (Cook et al. 1987; McLaughlin et al. 1987). Interestingly, this relationship was negative in the third quartile, 1969-1990, a period of peak acid deposition (Greaver et al. 2012) and documented red spruce decline (Hornbeck et al. 1987; Johnson et al. 1988). When warm winter temperatures cause thaws, red spruce can photosynthesize while sympatric species remain dormant; however, when cold temperatures return, freezing damage can

ensue. This process is exacerbated by acid deposition, which reduces the cold tolerance of red spruce foliage (Schaberg and DeHayes 2000).

Red spruce growth at the Mt. Mansfield study plots corresponds well with red spruce growth region-wide, implying that growth trends in this study are not a byproduct of local stand dynamics and, further, that climate- and deposition- growth relationships presented here may be representative of a region-wide phenomenon. Positive associations with measures of growing season length and temperature (e.g., water year T_{mean}, Jun-Sept T_{mean}, GDD, CDD) allude to continued favorable growth conditions and potential range expansion (e.g., Foster and D'Amato 2015) for red spruce into the future. This conclusion contrasts with to projected species range maps that depict red spruce range constriction in the future (Iverson et al. 2008). Interestingly, the period of most divergent growth between Mt. Mansfield and regional red spruce was from roughly 1980 through 2008. This period was interspersed with a series of winter injury events with varied intensities and legacies across the region (Lazarus et al. 2004, Kosiba et al. 2013). The higher than average growth at Mt. Mansfield relative to the regional chronology may indicate that red spruce on Mt. Mansfield experienced less winter injury than the regional norm. Likewise, the recent synchronous increase in growth evident in the chronologies indicates that this rebound is a regional phenomenon, similar to the ubiquitous decline in growth following the 2003 winter injury event.

In contrast with the other species, sugar maple growth at low elevation was not correlated with the selected variables, suggesting that they may be responding to micro-

site parameters not considered in this analysis (e.g., nutrient availability, stand dynamics, local soil moisture, etc.). For example, PDSI is a metric for the whole state of VT that does not consider site based soil and hydrological differences that may help explain tree growth. Others have also shown similar weak climate-growth relationships for sugar maple in the region (e.g., Bishop et al. 2015). Sugar maple growth at mid elevations exhibited a negative correlation with pSummer T_{mean} and T_{max}, indicating that elevated summer temperature due to climate change (Kunkel et al. 2013) could limit sugar maple growth further in the future.

Sugar maple at HBEF (Hansen 2015) had higher growth than those at Mt. Mansfield, particularly during the first half of the chronology. After 1982, the chronologies are more analogous. Sugar maple at Mt. Mansfield displayed a subdued decline in growth in the 1980s, but otherwise maintained consistent, low growth. It is unclear why sugar maple at HBEF had higher growth than those at Mt. Mansfield for the first part of the chronology, though higher acidic loading in the west of the region (e.g., Ollinger et al. 1993) could have stressed sugar maple trees there first. However, the near-steady growth of sugar maple at Mt. Mansfield since 1950 (Fig. 2.2) seems inconsistent with the possibility of early stress from acidic inputs. Another possibility is that Mt. Mansfield is a more marginal site for sugar maple growth, so baseline growth there was consistently lower.

Growth of Mt. Mansfield yellow birch did not correspond well to yellow birch growing at HBEF (Hansen 2015). One possible explanation for this could be the lower

sample size for yellow birch ($n = 34$ trees) relative to sugar maple ($n = 63$ trees) at Mt. Mansfield, which could reduce the accuracy of yearly growth mean estimates and increase the variation around those means. These results demonstrate the importance of having high replication when looking at region-wide patterns in tree cores.

Surprisingly, annual S and N deposition only related to poor growth for red spruce at low elevation, but not at mid and high elevations where documented declines have been tied to acid deposition (DeHayes 1992; Schaberg et al. 2006). While growth of sugar maple and red spruce, aside from low elevation, did display negative correlations with S deposition, these relationships were not significant. One possible reason for this outcome is the absence of long-term S and N deposition data. Datasets in this region only span from 1965-2012, which excludes over a decade of acid deposition inputs. In addition, detrending growth data with a flexible spline removes high frequency variation and biological trends while preserving decadal and longer trends. Nevertheless, a smoothing spline is one of the best options for reducing the effects of tree competition and age-related growth trends. Lastly, relating growth to annual deposition data may overlook more complex impacts of pollutant loading, such as long-term cumulative Ca depletion. For example, research has shown that red spruce growth was related to the historic accumulation of acidic inputs relative to the capacity of the site to buffer these inputs (Engle et al. 2016).

Atmospheric CO_2 concentration trends were not associated with growth (or residuals of growth-climate models after accounting for the effects of climate) for any of

the species or elevations. Our findings align with others who have shown no significant effect of elevated CO_2 concentration on stem growth (Bader et al. 2013; Girardin et al. 2016; Körner et al. 2005). While it is currently debated if elevated CO_2 concentrations will provoke changes in tree growth, there is evidence that CO_2 effects are muted or nonexistent on sites where other environmental factors, including soil fertility (particularly N-limitation) (Oren et al. 2001), temperature, and water (Körner et al. 2005), are more limiting to potential stem growth than C (Körner 2003; Silva and Anand 2013). Based on the strong associations with growth of trees in this study and measures of heat that we reported here, we hypothesize that temperature is more limiting to these trees than C availability.

2.6 Conclusions

We presented a comparison of growth trends for five key tree species. While this is a case study, by comparing the chronologies developed at this site to others in the region, we show that at least for red spruce, there is strong alignment to the broader region and propose that patterns evident here may be indicative of the region's forested ecosystems. Comparisons of the chronologies (Fig. 2.2) highlight that the five species often experienced changes in growth that were either species- or elevation-specific. There was a high degree of year-to-year variability in growth, likely due to local abiotic and biotic factors. For some species, the repeated stress of abiotic and biotic factors in succession may help explain prolonged growth declines.

For most species and elevations, there was a positive association between higher temperatures and growth during that same year, suggesting that contemporary warming has improved the competitive status of many trees. However, there are two noted exceptions to this trend. The first is that excessive heat (cumulative temperatures > 18.3°C) the previous year was broadly associated with lower growth the following year. Further investigation is needed to understand the complex interplay of elevated temperature and net growth in successive years and over time. The second exception is that sugar maple trees at low elevation showed no positive association with increased warming. This may provide field-based evidence of the particular sensitivity of sugar maple to the warming that has been projected by climate change range models (e.g., Iverson et al. 2008).

Declines of red spruce have also been well documented, but the recent and surprising growth surge had not been investigated. Here we show that it occurred across elevations and watersheds and that perhaps another species, red maple, has had a synchronous increase in growth. Both species show positive correlations with growing season temperatures, including CDD. Indeed, CDD was consistently associated with increased growth for most of species and elevations overall. This finding highlights the potential value of CDD as an integrated temperature index with particular relevance to tree growth in a warming world. While CDD was often positively associated with growth, pCDD often had a negative relationship. As CDD increases in the future, its influence on tree growth could be mixed. Results of this analysis suggest that some tree species may

be responding favorably to changing environmental conditions, while others are either declining or appear stable in growth. Though this specific study covered a small spatial scale, it opens avenues for future work to examine more fully some of the patterns that emerged here. Indeed, there have been relatively few studies that have examined growth trends and responses to the environment among species in the region; yet, this is of particular interest as the climate changes and the future state of forest health and productivity remains uncertain.

2.8 References

Aber, J., McDowell, W., Nadelhoffer, K., Alison, M., Berntson, G., Kamakea, M., McNulty, S., Currie, W., Rustad, L., and Fernandez, I. 1998. Nitrogen saturation in temperate forest ecosystems. BioScience **48**(11): 921-934.

Bader, M.K.F., Leuzinger, S., Keel, S.G., Siegwolf, R.T.W., Hagedorn, F., Schleppi, P., and Körner, C. 2013. Central European hardwood trees in a high-CO2 future: synthesis of an 8-year forest canopy CO2 enrichment project. Journal of Ecology **101**(6): 1509-1519. doi: 10.1111/1365-2745.12149.

Beckage, B., Osborne, B., Gavin, D.G., Pucko, C., Siccama, T., and Perkins, T. 2008. A rapid upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont. Proceedings of the National Academy of Sciences **105**(11): 4197-4202. doi: 10.1073/pnas.0708921105.

Bishop, D.A., Beier, C.M., Pederson, N., Lawrence, G.B., Stella, J.C., and Sullivan, T.J. 2015. Regional growth decline of sugar maple (Acer saccharum) and its potential causes. Ecosphere **6**(10): art179. doi: 10.1890/ES15-00260.1.

Bunn, A., Korpela, M., Biondi, F., Campelo, F., Merian, P., Qeadan, F., and Zang, C. 2015. dplR: Dendrochronology Program Library in R. R package version 1.6.3. http://r-forge.r-project.org/projects/dplr/.

Burns, D., Lynch, J., Cosby, B., Fenn, M., and Baron, J. 2011. National acid precipitation assessment program report to Congress 2011: an integrated assessment. US Environmental Protection Agency, Washington, DC, USA.

Burns, R., and Honkala, B. 1990. Silvics of North America: 1. Conifers; 2. Hardwoods Agriculture Handbook 654. US Department of Agriculture, Forest Service, Washington, DC.

Cogbill, C.V. 1996. Historical ecology of the upper Stevensville Brook watershed, Underhill, Vermont. For Vermont Department of Forest, Parks and Recreation and Vermont Monitoring Cooperative.

Cook, E.R., Johnson, A.H., and Blasing, T.J. 1987. Forest decline: modeling the effect of climate in tree rings. Tree Physiology **3**(1): 27-40. doi: 10.1093/treephys/3.1.27.

Cook, E.R., and Kairiukstis, L.A. (eds). 1990. Methods of Dendrochronology: Applications in the Envrionmental Sciences. Kluwer Academic Publishers, Dordrecht.

DeHayes, D.H. 1992. Winter injury and developmental cold tolerance of red spruce. *In* The Ecology and Decline of Red Spruce in the Eastern United States. *Edited by* C. Eagar and M.B. Adams. Springer-Verlag New York Inc., New York, NY, USA. pp. 295-337.

DeHayes, D.H., Schaberg, P.G., Hawley, G.J., and Strimbeck, G.R. 1999. Acid rain impacts on calcium nutrition and forest health. BioScience **49**(10): 789-800.

DeHayes, D.H., Schaberg, P.G., and Strimbeck, G.R. 2001. Red spruce cold hardiness and freezing injury susceptibility. *In* Conifer Cold Hardiness. *Edited by* F. Bigras. Kluwer Academic Publishers, Dordrecht, the Netherlands.

Duchesne, L., Ouimet, R., and Morneau, C. 2003. Assessment of sugar maple health based on basal area growth pattern. Canadian Journal of Forest Research **33**(11): 2074-2080. doi: 10.1139/x03-141.

Dupigny-Giroux, L.-A. 2002. Climate variability and socioeconomic consequences of Vermont's natural hazards: a historical perspective. Vermont History **70**: 19-39.

Engel, B.J., Schaberg, P.G., Hawley, G.J., Rayback, S.A., Pontius, J., Kosiba, A.M., and Miller, E.K. 2016. Assessing relationships between red spruce radial growth and pollution critical load exceedence values. Forest Ecology and Management **359**: 83-91.

Foster, J.R., and D'Amato, A.W. 2015. Montane forest ecotones moved downslope in northeastern US in spite of warming between 1984 and 2011. Global Change Biology: 4497-4507. doi: 10.1111/gcb.13046.

Gavin, D.G., and Peart, D.R. 1993. Effects of beech bark disease on the growth of American beech (Fagus grandifolia). Canadian Journal of Forest Research **23**(8): 1566-1575. doi: 10.1139/x93-197.

Girardin, M.P., Bouriaud, O., Hogg, E.H., Kurz, W., Zimmermann, N.E., Metsaranta, J.M., de Jong, R., Frank, D.C., Esper, J., Büntgen, U., Guo, X.J., and Bhatti, J. 2016. No growth stimulation of Canada's boreal forest under half-century of combined warming and CO2 fertilization. Proceedings of the National Academy of Sciences **113.52**: E8406-E8414. doi: 10.1073/pnas.1610156113.

Greaver, T.L., Sullivan, T.J., Herrick, J.D., Barber, M.C., Baron, J.S., Cosby, B.J., Deerhake, M.E., Dennis, R.L., Dubois, J.-J.B., Goodale, C.L., Herlihy, A.T., Lawrence, G.B., Liu, L., Lynch, J.A., and Novak, K.J. 2012. Ecological effects of nitrogen and sulfur air pollution in the US: what do we know? Frontiers in Ecology and the Environment **10**(7): 365-372. doi: 10.1890/110049.

Hansen, C.F. 2015. LiDAR remote sensing of forest canopy structure and integrity: Trophic interactions among forest health, productivity, insects and birds. MS Thesis, the University of Vermont.

Holmes, R.L. 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-ring Bulletin **43**: 69-78.

Hornbeck, J.W., Smith, R.B., and Federer, C.A. 1987. Growth decline in red spruce and balsam fir relative to natural processes. Water Air Soil Pollut **31**(1-2): 425-430. doi: 10.1007/BF00630860.

Hornbeck, J.W., and Smith, R.L. 1985. Documentation of red spruce growth decline. Canadian Journal of Forest Research **15**: 1199-1201.

Hufkens, K., Friedl, M.A., Keenan, T.F., Sonnentag, O., Bailey, A., O'Keefe, J., and Richardson, A.D. 2012. Ecological impacts of a widespread frost event following early spring leaf-out. Global Change Biology **18**(7): 2365-2377. doi: 10.1111/j.1365-2486.2012.02712.x.

Iverson, L.R., Prasad, A.M., Matthews, S.N., and Peters, M. 2008. Estimating potential habitat for 134 eastern US tree species under six climate scenarios. Forest Ecology and Management **254**(3): 390-406.

Johnson, A., Cook, E., and Siccama, T. 1988. Climate and red spruce growth and decline in the northern Appalachians. Proceedings of the National Academy of Sciences **85**(15): 5369-5373.

Johnson, A.H., Friedland, A.J., and Dushoff, J.G. 1986. Recent and historic red spruce mortality: Evidence of climatic influencee. Water, Air, & Soil Pollution **30**(1): 319-330. doi: 10.1007/bf00305203.

Johnson, A.H., and Siccama, T.G. 1983. Acid deposition and forest decline. Environmental Science & Technology **17**(7): 294A-305A. doi: 10.1021/es00113a001.

Körner, C. 2003. Carbon limitation in trees. Journal of Ecology **91**(1): 4-17. doi: 10.1046/j.1365-2745.2003.00742.x.

Körner, C., Asshoff, R., Bignucolo, O., Hättenschwiler, S., Keel, S.G., Peláez-Riedl, S., Pepin, S., Siegwolf, R.T.W., and Zotz, G. 2005. Carbon flux and growth in mature deciduous forest trees exposed to elevated CO_2. Science **309**(5739): 1360-1362. doi: 10.1126/science.1113977.

Kosiba, A.M., Schaberg, P.G., Hawley, G.J., and Hansen, C.F. 2013. Quantifying the legacy of foliar winter injury on woody aboveground carbon sequestration of red spruce trees. Forest Ecology and Management **302**: 363-371.

Kunkel, K.E., Stevens, L.E., Stevens, S.E., Sun, L., Janssen, E., Wuebbles, D., Hilberg, S., Timlin, M., Stoecker, L., and Westcott, N. 2013. Regional climate trends and scenarios for the US national climate assessment. Part 1. Climate of the Northeast U.S. NOAA Technical Report NESDIS 142-1.

Lazarus, B.E., Schaberg, P.G., DeHayes, D.H., and Hawley, G.J. 2004. Severe red spruce winter injury in 2003 creates unusual ecological event in the northeastern United States. Canadian journal of forest research **34**(8): 1784-1788.

LeBlanc, D.C. 1992. Spatial and temporal variation in the prevalence of growth decline in red spruce populations of the northeastern United States. Can. J. For. Res. **22**: 1351–1363.

Likens, G. 2010. Chemistry of Steamwater at HBEF WS-1. http://www.hubbardbrook.org/data/dataset.php?id=3 [Acessed 10/14/14].

Long, R.P., Horsley, S.B., Hallett, R.A., and Bailey, S.W. 2009. Sugar maple growth in relation to nutrition and stress in the northeastern United States. Ecological Applications **19**(6): 1454-1466. doi: 10.1890/08-1535.1.

McLaughlin, S.B., Downing, D.J., Blasing, T.J., Cook, E.R., and Adams, H.S. 1987. An analysis of climate and competition as contributors to decline of red spruce in high elevation Appalachian forests of the Eastern United states. Oecologia **72**(4): 487-501. doi: 10.1007/BF00378973.

Minocha, R., Long, S., Thangavel, P., Minocha, S.C., Eagar, C., and Driscoll, C.T. 2010. Elevation dependent sensitivity of northern hardwoods to Ca addition at Hubbard Brook Experimental Forest, NH, USA. Forest Ecology and Management **260**(12): 2115-2124. doi: http://dx.doi.org/10.1016/j.foreco.2010.09.002.

National Atmospheric Deposition Program. 2016. NADP/NTN Monitoring. US Geological Survey [accessed 4 May 2016].

National Drought Mitigation Center. 2012. SPEI. University of Nebraska, Lincoln. http://droughtatlas.unl.edu/About.aspx [acessed 15 March 2015].

National Drought Mitigation Center. 2014. Drought Risk Atlas. http://droughtatlas.unl.edu/Data.aspx [Accessed 10/10/13].

NOAA Earth System Research Laboratory Global Monitoring Division. 2016. Monthly Average Mauna Loa CO_2. http://www.esrl.noaa.gov/gmd/ccgg/trends/ [accessed 6 October 2016].

NOAA National Weather Service. 2014. Monthly total growing degree days for Burlington, VT. http://www.weather.gov/btv/climo_gdd [Accessed 4/23/14].

Ollinger, S.V., Aber, J.D., Lovett, G.M., Millham, S.E., Lathrop, R.G., and Ellis, J.M. 1993. A spatial model of atmospheric deposition for the northeastern US. Ecological Applications **3**(3): 459-472.

Oren, R., Ellsworth, D.S., Johnsen, K.H., Phillips, N., Ewers, B.E., Maier, C., Schäfer, K.V., McCarthy, H., Hendrey, G., and McNulty, S.G. 2001. Soil fertility limits carbon sequestration by forest ecosystems in a CO2-enriched atmosphere. Nature **411**(6836): 469-472.

Pederson, N., Bell, A.R., Cook, E.R., Lall, U., Devineni, N., Seager, R., Eggleston, K., and Vranes, K.J. 2013. Is an Epic Pluvial Masking the Water Insecurity of the Greater New York City Region? Journal of Climate. doi: 10.1175/jcli-d-11-00723.1.

PRISM Climate Group. 2004. Available from http://prism.oregonstate.edu/ [accessed 5/10/14 2014].

R Development Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rhoads, A.G., Hamburg, S.P., Fahey, T.J., Siccama, T.G., Hane, E.N., Battles, J., Cogbill, C., Randall, J., and Wilson, G. 2002. Effects of an intense ice storm on the structure of a northern hardwood forest. Canadian Journal of Forest Research **32**(10): 1763-1775. doi: 10.1139/x02-089.

Salzer, M.W., Hughes, M.K., Bunn, A.G., and Kipfmueller, K.F. 2009. Recent unprecedented tree-ring growth in bristlecone pine at the highest elevations and possible causes. Proceedings of the National Academy of Sciences **106**(48): 20348-20353. doi: 10.1073/pnas.0903029106.

Schaberg, P.G., and DeHayes, D.H. 2000. Physiological and envrionmental causes of freezing injury to red spruce. *In* Responses of Northern U.S. Forests to Environmental Change. *Edited by* R.A. Mickler and R.A. Birdsey and J.L. Hom. Springer-Verlag, New York. pp. 181-227.

Schaberg, P.G., Tilley, J.W., Hawley, G.J., DeHayes, D.H., and Bailey, S.W. 2006. Associations of calcium and aluminum with the growth and health of sugar maple trees in Vermont. Forest Ecology and Management **223**(1–3): 159-169. doi: http://dx.doi.org/10.1016/j.foreco.2005.10.067.

Siccama, T.G. 1971. Presettlement and Present Forest Vegetation in Northern Vermont with Special Reference to Chittenden County. American Midland Naturalist **85**(1): 153-172.

Silva, L.C.R., and Anand, M. 2013. Probing for the influence of atmospheric CO2 and climate change on forest ecosystems across biomes. Global Ecology and Biogeography **22**(1): 83-92. doi: 10.1111/j.1466-8238.2012.00783.x.

Soil Survey Staff. 2015. Natural Resources Conservation Service, United States Department of Agriculture. Web Soil Survey. http://websoilsurvey.nrcs.usda.gov/ [Accessed 08/15/2015].

Soule, P.T., and Knapp, P.A. 2006. Radial growth rate increases in naturally occurring ponderosa pine trees: a late-20th century CO2 fertilization effect? The New phytologist **171**(2): 379-390. doi: 10.1111/j.1469-8137.2006.01746.x.

Speer, J.H. 2010. Fundamentals of Tree-Ring Research. University of Arizona Press.

Stokes, M., and Smiley, T. 1996. An Introduction to Tree-Ring Dating. University of Chicago Press.

van Doorn, N.S., Battles, J.J., Fahey, T.J., Siccama, T.G., and Schwarz, P.A. 2011. Links between biomass and tree demography in a northern hardwood forest: a decade of stability and change in Hubbard Brook Valley, New Hampshire. Canadian Journal of Forest Research **41**(7): 1369-1379. doi: 10.1139/x11-063.

Vermont Agency of Natural Resources Department of Forest Parks & Recreation. 2010. Forest insects and disease conditions in Vermont 2010. Waterbury, VT.

Vermont Agency of Natural Resources Department of Forest Parks & Recreation. 2013. Combined Master Dataset of Aerial Defoliation Surveys, 1985 to 2013 [downloaded July 25, 2014, http://www.uvm.edu/vmc/research/data.php?id=66]. Hosted by Vermont Monitoring Cooperative.

West, P.W. 1980. Use of diameter increment and basal area increment in tree growth studies. Canadian Journal of Forest Research **10**(1): 71-77. doi: doi:10.1139/x80-012.

Weverka, A.S. 2012. Remote sensing of productivity in northeastern forests. MS Thesis. Rubenstein School of Envrionment and Natural Resources, University of Vermont.

Whitney, G. 1994. From coastal wilderness to fruited plain: An environmental history of the eastern US. 1500 to present. Cambridge University, Cambridge, MA.

World Data Center for Paleoclimatology and NOAA Paleoclimatology Program. Law Dome ice core data. ftp://ftp.ncdc.noaa.gov/pub/data/paleo/icecore/antarctica/law/law2006.txt [Access date: 10 October 2016].

Yamaguchi, D.K. 1991. A simple method for cross-dating increment cores from living trees. Canadian Journal of Forest Research **21**(3): 414-416. doi: 10.1139/x91-053.

Zang, C., and Biondi, F. 2015. treeclim: an R package for the numerical calibration of proxy-climate relationships. Ecography **38**(4): 431-436. doi: 10.1111/ecog.01335.

2.9 Supplementary Materials
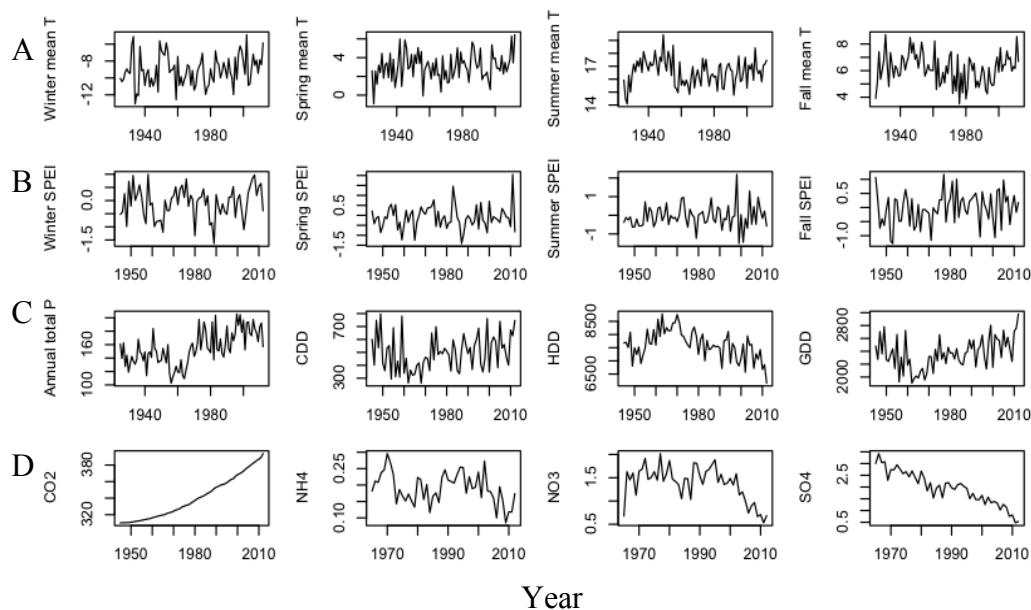
Fig. S2.1: (A) Mean seasonal (Winter [p Dec-Feb], Spring [Mar-May], Summer [Jun-Aug], and Fall [Sep-Nov]) temperatures (°C; 1925-2012) for the study location (see Methods for more details). **(B)** Seasonal Standardized Precipitation-Evapotranspiration Index (SPEI; 1945-2012) for Vermont (VT). **(C)** Annual total precipitation (cm) for the study location (1925-2012); cooling degree days (CDD, measured as degrees > 18.3°C, 1945-2012), heating degree days (HDD, < 18.3°C, 1945-2012) and growing degree days (GDD, > 5°C, 1945-2012) for VT. **(D)** Atmospheric CO_2 concentration (ppm, 1945-2012) from Mauna Loa, HI; deposition (1965-2012, mg/L, by water year) of ammonium (NH_4^+), nitrate (NO_3^-), and sulfate (SO_4^-) from Hubbard Brook Experimental Forest (Thorton, NH) and Mt. Mansfield (VT).

Table S2.1: Raw tree ring data and statistics listed by species per elevational zone across the three watersheds.

Species	Elev. Zone[a]	N trees	Mean DBH ± SD[b]	Age at BH ± SD[c]	Mean BAI ± SD[d]	Inter-series corr.[e]	Mean Sens.[e]	Max. BAI ± SD[f]
Balsam fir	High	34	23.4 ± 3.4	77.9 ± 20.4	7.9 ± 3.4	0.583	0.209	10 ± 2.2 (2001)
Red maple	Low	28	39.6 ± 8.4	90.0 ± 25.2	19.6 ± 11.2	0.514	0.225	29.8 ± 5.8 (2012)
Red spruce	Low	31	34 ± 9.3	142.7 ± 55.8	11.3 ± 9.3	0.519	0.257	18.1 ± 3.4 (2012)
	Mid	34	41.5 ± 10.2	165.5 ± 51	16.1 ± 10.2	0.559	0.254	27.9 ± 4.0 (2012)
	High	41	23.5 ± 8.2	86.7 ± 32.8	8.1 ± 4.1	0.579	0.236	13.2 ± 3.4 (2012)
Sugar maple	Low	29	32.5 ± 5.8	95.9 ± 20.3	9.9 ± 5.8	0.474	0.304	14.2 ± 1.1 (1994)
	Mid	34	28.2 ± 6.8	93.1 ± 23.8	7 ± 3.4	0.466	0.325	10.5 ± 2.3 (1983)
Yellow birch	Mid	34	43.2 ± 10.2	101.1 ± 27.2	18 ± 10.2	0.467	0.286	22.7 ± 0.6 (1982)

[a] Low = 450-650 m a.s.l., mid = 750-850 m, and high = 900-1000 m
[b] Mean diameter (± SD)(cm) measured at breast height (DBH 1.37 m).
[c] Age in years is approximate, based on number of rings at breast height and distnace to pith.
[d] Mean basal area increment (cm^2) calculated using the follwing formula $BAI = \pi(R_n^2 - R_{n-1}^2)$ (West 1980).
[e] Interseries correlation and mean sensitivity, from COFECHA output.
[f] Maximum basal area increment (cm^2) and year of occurance.

Table S2.2: Chronology statistics from Mt. Mansfield, VT, detrended with a 67% cubic smoothing spline and prewhitened, computed for 30-year time periods with 15-year overlap from 1923-2012.

Species	Elevation[a]	Stat[b]	Time period				
			1923-1952	1938-1967	1953-1982	1968-1997	1983-2012
Balsam fir	High	n cores	40	53	59	59	59
		n trees	24	30	34	34	34
		Rbar	0.22	0.44	0.38	0.30	0.31
		EPS	0.82	0.95	0.95	0.94	0.94
		SNR	4.67	18.83	18.68	14.52	15.26
Red maple	Low	n cores	63	77	86	86	86
		n trees	39	46	51	51	51
		Rbar	0.15	0.21	0.16	0.13	0.08
		EPS	0.82	0.91	0.91	0.88	0.82
		SNR	4.57	10.06	8.55	7.11	4.69
Red spruce	Low	n cores	54	56	56	56	56
		n trees	31	31	31	31	31
		Rbar	0.28	0.40	0.34	0.26	0.28
		EPS	0.91	0.95	0.94	0.92	0.93
		SNR	10.13	19.89	16.13	10.70	12.27
	Mid	n cores	74	78	78	78	78
		n trees	38	39	39	39	39
		Rbar	0.45	0.47	0.41	0.35	0.43
		EPS	0.97	0.97	0.96	0.96	0.97
		SNR	29.05	33.09	26.51	21.00	29.01
	High	n cores	60	72	78	78	78
		n trees	33	40	41	41	41
		Rbar	0.46	0.43	0.41	0.31	0.41
		EPS	0.95	0.96	0.96	0.95	0.97
		SNR	17.36	23.69	26.39	18.65	28.03
Sugar maple	Low	n cores	45	47	47	48	48
		n trees	30	31	31	31	31
		Rbar	0.16	0.12	0.13	0.22	0.34
		EPS	0.80	0.80	0.82	0.90	0.94
		SNR	3.90	3.97	4.39	8.55	15.89
	Mid	n cores	46	56	57	57	57
		n trees	29	34	34	34	34
		Rbar	0.30	0.25	0.26	0.24	0.19
		EPS	0.89	0.91	0.92	0.92	0.89
		SNR	8.44	9.51	11.64	10.82	8.20
Yellow birch	Mid	n cores	46	56	59	59	59
		n trees	29	32	34	34	34
		Rbar	0.26	0.25	0.16	0.22	0.20
		EPS	0.90	0.91	0.86	0.90	0.90
		SNR	8.74	9.59	6.14	9.45	8.65

[a] Low = 450-650 m a.s.l., mid = 750-850 m, and high = 900-1000 m
[b] R bar = Effective R bar, a weighted average of RBT (R bar betweenn trees) and RWT (R bar within trees) and thus a measure of correlation among and between cores, EPS = expressed population signal, SNR = signal to noise ratio.

CHAPTER 3: EXPLORING POSSIBLE CAUSES FOR THE SURPRISING RECOVERY OF RED SPRUCE GROWTH IN THE NORTHEASTERN UNITED STATES

Alexandra M. Kosiba[a*], Paul G. Schaberg[b], Shelly A. Rayback[c], and Gary J. Hawley[a]

[a] The University of Vermont, Rubenstein School of Environment and Natural Resources,

Burlington, VT 05405, USA, akosiba@uvm.edu, ghawley@uvm.edu

[b] Forest Service, U.S. Department of Agriculture, Northern Research Station, Burlington,

VT 05405, USA, pschaberg@fs.fed.us

[c] The University of Vermont, Department of Geography, Burlington, VT 05405, USA,

srayback@uvm.edu

[*] Corresponding author. akosiba@uvm.edu (A.M. Kosiba).

3.1 Abstract

Following decades of documented growth declines and increased mortality quantitatively linked to acid deposition-induced calcium depletion, red spruce in the northeastern United States appear to be experiencing a recovery. We found that over 75% of red spruce trees and 90% of the plots examined in this study exhibited increasing growth over the past decade (since 2001). To understand the possible factors involved in this observed phenomenon, we examined the relationship between growth and factors that may influence growth: tree age and diameter, disturbance, plot characteristics (elevation, slope, aspect, geographical position), and a suite of environmental variables (temperature, precipitation, climate and precipitation indices [degree days, SPEI [standardized precipitation evapotranspiration index], acid deposition [SO_4-, NO_3-, pH of rainfall, cation:anion ratio of rainfall]) for 52 plots (661 trees) from five states (spanning 2.5 °N x 5°W). Examining the growth relationships from 1925 to 2012, we found that while there was variability in response to climate and acid deposition by elevation and location, site and tree factors did not adequately explain growth. Higher temperatures outside the traditional growing season (e.g., fall, winter, and spring) were related to increased growth. Nitrogen deposition was related to lower growth, but the strength of this relationship may be lessening over time. Overall, we predict continued favorable conditions for red spruce in the near term as acid deposition continues to decline and fall through spring temperatures moderate, provided overall temperatures and precipitation remain adequate for growth.

Key words: Picea rubens*, acid deposition, nitrate, dendrochronology, woody growth, climate change, winter temperature*

3.2 Introduction

Beginning in the mid-1960s, red spruce (*Picea rubens* Sarg.) in the northeastern United States (US) began to suffer from needle damage, crown deterioration, reductions in growth, and increased mortality (Johnson et al. 1988; McLaughlin et al. 1987; Scott et al. 1984). In the following decades, red spruce decline became one of the most intensively studied examples of forest degeneration in the US (Eagar and Adams 1992). Through this inquiry, the decline was attributed to winter injury, provoked by acid deposition-induced calcium [Ca] depletion (DeHayes et al. 1999; Schaberg et al. 2000). A number of factors contribute to a severe winter injury event, including both predisposing stresses (e.g., weather events that reduced carbon [C] capture in the prior growing season, like drought or extreme temperature [T] stress) and inciting stresses (e.g., extreme minimum T [T_{min}] and/or winter freeze-thaw cycles) (Schaberg et al. 2011). Pollution controls were enacted through the Clean Air Act and subsequent amendments, resulting in declines in acidic deposition (Driscoll et al. 2001). However, red spruce winter injury persisted and a severe region-wide event occurred as recently as 2003 (Lazarus et al. 2004) (Fig. S3.1).

Therefore, it was unexpected to discover that red spruce in the region recently exhibited a prominent increase in growth (Kosiba et al. 2013). Although Kosiba *et al.* (2013) were the first to report this growth upturn, other studies have noted the phenomena in red spruce stands from New England and New York (Engel et al. 2016; Kosiba et al. 2014; Wason et al. 2014). There is also evidence that red spruce regeneration has

increased since previous inventories (Foster and D'Amato 2015; van Doorn et al. 2011). However, to date, no investigations have examined the possible factors involved in these changes to red spruce growth or demography.

Red spruce has been likened to the proverbial "canary in a coal mine" for its high sensitivity to acid deposition relative to co-occurring tree species. This sensitivity has been attributed to the species' marginal cold tolerance (DeHayes et al. 2001), comparably low genetic diversity (Hawley and DeHayes 1994), and unique capacity to deharden and photosynthesize during the traditional dormant season when T is favorable (e.g., during January thaws) (Schaberg et al. 1998; Schaberg et al. 1995; Schwarz et al. 1997). However, dehardening increases the susceptibility of the foliage to freezing injury when low temperatures return (DeHayes et al. 2001; Schaberg and DeHayes 2000). While these adaptions have made red spruce particularly vulnerable to acid deposition, they may now allow the species a competitive advantage with climate change. The ability of red spruce to photosynthesize when T is favorable could result in increased opportunities for photosynthesis as T increases, particularly if those increases occur outside the traditional growing season (e.g., fall, winter, and early spring) when co-occurring species remain leafless or dormant.

In the northeastern US, climatic trends over the past decade have included anomalously higher fall, winter, and spring T (Kunkel et al. 2013; NOAA National Climatic Data Center 2010), which would reduce the chance of foliar freezing injury for

red spruce (C loss) and increase opportunities for photosynthesis (C gain). Concurrent with increasing T, atmospheric carbon dioxide (CO_2) concentrations have risen steadily. Although debated, some studies have reported a fertilization effect of elevated CO_2 on tree C sequestration (Ainsworth and Long 2005; Salzer et al. 2009; Soule and Knapp 2006). If combined with reductions in acidic pollutant inputs, these factors could allow for an overall increase in C sequestration for red spruce trees. Further, considering the relatively uniform genetics of the species (DeHayes 1992), red spruce may exhibit a more unified response to environmental change compared to other species.

To this end, we investigated the patterns of red spruce growth across five states where it is an important component of the forested ecosystem. We examined if recent pollution controls, which have reduced emissions of sulfur (S) and, to a lesser extent, nitrogen (N) based compounds (Driscoll et al. 2001), plot characteristics (e.g., stand dynamics, age, location), observed changes in climate, and recorded increases in atmospheric CO_2 may have contributed to the recent growth increase of red spruce trees. Although the possible drivers of xylem growth are varied and complex, we examined five hypotheses to disentangle the factors affecting red spruce growth:

H$_1$ The legacy of historical land use and/or stand demographics have resulted in a synchronous increase in growth.

H$_2$ Changes in the climate, particularly changes in the length of the growing season and increases in T outside the traditional growing season (in fall, winter and

spring), have simultaneously reduced the likelihood of foliar winter injury (C loss) and increased photosynthesis (C capture).

H₃ Reductions in pollution deposition have alleviated a predisposing stress that contributed to past declines and resulted in C losses.

H₄ Increases in CO_2 have allowed for higher C capture and growth.

It is likely, however, that recent growth increases of red spruce are the result of a complex interplay between multiple factors. Indeed, previous studies of the climatic drivers of red spruce growth showed a strong de-coupling of growth and climate relationships around the start of red spruce decline (Johnson et al. 1988; McLaughlin et al. 1987), suggesting that the trees were no longer responding to the same environmental cues as they had prior to increased acid loading.

3.3 Materials and Methods

3.3.1 Study sites

Red spruce tree cores were collected from five northeastern US states (NY, VT, NH, MA, and ME; study region: 42.67-45.04°N, 73.79-68.63°W) by the authors or affiliates (Engel et al. 2016; Kenefic 2015; Kosiba et al. 2013; Kosiba et al. 2014; Pontius and Halman 2012; Rayback 2012; Wason et al. 2012; Weverka 2012) (Fig. 3.1). Red spruce sites (*n*=52 plots) were included based on the strength of the common growth signal (i.e., r-bar; expressed population signal [EPS] >0.80) (see details below). Plots were categorized by elevation (Low<650m, Mid 700-900m, and High>950m) and region

(East or West of study area, divided along the North-South spine of the Green Mountains of VT) to examine how landscape position that strongly affects weather and pollution deposition patterns in the region (Ollinger et al. 1993), may also alter growth. (Fig. 3.1).

Plot aspect, elevation, and percent slope were extracted from a digitized elevation model and hillshade layers. Sites encompassed a range of elevation, aspect, slope, mean tree age, and mean diameter at breast height (DBH, 1.37 m above ground level) (Table S3.1). While the region has experienced historic, widespread land-clearing and subsequent reforestation (Foster 1992), we did not select plots based on stand age or DBH; rather, we attempted to obtain a range of tree ages and site characteristics in order to characterize red spruce growth dynamics region-wide.

For the study area, the annual T_{mean} is 6.3°C. January is the coldest month (-7.5°C average 1925-2012) and July the warmest (19.4°C) (Fig. S3.2) (NOAA National Centers for Environmental Information 2016). An average of 106 cm of precipitation [P] is deposited uniformly throughout the year. In general, precipitation increases with elevation (NOAA National Centers for Environmental Information 2016) .
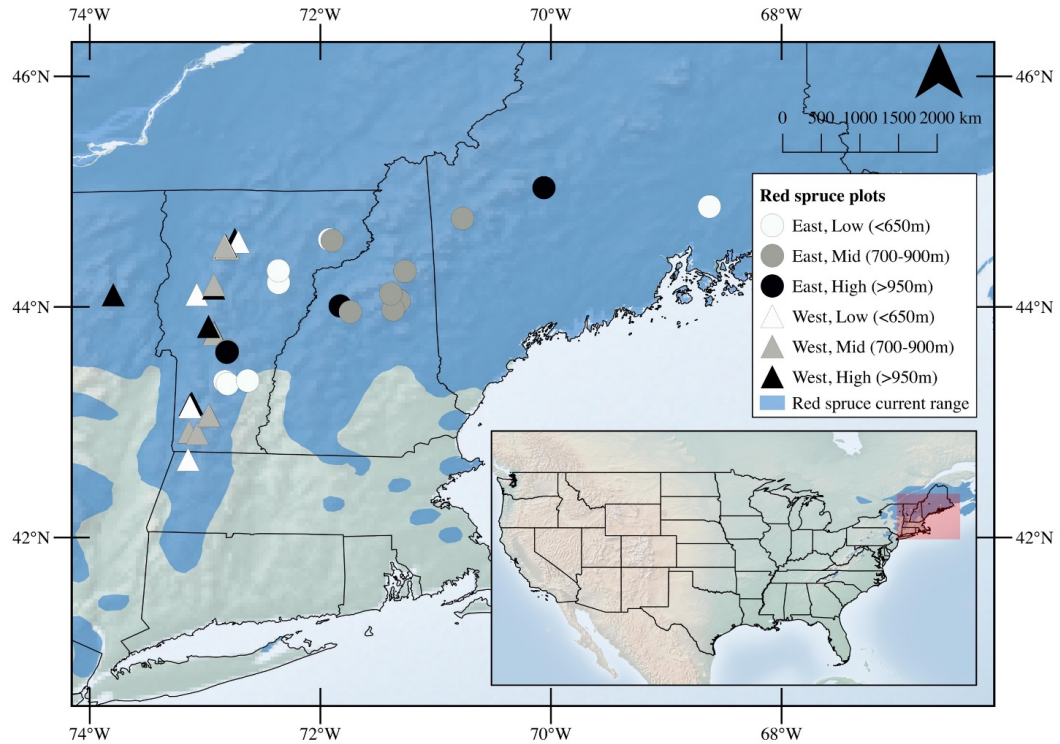
Figure 3.1: Locations of red spruce (*Picea rubens* Sarg.) tree ring plots in NY, VT, NH, ME, and MA. Plots are designated by elevation (Low, Mid, and High) and region (East, West of the study area), and overlaid on the current range of red spruce (in blue) (U.S. Geological Survey 2016). Although 52 plots were sampled, nearby plots appear overlapping and/or obscured in this representation.

3.3.2 Dendrochronology

Selected red spruce trees (*n*=661) were increment cored following standard dendrochronological techniques (Speer 2010; Stokes and Smiley 1996). For all datasets, two 5 mm increment cores were collected per tree at stem DBH, 180° to each other, and perpendicular to the dominant slope. For datasets with fewer than nine dominant or co-

dominant trees per plot and where multiple plots from one area were available, nearby plots were combined to create a stronger common growth signal. This step was only necessary for four plots. Following collection, cores were air dried, mounted in grooved wooden blocks, and sanded with progressively finer grit sandpaper. Cores were visually crossdated using the list method (Yamaguchi 1991) and microscopically measured to 0.001 mm resolution using a Velmex sliding stage unit (Velmex Inc., Bloomfield, NY) with MeasureJ2X software (VoorTech Consulting, Holderness, NH). We used COFECHA software (Holmes 1983) to detect and correct for potential crossdating errors (±0 years) (Speer 2010). To retain a strong common growth signal, individual cores were discarded if they were poorly correlated with the master chronology (i.e., below Pearson critical correlation level of 0.328 [99% confidence level]). We calculated approximate tree age at breast height using the maximum number of rings per tree if pith was evident or estimated per core using a pith indicator (Speer 2010) if pith had not been reached and pith location could be approximated based on the curvature of innermost rings. For incomplete cores where pith could not be estimated, age was not assessed. Trees were categorized into age and size (DBH) groups based on approximately equal sample sizes: <100, 100-200, and >200 years old at breast height and <30, 30-40, and >40 cm DBH.

Standard dendrochronological statistical parameters (Fritts 1976; Wigley et al. 1984) were computed for each plot (Tables S1, S2). Specifically, from the raw ring width (RRW) chronologies the parameters were series intercorrelation (SI), mean sensitivity

(MS), mean value of tree-ring width (RW±SD), first-order autocorrelation coefficient (AC), EPS, and signal to noise ratio (SNR). From the residual RWI chronologies, we computed the average correlation between individual series in a plot (R-bar), EPS, and SNR. All 52 resulting plot chronologies were truncated at the year when the EPS value fell below 0.80; for all plot-level chronologies this was 1925. We first averaged RRW by tree, then detrended, standardized, and prewhitened each series using the *dplR* package (Bunn et al. 2015) for R (Version 3.1.1) (R Development Core Team 2016).

We detrended with the Friedman Super Smoother (FSS) (tweeter=5), a variable span smoother used to reduce the influence of disturbance on each series (Friedman 1984; Pederson et al. 2013). We developed chronologies at plot and regional scales, as well as aggregated by age-, size-, and elevation-class and divided into east and west groupings. Plots were divided along the dominant north-south ridge of the Green Mountains (VT) to examine if a relationship with acid deposition was associated with distance from pollution sources (e.g., pollution deposition increases west to east (Ollinger et al. 1993)). Plot, and age- and size-class chronologies, were calculated by aggregating individual tree chronologies with a Tukey's biweight robust mean. Regional, elevational, and east-west chronologies were calculated as a mean of the plot chronologies. Detrended chronologies were standardized to a dimensionless index by dividing the observed by the expected value and stripped of temporal autocorrelation through autoregressive modeling to create prewhitened (residual) chronologies (Cook 1985) (RWI). The residual chronologies are

preferred for analysis because through the process of detrending, standardizing, and prewhitening, the remaining interannual variance can be attributed to exogenous factors (Cook and Peters 1997).

3.3.3 Growth trends

Using RRW and RWI chronologies, the slope of recent growth was assessed from 2001 to the end of chronology or 2012, whichever came first (termed "recent growth trends"). The year 2001 was chosen as the start of the slope assessment because it captures recent growth increases while allowing for inclusion of the region-wide winter injury event (2003) with preceding years (2001, 2002), which is consistent with methods of Kosiba *et al*. (2013) and Engel *et al*. (2016). We tested the effects of plot characteristics (e.g., slope, aspect, latitude, longitude, elevation, mean age, mean DBH) on recent growth trends.

Release events were detected two ways: (1) per tree RWW following Fraver (2009) using a 10-year running mean and an absolute threshold increase of 0.58 mm (a metric developed specifically for red spruce in the northeastern US); and (2) per plot RRW following Lorimer and Frelich (1989) using a percent threshold of 60% and series threshold of 75%, over 10 years. We also examined if mortality (log transformed) following the 2003 winter injury event (and in the subsequent seven years) was positively correlated to growth of surviving trees.

3.3.4 Climate, acid deposition, and atmospheric data

We aggregated climate data (mean, maximum, and minimum monthly T [T_{mean}, T_{max}, T_{min}], and total monthly P; 1925-2012) from eight weather stations (NOAA Regional Climate Centers 2016) (Table S3.2) in order to better characterize the regional climate over the spatial range of study plots. From these, we computed seasonal (Winter: Dec-Feb, Spring: Mar-May, Summer: Jun-Aug, Fall: Sep-Nov) and water year (Wyr) (previous Oct- current Sep) values.

We included several climate indices in our analysis. Specifically, we used standardized precipitation-evapotranspiration index (SPEI; a multi-scalar climatic drought index; version 3.23) at time scales of one, six (SPEI06 ending in Sep), and nine (SPEI09 ending in Sep) months (National Drought Mitigation Center 2012; Vicente-Serrano et al. 2010). We averaged the monthly indices of extreme T and P generated by NOAA for the stations within the study region (NOAA National Centers for Environmental Information 2016) (Table S3.2). These data included three measures of degree days: growing degree days (GDD, measured as cumulative degrees >5°C [41°F]), cooling degree days (CDD, >18.3°C [65°F]) and heating degree days (HDD, <18.3°C [65°F]); indices of extreme heat (*n* days with $T_{max} \geq 32°C$, extreme T_{max}) and cold (*n* days with $T_{min} \leq -18°C$ and $\leq 0°C$); and indices of extreme P (*n* days with ≥ 2.2 cm P, departure from normal P, total snowfall). While CDD and HDD were derived for estimating

building heating and cooling needs, respectively, previous research using these metrics have shown promise with relationship to tree growth (Kosiba et al. In press; Miller et al. 2014) and they can be used as proxies for higher and lower temperature accumulation over time. From these, we computed seasonal and Wyr values.

To obtain an adequate temporal dataset of annual atmospheric CO_2 concentration for tree growth comparison (e.g., 1925-2012), we combined data from the Mauna Loa Observatory, HI, US (NOAA Earth System Research Laboratory Global Monitoring Division 2016) and Law Dome, Antarctica ice core data (World Data Center for Paleoclimatology and NOAA Paleoclimatology Program). Lastly, pollutant deposition data (SO_4^-, NO_3^-, NH_4^+, cation:anion ratio, and rainfall pH) were averaged from all National Atmospheric Deposition Program (NADP) stations within the study region (National Atmospheric Deposition Program 2016) (Table S2). This dataset is limited to 1980-2012.

3.3.5 Comparisons of growth with climate and acid deposition data

We used the package *treeclim* (Zang and Biondi 2015) for R to assess the relationship between a suite of climatic and environmental variables and the mean RWI chronologies (RWI_{RCS}, RWI_{FSS}, RWI_{BAI}). We analyzed climate and pollution deposition relationships with growth over two years ($year_t$ and $year_{t-1}$). This allowed us to examine the effect of the previous year's climate and pollution deposition on the follow year's

growth. *Treeclim* uses time-dependent bootstrapped resampling (1000 iterations) to test for linear correlations between the residual ring width data and each subvector of the climate matrix (Zang and Biondi 2015). This step was to assess for any possible emergence of predictor variables that we would not have known *a priori* (Cook and Pederson 2011) and to assist in variable selection for subsequent climate-growth models. To select the strongest relationships, variables were considered significant at the $\alpha=0.01$ level.

We created models of red spruce growth based on four time periods: the entire chronology 1925-2012; 1925-1960 (period before acid deposition and red spruce decline); 1960-2012 (period of peak acid deposition and red spruce decline but lacking complete pollutant deposition data); and 1980-2012 (period with pollutant deposition data). This method was first proposed to examine forest decline (Cook et al. 1987) rather than rebound, but also is informative to identify changes in climate-growth relationships through time. First differences of all input variables were calculated to remove trends and serial autocorrelation, as well as to enhance the magnitude of annual predictor variables. We limited inclusion to significant factors from the previous analysis and variables without significant multicollinearity. With this subset, we used stepwise linear regression, using AIC criteria, to further restrict linear model input variables. Using the residuals from these models, we looked for trends not explained by the model parameters and regressed these values with CO_2. Lastly, we computed running correlations between

the predicted and observed growth (methods follow Johnson et al. 1988), and between NO_3^- deposition and growth over time. To investigate possible spatial patterns between acid deposition and growth, we tested the fit of these models by the elevational and regional (east-west) RWI chronologies following similar methods as previously outlined.

3.4 Results

3.4.1 Growth trends and patterns

Red spruce trees in this study displayed a range of DBH (13-70.3 cm) and estimated age at breast height (41-373 years) (Fig. S3.4a, b). Most trees (78%) showed positive recent RRW growth (measured as slope of growth from 2001- end of chronology), and it did not vary by DBH ($P = 0.81$, ANOVA) or age class ($P = 0.33$, Wilcoxon Rank Sum test due to unequal variances). This same pattern held when we examined the slope of recent growth using tree RWI (DBH class $P = 0.55$; age class $P = 0.37$; ANOVA) (Fig. S3.4a, b).

When aggregated, over 90% of the red spruce plots displayed positive, recent growth trends (Table S3.1). Plot locations encompassed a range of latitude/longitude, aspect, elevation (Fig. 3.1), slope, and average tree age and DBH (Table S3.1). If, as we stated in H_1, observed growth patterns were a result of natural stand dynamics, then variations in growth should have been related to plot factors (e.g., elevation, aspect, location, mean DBH, mean age), as opposed to factors with a broad spatial extent (e.g., weather, pollution deposition). However, when we modeled RWI using these fixed plot

86

characteristics (with "state" as a random factor in a mixed-effects model), none of these

plot factors were significant in predicting recent growth.
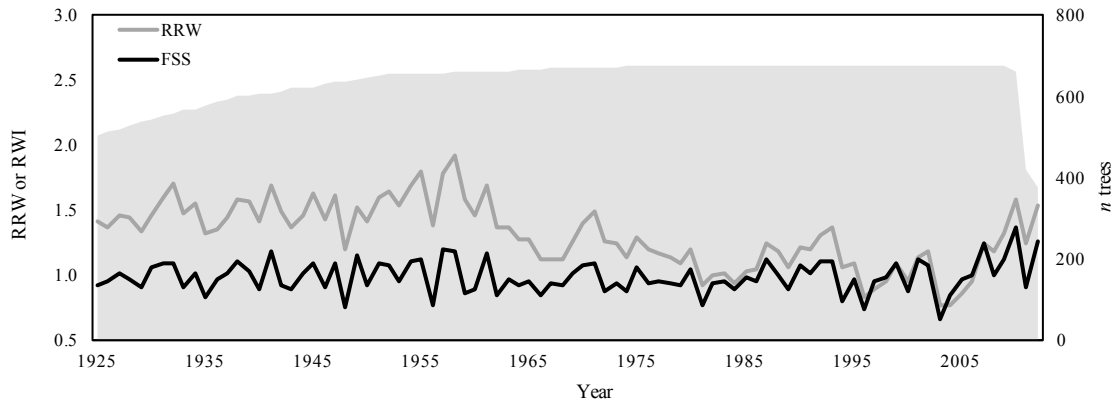
Figure 3.2: Red spruce (*Picea rubens* Sarg.) mean raw ring width (RRW, grey line, cm) and detrended and standardized residual mean ring width indices (RWI, unitless) using Friedman's Super Smoother (FSS) from 1925-2012. Number of trees contributing to chronologies shown in light grey.

Further, if recent growth increases were due to stand dynamics, we would expect

to see large increases in growth following known disturbance events. No major release

events were detected in individual trees or by plot since 1935 using either release

detection method. Neither were trees that survived known winter injury events growing

at a higher rate. Examining past data we collected (see Kosiba *et al.* 2013), we found that

9.6% of trees we assessed for winter injury in 2003 and reassessed seven years later

(2010) were dead. To assess if mortality rates following the 2003 winter injury event

(and in the subsequent seven years) may have impacted future growth of surviving trees,

we looked at the relationship between recent RRW growth (assessed as the slope of

growth since 2001) and the mortality assessment per plot (log transformed) and found no

87

relationship between the two factors (R_{adj}^2=0.0006, P=0.17) (Fig. S3.5). Further, we did not find differences in growth based on tree DBH or estimated age at DBH, nor by elevation or east-west location in the study area (Fig. S3.4). Based on these combined results, we rejected H_1.

3.4.2 Climate and acid deposition related growth trends

We found that various metrics of heat accumulation (e.g., degree days) were important for red spruce growth, particularly in the fall and spring seasons (Fig. 3.3). Both Wyr GDD (a measure of cumulative heat above 18.3°C) and T_{mean} were significantly related to growth (r=0.31 and r=0.38, $P \leq 0.01$) and have increased regionally since 1925 (NOAA National Weather Service 2014) (Fig. S3.3) (P<0.001). In November before growth, measures of higher T (T_{mean} and T_{max}) were associated with greater growth (r=0.38 and 0.35, respectively; $P \leq 0.01$), while lower T during this time (extreme T_{min} e.g., <0°C and <-18°C) showed the opposite effect (r=0.38, $P \leq 0.01$). Snow fall in November preceding growth was also negatively correlated (r=-0.23, $P \leq 0.01$), likely due to associated low T or cloud cover (which reduced light needed for photosynthesis). Similarly, reductions in heat accumulation in the spring were linked to reduced growth. April T_{mean} and May cooling degree days (CDD) – a measure of heat accumulation >18.3°C – were positively associated with growth the following year (r=0.38, $P \leq 0.01$), while April HDD, a measure of cold, was negatively correlated to growth.
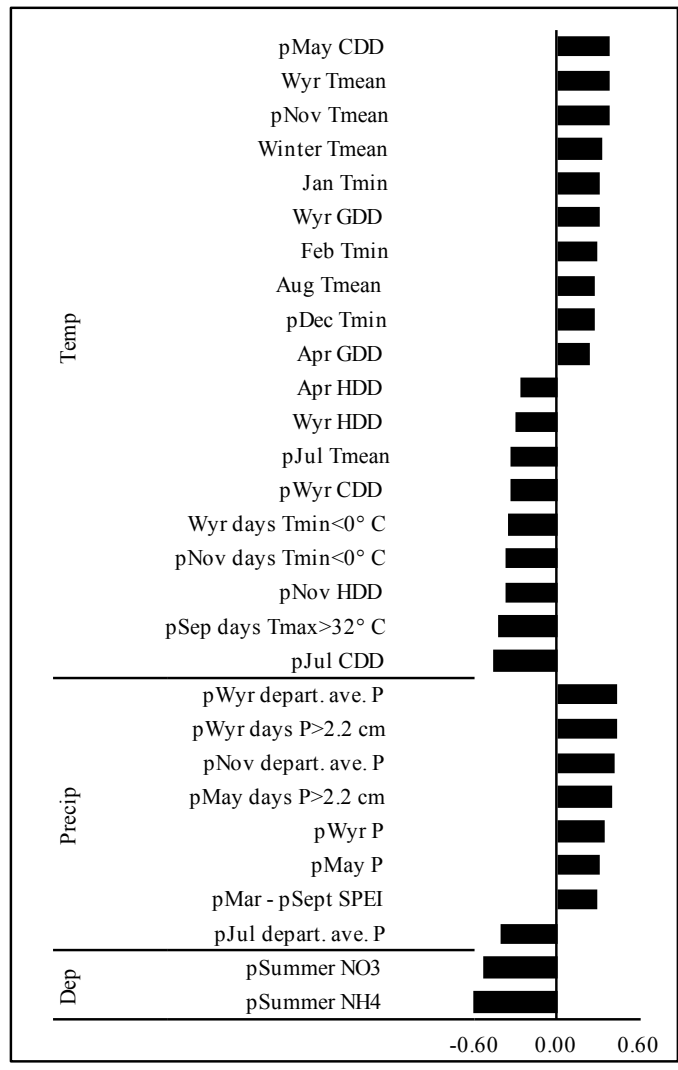
Figure 3.3: Significant bootstrapped climate- and deposition-growth correlations (r) with mean RWI by variable type: temperature (Temp), precipitation (Precip), and atmospheric deposition (Dep). Coefficients were considered significant if *P*≤0.01. Abbreviations: p = previous year, N = number, Depart.= departure, T = temperature, P = precipitation, Min = minimum, GDD = growing degree days (cumulative degrees > 5°C [41°F]), HDD = heating degree days (cumulative days < 18.3°C [65°F]), CDD = cooling degree days (cumulative degrees > 18.3°C [65°F]), Winter= previous December–February, SPEI= standardized precipitation evapotranspiration index, Wyr= water year (previous October to current September), NO3= nitrate deposition, NH4= ammonium deposition. For more information on variables see methods.

89

As expected, winter T was important for red spruce. Specifically, we found that higher winter and Jan T_{mean} (r=0.33 and 0.27, respectively; $P \leq 0.01$), and Dec-Feb extreme T_{min} (r=0.27, 0.31, and 0.30, respectively; $P \leq 0.01$), were related with greater growth. When we combined these findings with the strong associations between red spruce growth and fall and spring T, we conclude that we cannot reject H_2, which hypothesized that increases in T, particularly outside the traditional growing season (e.g., fall, winter and spring), were related to increased red spruce growth.

Summer T demonstrates the complicated relationship between red spruce growth and T. While summer T was often positively associated with growth, previous (p) summer T displayed the opposite relationship (Fig. 3.3). We found that high T in July (CDD, GDD, T_{mean}, and T_{max}) were negatively correlated with growth the subsequent year. However, during the summer of growth, red spruce shows a strong, positive association with Aug T_{mean} (r=0.28; $P \leq 0.01$).

During summer, red spruce also displayed an increased sensitivity to pollution deposition. Both NH_4^+ and NO_3^- deposition in the summer were strongly, negatively correlated to growth the following year (r=-0.60 and -0.53, respectively; $P \leq 0.01$) (Fig. 3.3). While we found that pH of rainwater and cation:anion ratio of deposition were both positively associated with red spruce growth ($P \leq 0.05$), neither of these associations were strong enough to warrant inclusion in further analyses. These results strongly suggest a continued relationship between acid deposition and red spruce growth; thus, we cannot

reject H_3, which proposed that declines in acid deposition could be related to increased growth.

Although not accounted for in our hypotheses, moisture availability was important for red spruce growth, particularly in antecedent years (Fig. 3.3). SPEI of pMay-Sept and pWyr P were associated with increases in growth (r=0.29 and 0.34, respectively; $P \leq 0.01$), but interestingly, we found that measures of extreme P, such as number of days with rainfall >2.2 cm and overall departure from normal rainfall, had stronger correlations with growth (r=0.43 and 0.44, respectively; $P \leq 0.01$). Examining these patterns over the seasons, we find strong, positive relationships between subsequent growth and spring and fall P (pMay and Nov extreme P, May P). If we couple these findings with the negative associations between growth and pSummer T, it suggests a drought response for the species. However, since extreme rainfall in the prior summer (e.g., pJuly) was associated with reduced growth, it may be that red spruce is more sensitive to low water availability during the spring and fall seasons, compared to summer. Lastly, we failed to find an association between CO_2 and red spruce growth (overall and using residuals). Therefore, at this point, we reject our hypothesis that CO_2 positively influenced red spruce growth (H_4).

3.4.3 Growth models

Overall, the best model predictors for mean annual change in growth (1925-2012, R_{adj}^2=0.60, RMSE=0.12, P<0.0001) across the study site were Jan T_{min} (R_{adj}^2=0.06, P=0.0014), pNov HDD (R_{adj}^2=0.14, P<0.0001), April GDD (R_{adj}^2=0.03, P<0.0001), and pWyr P and CDD (R_{adj}^2=0.07, P=0.0002 and R_{adj}^2=0.31, P<0.0001, respectively) (Table 3.1, Fig. 3.4c) Of these predictors, pNov HDD and pWyr CDD had a negative association with growth, while the others were positively associated. Temperature preceding the growing season (e.g., pNov HDD, pWyr CDD, Jan T_{min}) in total explained 58% of the variance in growth, with pWyr P explaining 10% and April GDD, 13%. In total, this model explained 81% of the total variance seen in the mean chronology. The residuals of the climate models did not display a linear trend and further, did not have a significant correlation with CO_2 (Fig. S3.6).

However, we found that predictor variables were not consistent though time or space (Table 3.1, Fig. 3.4). When we modeled growth using data before acid deposition-related decline ($RWI_{1925-1960}$) (Adj. R^2=0.58, RMSE=0.13, P<0.0001), the model was not as strong at forecasting growth post-1960 (r=0.78 and r=0.40, respectively) (Fig. 3.4a). Interestingly, this model only included T (i.e., April GDD, pWyr CDD, Jan T_{min}), while the models using post-1960s data included P. A similar pattern emerged when we created a model of RWI_{FSS} growth using only 1960 to 2012 data ($RWI_{1960-2012}$) and predicted pre-1960 growth (Fig. 3.4b). However, this model more accurately forecasted recent growth

trends than the earlier model ($RWI_{1925\text{-}1960}$) (2001-2012; r=0.97 and r=0.65, respectively).

When we modeled growth to include deposition ($RWI_{1980\text{-}2012}$) (Fig. 3.4d), we found that

a negative effect of pSummer NO_3^- increased the model fit, particularly for recent growth

(r=0.98).

Table 3.1: Model results (ANOVA, *P*<0.001) predicting mean RWI for four time periods: Predicted RWI$_{1925\text{-}1960}$, pre-acid deposition (Adj. R^2=0.58, RMSE=0.13, *P*<0.0001); predicted RWI$_{1960\text{-}2012}$ (Adj. R^2=0.78, RMSE=0.08, *P*<0.0001); predicted RWI$_{1925\text{-}2012}$ (Adj. R^2=0.60, RMSE=0.12, *P*<0.0001), the full chronology; and predicted RWI$_{1980\text{-}2012}$, this latter time period included possible influences of pollutant deposition data that was limited to 1980-2012 (Adj. R^2=0.88, RMSE=0.07, *P*<0.0001). Model terms, expressed as first differences, were first selected via bootstrapped correlation function analysis, stepwise linear regression, and assessment of collinearity.

Time period for model construction	Term[a]	R_{adj}^2	Estimate	SS	F Ratio	Prob > F	Variance explained
	Jan T_{min}	0.06	0.005±0.001	0.15	10.96	0.0014	8%
	pNov HDD	0.14	0.000±0.000	0.34	25.49	<0.0001	18%
1925-2012	April GDD	0.03	0.002±0.000	0.26	19.14	<0.0001	13%
	pWyr P	0.07	0.008±0.002	0.20	14.71	0.0002	10%
	pWyr CDD	0.31	-0.001±0.000	0.62	45.75	<0.0001	32%
	Jan T_{min}	0.002	0.006±0.003	0.08	4.75	0.0372	10%
1925-1960	April GDD	0.33	0.003±0.001	0.44	27.88	<0.0001	58%
	pWyr CDD	0.23	-0.001±0.000	0.20	12.46	0.0014	26%
	Jan T_{min}	0.16	0.005±0.001	0.08	12.83	0.0008	6%
	pNov T_{mean}	0.12	0.014±0.003	0.17	27.23	<0.0001	13%
1960-2012	Aug T_{max}	0.32	0.010±0.003	0.08	12.94	0.0008	6%
	April GDD	0.004	0.001±0.000	0.03	5.08	0.0291	2%
	pWyr P	0.28	0.008±0.002	0.13	20.06	<0.0001	9%
	pWyr CDD	0.36	-0.001±0.000	0.28	44.69	<0.0001	21%
	pNov HDD	0.14	0.000±0.000	0.06	14.13	0.0009	6%
	pJul CDD	0.20	-0.001±0.000	0.12	27.20	<0.0001	11%
1980-2012	Jan T_{min}	0.06	0.010±0.002	0.14	30.75	<0.0001	13%
	pSummer NO_3^-	0.50	-0.282±0.072	0.07	15.46	0.0006	6%
	pWyr P	0.07	0.007±0.002	0.08	17.22	0.0003	7%

[a]p = previous year, T = temperature, P = precipitation, Min = minimum, Max = maximum, GDD = growing degree days (cumulative degrees > 5°C [41°F]), HDD = heating degree days (cumulative days < 18.3°C [65°F]), CDD = cooling degree days (cumulative degrees > 18.3°C [65°F]), Summer: June-August, Wyr: water year, previous October to current September, NO_3^-: nitrate deposition. For more information on variables see methods.

(a)

- - - - RWI
Pred RWI 1960-2012

r=0.76, *P*<0.0001

2001-2012
r=0.95, *P*<0.0001

r=0.57, *P*=0.0005

r=0.88, *P*<0.0001

(b)

- - - - RWI
Pred RWI 1925-1960

r=0.78, *P*<0.0001

2001-2012
r=0.65, *P*=0.02

r=0.58, *P*<0.0001

r=0.40, *P*=0.003

(c)

- - - - RWI
Pred RWI 1925-2012

r=0.79, *P*<0.0001

2001-2012
r=0.97, *P*<0.0001

r=0.72, *P*<0.0001

r=0.76, *P*<0.0001

(d)

- - - - RWI
Pred RWI 1980-2012

2001-2012
r=0.98, *P*<0.0001

r=0.95, *P*<0.0001
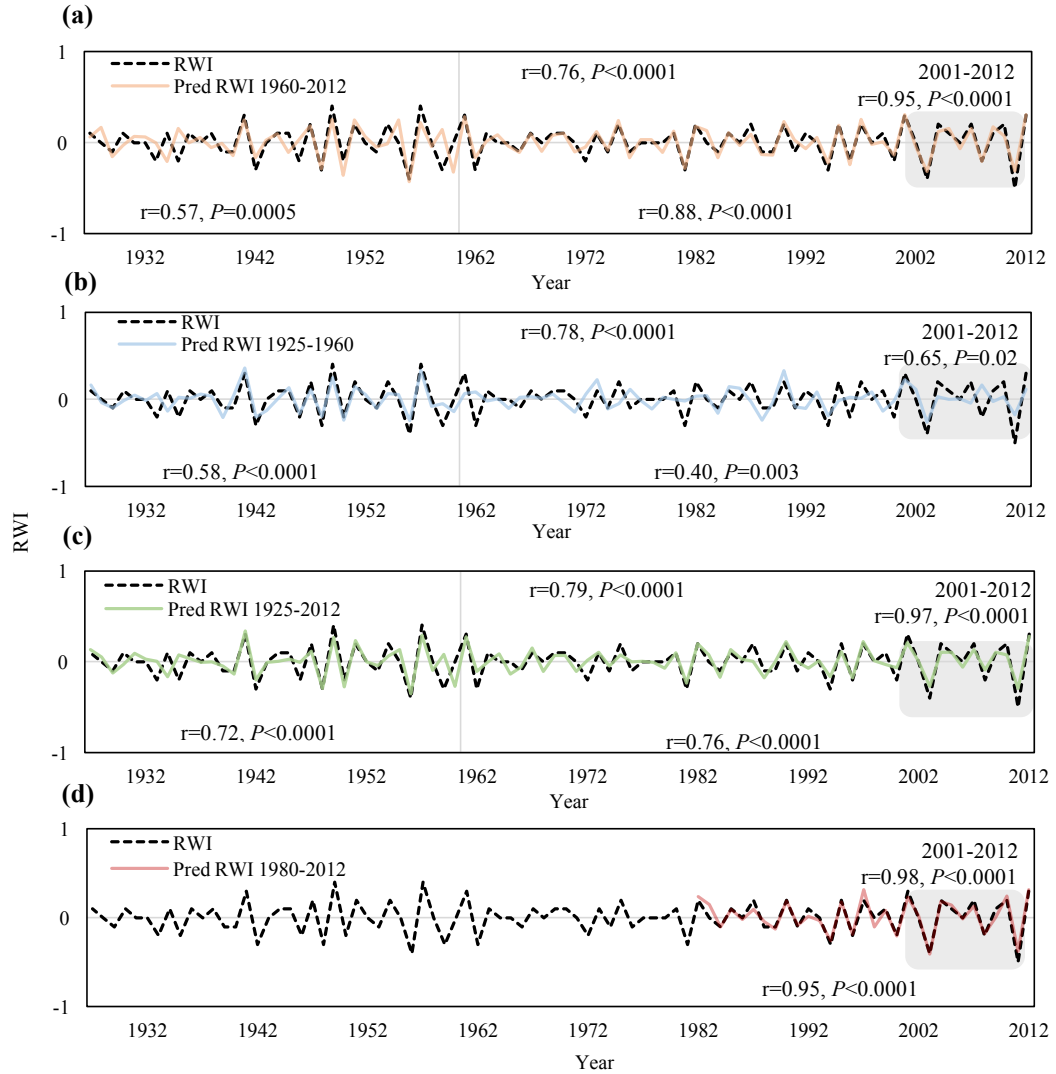
Figure 3.4: First differences of observed mean red spruce tree ring chronology (RWI$_{FSS}$, black dashed line) compared to predicted chronology modeled using growth and climate data from three time periods: (a) predicted RWI$_{1925-2012}$ (Adj. R^2=0.60, RMSE=0.12, *P*<0.0001), the full chronology: (b) predicted RWI$_{1925-1960}$ (Adj. R^2=0.58, RMSE=0.13, *P*<0.0001), before acid deposition and red spruce decline; (c) predicted RWI$_{1960-2012}$ (Adj. R^2=0.80, RMSE=0.08, *P*<0.0001); and (d) predicted RWI$_{1980-2012}$ (Adj. R^2=0.88, RMSE=0.07, *P*<0.0001), the most recent growth and period of pollutant deposition data. Correlations between the Mean RWI chronology (expressed as first differences) and the predicted chronologies a-c and associated *P*-values are shown for different time periods: 1925-2012 at the top, and both 1925-1960 and 1960-2012 at the bottom of each figure. Predicted RWI$_{1980-2012}$ could not be modeled back in time as it uses deposition data that begins in 1980. Correlations with recent growth (2001-2012, denoted with grey box) are displayed at the top right.

94

Running correlations between each model prediction and RWI_{FSS} show how these models failed to accurately predict growth through time (Fig. 3.5). For the three models that predict growth from 1960-1980, there are sharp declines, and even reversals, in correlation with RWI_{FSS}. The predicted $RWI_{1980-2012}$ model (includes NO_3^- deposition) had a consistently strong fit, but due to the data limits of the acid deposition record, we cannot assess the strength of this relationship pre-1980. Further, we found that the correlation between growth and NO_3^- deposition was not consistent through time (1980-2012), even for this limited dataset (Fig. 3.6). However, this analysis suggests that the strongly negative relationship between the two factors has decreased recently and may lead to more favorable conditions for the species.
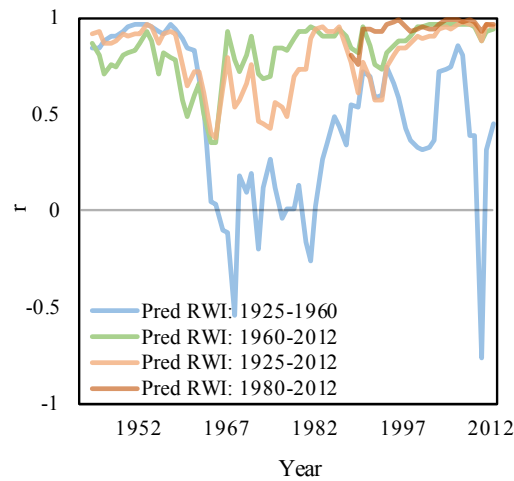
Figure 3.5: Seven-year running Pearson's product moment correlations between mean RWI and predicted RWI based on four models. Methods follow Johnson et al. 1988.
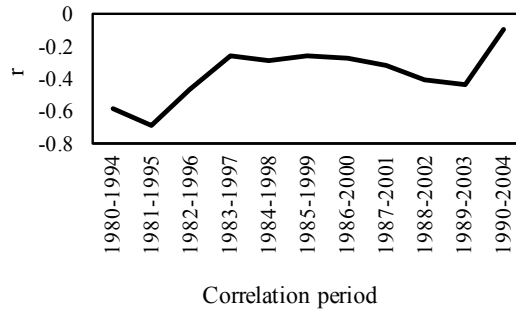
Figure 3.6: Running 15-year bootstrapped correlations between RWI and NO$_3^-$ deposition from 1980-2012.

Testing the predicted RWI$_{1980-2012}$ model by RWI$_{FSS}$ elevation class chronology, we see differing response by elevation grouping (Table 3.2). All the model parameters imputed from the RWI$_{1980-2012}$ model are strong predictors of growth at Mid (RWI$_{Mid}$ R$_{adj}^2$=0.81, RSME=0.09, P<0.0001) and High (RWI$_{High}$ R$_{adj}^2$=0.76, RSME=0.12, P<0.0001) elevations, but not at Low elevation. Therefore, we used a reduced model for Low elevation. All elevation groups displayed a negative relationship with NO$_3^-$ deposition, but again, this relationship was stronger for Mid and High elevations (RWI$_{High}$ R$_{adj}^2$= 0.47, P=0.055; RWI$_{Mid}$ R$_{adj}^2$= 0.49, P=0.015, and RWI$_{Low}$ R$_{adj}^2$= 0.36, P=0.038). For Low elevation, the other best predictor variables were the negative growth relationship with pNov HDD (R$_{adj}^2$= 0.13) and pJuly CDD (R$_{adj}^2$= 0.11). We did not see a division in growth based on geographic relationship to the prevailing pollution deposition trends (Ollinger et al. 1993). Further, the predicted RWI$_{1980-2012}$ model fit both chronologies well (RWI$_{East}$ R$_{adj}^2$=0.76, RSME=0.12, P<0.0001; RWI$_{West}$ R$_{adj}^2$=0.50,

RSME=0.12, P<0.0001) (Table 3.3), and we did not detect stronger effects of NO_3^-

deposition for RWI$_{West}$ as expected.

Table 3.2: Predicted RWI$_{1980-2012}$ models by plot elevation class: High (R_{adj}^2=0.76, RSME=0.12, P<0.0001), Mid (R_{adj}^2=0.81, RSME=0.09, P<0.0001), and Low (R_{adj}^2=0.50, RSME=0.12, P<0.0001). All variables were converted into first differences prior to model building.

Elevation Class	Term[a]	Estimate± SE	R_{adj}^2	SS	F Ratio	Prob > F	Variance explained
	pSummer NO_3^-	-0.256±0.127	0.47	0.06	4.05	0.0551	4%
	pWyr P	0.011±0.003	0.13	0.16	11.42	0.0024	11%
High (>950m)	pJul CDD	-0.002±0.000	0.11	0.22	15.70	0.0005	15%
	pNov HDD	-0.001±0.000	0.11	0.09	6.34	0.0186	6%
	Jan T_{min}	0.006±0.002	0.07	0.09	6.54	0.017	6%
	pSummer NO_3^-	-0.266±0.122	0.49	0.06	6.79	0.0152	5%
	pJul CDD	-0.001±0.000	0.21	0.11	13.09	0.0013	10%
Mid (700-900m)	pNov HDD	-0.001±0.000	0.14	0.11	12.98	0.0014	10%
	pWyr P	0.009± 0.002	0.06	0.12	14.01	0.001	10%
	Jan T_{min}	0.006±0.002	0.05	0.09	11.10	0.0027	8%
	pSummer NO_3^-	-0.266±0.07	0.36	0.07	4.78	0.0377	14%
Low (<650m)	pNov HDD	-0.001±0.000	0.13	0.13	8.37	0.0075	25%
	pJul CDD	-0.001±0.000	0.11	0.10	6.74	0.0151	20%

[a]p = previous year, T = temperature, P = precipitation, Min = minimum, HDD = heating degree days (cumulative days < 18.3°C [65°F]), CDD = cooling degree days (cumulative degrees > 18.3°C [65°F]), Summer = Jun-Aug, Wyr: water year, previous October to current September, NO_3^-: nitrate deposition. For more information on variables see methods.

Table 3.3: Predicted RWI$_{1980\text{-}2012}$ models by regional grouping: East (R$_{adj}^2$=0.76, RSME=0.12, P<0.0001) and West (R$_{adj}^2$=0.50, RSME=0.12, P<0.0001) of the study area, approximately divided by the Green Mountains, VT (see Fig. 1). All variables were converted into first differences prior to model building.

Regional Grouping	Term[a]	Estimate ± SE	R$_{adj}^2$	SS	F Ratio	Prob > F	Variance explained
East	pSummer NO$_3^-$	-0.236±0.094	0.49	0.05	6.28	0.019	5%
	pJul CDD	-0.001±0.000	0.29	0.14	17.43	0.000	13%
	pNov HDD	-0.001±0.000	0.13	0.07	8.74	0.007	6%
	pWyr P	0.008±0.002	0.06	0.10	12.51	0.002	9%
	Jan T$_{min}$	0.006±0.002	0.06	0.09	12.06	0.002	9%
West	pSummer NO$_3^-$	-0.217±0.091	0.48	0.04	5.76	0.024	4%
	pJul CDD	-0.001±0.000	0.19	0.12	16.00	0.001	11%
	pNov HDD	-0.001±0.000	0.16	0.14	19.89	0.000	13%
	pWyr P	0.009±0.002	0.09	0.13	17.43	0.000	12%
	Jan T$_{min}$	0.005±0.002	0.05	0.06	8.17	0.009	5%

[a]p = previous year, T = temperature, P = precipitation, Min = minimum, HDD = heating degree days (cumulative days < 18.3°C [65°F]), CDD = cooling degree days (cumulative degrees > 18.3°C [65°F]), Summer = Jun-Aug, Wyr: water year, previous October to current September, NO$_3^-$: nitrate deposition. For more information on variables see methods.

3.5 Discussion

Based on the range of tree ages and DBH, variety of plot locations and characteristics (Table S3.1), failure to detect substantial stand disturbance (even following the recent [2003] winter injury event [Fig. S3.5]), and the strong alignment of three detrending techniques (Fig. 3.2), we feel confident that the trends depicted here are representative of the regional red spruce population. Further, this analysis is conservative as we include all red spruce plots for assessment, not only those exhibiting recent increases in growth (10% plots did not show positive growth trends since 2002). While we did not assess soil nutrition, a recent analysis indicated that recent growth increases occurred regardless of the combination of site nutrition and pollution inputs (assessed via Critical Load Exceedence models) (Engel et al. 2016) and recent work has shown that

soils have only just begun to recover from decades of acidic inputs (Lawrence et al. 2015; Lawrence et al. 2012). Together, these results lead us to reject H_1 and conclude that alterations to the regional environment are most likely responsible for recent increases in red spruce growth. While we did not study intermediate and suppressed red spruce trees, we postulate that similar growth trends and response to climate would be seen in these trees, although with a more muted response due to the effects of competition (Martín-Benito et al. 2008).

Through this study, we demonstrated the complex relationship between tree growth and T. For example, higher summer T was negatively associated with subsequent growth, but positively associated with current growth (Fig. 3.3). There are a few possible reasons for this difference, which has also been reported for other conifer species (Girardin et al. 2016). Higher T could increase current-year growth if the tree favors consumption of C for short-term needs rather than for storage as non-structural carbohydrates to support growth the following year (Rennenberg et al. 2006). Further, T-induced increases in growth could result in the sequestration of other nutrients (e.g., N, Ca) that temporarily become limiting and indirectly suppress growth the following year (Rennenberg et al. 2006).

While negative relationships between high T and growth the following year suggest a legacy effect of higher T, conceivably through limitations of C or other compulsory elements, when combined with the strong positive relationship with pWyr

P, it could indicate a negative response to drought for the species. This was unexpected considering that the high moisture availability in the region (Pederson et al. 2013) that is projected to increase (Kunkel et al. 2013). There is some evidence that acid deposition increases a tree's susceptibility to drought through a reduction in fine root biomass (Persson et al. 1995), which may partially explain the increase in strength of the relationship between growth and P after 1960 (Table 3.1). Additionally, for red spruce, it has been asserted that weather events in the preceding growing season that reduce C capture and nutrient uptake – for example drought – can predispose trees to winter injury (Schaberg et al. 2011), and thus cause reductions in growth due to C losses. However, for all analyses, we found that water availability (P, extreme P, SPEI) did not have as strong of an association or explain as much variance as T (Table 3.1), suggesting that T limits red spruce growth more than P.

We also demonstrated the importance of favorable T outside the traditional growing season—fall, winter, and spring seasons (Fig. 3.3). Positive relationships between T during the spring and fall imply that low T restricted red spruce growth in these seasons. While extreme cold and heat in the fall can be detrimental to growth, favorable T could allow for an extended period for C capture. Further, an extended fall growing season could allow for more root elongation (Joslin and Wolfe 1992), and increase water and nutrient uptake. Similarly, we saw a positive relationship of growth with April GDD. At this time in the year, most deciduous hardwoods have not fully

undergone leaf expansion; typically, that does not occur until May (Hufkens et al. 2012).

Higher temperatures in April, especially ones that accumulate GDD (i.e., >5°C), may

confer a competitive advantage for red spruce trees and perhaps other conifers (Girardin

et al. 2016) that are similarly able to rapidly increase photosynthetic activity compared

to sympatric species (DeHayes et al. 2001). Likewise, the physiological ability of red

spruce to photosynthesize in the winter when T moderates (e.g., during winter thaws)

could also confer a competitive advantage if winter T were favorable for photosynthesis.

Aligning with previous findings (Johnson et al. 1988; McLaughlin et al. 1987), we saw

that Jan T_{min}, the coldest month, was a strong predictor of growth, particularly for trees

at both Mid and High elevations. Additionally, we found degree day indices to be a strong

associate with growth. We established that both indices CDD (integrated heat exposure

>18.3 C) and HDD (integrated cold exposure <18.3 C) were consistently associated with

red spruce growth (Fig. 3.3). A strong relationship with CDD and radial growth has been

found in other co-occurring tree species as well (Kosiba et al. In press).

These results support the hypothesis that heat accumulation outside the traditional

growing season (e.g., fall, winter, early spring) positively relate to red spruce growth

(H_2). If we continue to observe increasing T in these seasons, conditions may be

favorable for the species. However, as the magnitude of the negative relationship

between growth and pJuly T was larger than the positive relationship with Aug T (Fig.

3.3), the net effect could be an overall negative effect of summer T on growth. Therefore,

101

rising T outside the summer may be beneficial, but increases during the summer months may be detrimental to growth.

Considering the plethora of research on the impact of acid deposition on red spruce growth and vigor (DeHayes et al. 1997; Engel et al. 2016; Schaberg et al. 2001), we were not surprised to find a strong, negative correlation between N-deposition and growth the subsequent year. N-deposition in the summer likely created nutrient imbalances approaching winter when Ca, in particular, is needed for winter cold tolerance (Schaberg et al. 2001). However, the negative correlation between growth and NO_3^- is lessening over time (Fig. 3.6), providing support for H_3. Unfortunately, the instrumental collection of acid deposition data began in the late 1970s, after acid deposition related decline in red spruce had already been evident (Johnson et al. 1988). Thus, acid deposition cannot be included in our long-term growth models and we cannot assess how increases – as opposed to contemporary decreases– in acid deposition may have impacted red spruce growth.

It has been show that acid deposition can increase the availability of soil-bound and toxic aluminum (Al), decrease accessibility of Ca (Joslin and Wolfe 1992; Persson et al. 1995), and reduce mycorrhizal associations (Reich et al. 1986), which can alter biomass (Park et al. 2008) and nutrient uptake of fine roots (Persson et al. 1995). Taken together, these impacts could reduce C availability through reductions in water and nutrient uptake, and thus, retard C allocation to radial growth. Chronic N deposition has

102

been identified as especially problematic to alterations in C allocation by reducing fine root biomass and critical nutrient uptake (Persson et al. 1995).

Interestingly, we found the strongest negative associations with NO_3^- deposition at Mid elevation, followed by High elevation. Low elevation displayed a weaker relationship with NO_3^-, which aligns with research demonstrating increasing acid deposition (Cogbill and Likens 1974) and red spruce winter injury severity (Lazarus et al. 2006) with elevation. However, why Mid elevation red spruce show a stronger growth relationship with NO_3^- is unclear, but it was also indicated in previous work (Engel et al. 2016). Nevertheless, we predict that as acid deposition continues to decline we should see fewer winter injury events and more C capture, particularly for Mid and High elevation locations where winter injury had been severe in the past (Lazarus et al. 2006).

We were surprised that not all measures of acid deposition, particularly SO_4^{2-}, were significantly related to growth, but this may do with spatial variability and the legacy effects of acid deposition on tree growth (e.g., Engle et al., 2016) as opposed to year-to-year relationships we focused on here. One additional reason for the lack of relationship with SO_4^{2-} may be the robust interaction between NO_3^-, cation leaching, and water flux reported by Joslin and Wolfe (1992). They found that NO_3^- was more strongly associated with cation leaching in both organic and mineral soil layers and had more temporal variability than SO_4^{2-}. Further, during periods of low water flux, soil NO_3^- increased strongly, and decreased during high water flux. This effect was so strong that

during periods of drought, NO_3^- was found to be much more important on a charge equivalent basis, than SO_4^{2-} (Joslin and Wolfe 1992). The interaction between NO_3^- and rainfall may partially explain the strengthening positive relationship after 1960 between Wyr P and subsequent growth, as well as the positive relationships with measures of extreme rainfall (i.e., departure from average P, N days P>2.2 cm) (Fig. 3.3). However, others have reported greater detrimental effects to red spruce – including larger reductions in cold tolerance – with application of SO_4^{2-} compared to NO_3^- (Cape et al. 1991; Jacobson et al. 1990)

We failed to find an association between CO_2 and red spruce growth through various methods (e.g., annual growth, residuals of growth after accounting for the effects of climate and deposition (Fig. S3.6)) and reject H_4. This lack of association aligns with others who have shown no significant effect of CO_2 on radial growth (Bader et al. 2013; Girardin et al. 2016; Körner et al. 2005). While there is considerable debate if elevated CO_2 will provoke changes in tree growth and/or water use efficiency (Silva and Horwath 2013), it is a difficult relationship to properly assess *in situ*. While some analyses of forest growth and instrumental CO_2 records have also attempted to find a relationship (Girardin et al. 2016), there is evidence that CO_2 effects are muted or nonexistent on sites where other environmental factors (e.g., T, P, and nutrients) are more limiting to growth than C availability (Körner 2003; Saurer et al. 2014). Based on the strong associations between red spruce growth and climate measures that we reported here, we hypothesize that other

104

factors, namely T, water accessibility, and nutrient leaching via acidifying agents, are currently more limiting to red spruce than C availability.

Following decades of declines, this work suggests a recovery for red spruce trees in the northeastern US. With decreases in acid deposition and increases in favorable climate conditions, the species' current growth surge should persist - at least in the short term, and particularly for stands at elevations over 650m. Considering these results, we predict that with continued increases in fall, winter, and spring T, coupled with reductions in pollutant loading, red spruce trees may even increase C capture further – if summer T does not exceed physiological thresholds and P is not limiting.

While the near-term predictions for red spruce may be favorable, the species could be vulnerable to change in the future, due to its low genetic diversity, past region-wide decline, and high spatial synchrony in growth patterns. The uncertainty lies in how P and T regimes will change in the future. If moisture availability (e.g., annual P, extreme P) continues to increase in the northeastern US, red spruce may have adequate water for increased C capture. However, if extreme weather events, such as prolonged drought or periods of extreme T become more frequent (especially in the summer), C capture could be limited. Indeed, the USDA Forest Service Climate Change Atlas projects that red spruce habitat suitability will decrease into the future primarily due to increases in July T (Prasad et al. 2007-ongoing).

Here we present the first comprehensive analysis of novel growth changes observed for red spruce trees in the northeastern US. While attributing cause and effect to *in situ* tree growth is challenging, we have identified significant correlations between growth and environmental variables, and have demonstrated that growth is synchronous across a wide spatial scale, and independent of a suite of site-based factors, suggesting that large-scale climate and pollutant deposition conditions are likely effecting this growth surge. When paired with declines in acid deposition, which have caused protracted declines in growth, the species could benefit in the short-term. More broadly, this work demonstrates the importance of scientific inquiry to identify ecological problems (here acid deposition-induced decline), policy decisions to mitigate those issues (the Clean Air Act and subsequent amendments), and evidence of resultant biological recovery (this research).

3.6 Acknowledgements

3.7 References

Ainsworth, E.A., and Long, S.P. 2005. What have we learned from 15 years of free-air CO2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO2. New Phytologist **165**(2): 351-372.

Bader, M.K.F., Leuzinger, S., Keel, S.G., Siegwolf, R.T.W., Hagedorn, F., Schleppi, P., and Körner, C. 2013. Central European hardwood trees in a high-CO2 future: synthesis of an 8-year forest canopy CO2 enrichment project. Journal of Ecology **101**(6): 1509-1519. doi: 10.1111/1365-2745.12149.

Bunn, A., Korpela, M., Biondi, F., Campelo, F., Merian, P., Qeadan, F., and Zang, C. 2015. dplR: Dendrochronology Program Library in R. R package version 1.6.3. http://r-forge.r-project.org/projects/dplr/.

Cape, J.N., Leith, I.D., Fowler, D., Murray, M.B., Sheppard, L.J., Eamus, D., and Wilson, R.H.F. 1991. Sulphate and ammonium in mist impair the frost hardening of red spruce seedlings. New Phytologist **118**(1): 119-126. doi: 10.1111/j.1469-8137.1991.tb00572.x.

Cogbill, C.V., and Likens, G.E. 1974. Acid precipitation in the northeastern United States. Water Resources Research **10**(6): 1133-1137. doi: 10.1029/WR010i006p01133.

Cook, E.R. 1985. A time series analysis approach to tree ring standardization (dendrochronology, forestry, dendroclimatology, autoregressive process). *In* Renewable Natural Resources. University of Arizona, Tucson, AZ.

Cook, E.R., Johnson, A.H., and Blasing, T.J. 1987. Forest decline: modeling the effect of climate in tree rings. Tree Physiology **3**(1): 27-40. doi: 10.1093/treephys/3.1.27.

Cook, E.R., and Pederson, N. 2011. Uncertainty, emergence, and statistics in dendrochronology. *In* Dendroclimatology. Springer. pp. 77-112.

Cook, E.R., and Peters, K. 1997. Calculating unbiased tree-ring indices for the study of climatic and environmental change. The Holocene **7**(3): 361-370.

DeHayes, D.H. 1992. Winter injury and developmental cold tolerance of red spruce. *In* The Ecology and Decline of Red Spruce in the Eastern United States. *Edited by* C. Eagar and M.B. Adams. Springer-Verlag New York Inc., New York, NY, USA. pp. 295-337.

DeHayes, D.H., Schaberg, P.G., Hawley, G.J., Borer, C.H., Cumming, J.R., and Strimbeck, G.R. 1997. Physiological implications of seasonal variation in membrane-associated calcium in red spruce mesophyll cells. Tree Physiology **17**(11): 687-695. doi: 10.1093/treephys/17.11.687.

DeHayes, D.H., Schaberg, P.G., Hawley, G.J., and Strimbeck, G.R. 1999. Acid rain impacts on calcium nutrition and forest health. BioScience **49**(10): 789-800.

DeHayes, D.H., Schaberg, P.G., and Strimbeck, G.R. 2001. Red spruce cold hardiness and freezing injury susceptibility. *In* Conifer Cold Hardiness. *Edited by* F. Bigras. Kluwer Academic Publishers, Dordrecht, the Netherlands.

Driscoll, C.T., Lawrence, G.B., Bulger, A.J., Butler, T.J., Cronan, C.S., Eagar, C., Lambert, K.F., Likens, G.E., Stoddard, J.L., and Weathers, K.C. 2001. Acidic deposition in the northeastern United States: sources and inputs, ecosystem effects, and management strategies. BioScience **51**(3): 180-198. doi: 10.1641/0006-3568(2001)051[0180:aditnu]2.0.co;2.

Eagar, C., and Adams, M.B. 1992. Ecology and decline of red spruce in the eastern United States. Springer-Verlag, New York.

Engel, B.J., Schaberg, P.G., Hawley, G.J., Rayback, S.A., Pontius, J., Kosiba, A.M., and Miller, E.K. 2016. Assessing relationships between red spruce radial growth and pollution critical load exceedence values. Forest Ecology and Management **359**: 83-91.

Foster, D.R. 1992. Land-Use History (1730-1990) and Vegetation Dynamics in Central New England, USA. Journal of Ecology **80**(4): 753-771.

Foster, J.R., and D'Amato, A.W. 2015. Montane forest ecotones moved downslope in northeastern US in spite of warming between 1984 and 2011. Global Change Biology: 4497-4507. doi: 10.1111/gcb.13046.

Fraver, S., White, A.S., and Seymour, R.S. 2009. Natural disturbance in an old-growth landscape of northern Maine, USA. Journal of Ecology **97**(2): 289-298. doi: 10.1111/j.1365-2745.2008.01474.x.

Friedman, J.H. 1984. A variable span smoother. DTIC Document.

Fritts, H.C. 1976. Tree Rings and Climate. Academic Press, New York.

Girardin, M.P., Bouriaud, O., Hogg, E.H., Kurz, W., Zimmermann, N.E., Metsaranta, J.M., de Jong, R., Frank, D.C., Esper, J., Büntgen, U., Guo, X.J., and Bhatti, J. 2016. No growth stimulation of Canada's boreal forest under half-century of combined warming and CO2 fertilization. Proceedings of the National Academy of Sciences **113.52**: E8406-E8414. doi: 10.1073/pnas.1610156113.

Hawley, G.J., and DeHayes, D.H. 1994. Genetic diversity and population structure of red spruce (Picea rubens). Canadian Journal of Botany **72**(12): 1778-1786. doi: 10.1139/b94-219.

Holmes, R.L. 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-ring Bulletin **43**: 69-78.

Hufkens, K., Friedl, M.A., Keenan, T.F., Sonnentag, O., Bailey, A., O'Keefe, J., and Richardson, A.D. 2012. Ecological impacts of a widespread frost event following early spring leaf-out. Global Change Biology **18**(7): 2365-2377. doi: 10.1111/j.1365-2486.2012.02712.x.

Jacobson, J.S., Heller, L.I., Yamada, K.E., Osmeloski, J.F., Bethard, T., and Lassoie, J.P. 1990. Foliar injury and growth response of red spruce to sulfate and nitrate acidic mist. Canadian Journal of Forest Research **20**(1): 58-65. doi: 10.1139/x90-009.

Johnson, A., Cook, E., and Siccama, T. 1988. Climate and red spruce growth and decline in the northern Appalachians. Proceedings of the National Academy of Sciences **85**(15): 5369-5373.

Joslin, J., and Wolfe, M. 1992. Red spruce soil solution chemistry and root distribution across a cloud water deposition gradient. Canadian Journal of Forest Research **22**(6): 893-904.

Kenefic, L. 2015. Red spruce tree cores from the Penobscot Experimental Forest, Maine. USDA Forest Service.

Körner, C. 2003. Carbon limitation in trees. Journal of Ecology **91**(1): 4-17. doi: 10.1046/j.1365-2745.2003.00742.x.

Körner, C., Asshoff, R., Bignucolo, O., Hättenschwiler, S., Keel, S.G., Peláez-Riedl, S., Pepin, S., Siegwolf, R.T.W., and Zotz, G. 2005. Carbon flux and growth in mature deciduous forest trees exposed to elevated CO_2. Science **309**(5739): 1360-1362. doi: 10.1126/science.1113977.

Kosiba, A.M., Schaberg, P.G., Hawley, G.J., and Hansen, C.F. 2013. Quantifying the legacy of foliar winter injury on woody aboveground carbon sequestration of red spruce trees. Forest Ecology and Management **302**: 363-371.

Kosiba, A.M., Schaberg, P.G., Hawley, G.J., and Rayback, S.A. 2014. Using dendroecological techniques to interpret the response of trees to environmental change at Vermont Monitoring Cooperative's Mount Mansfield study site. Vermont Monitoring Cooperative.

Kosiba, A.M., Schaberg, P.G., Rayback, S.A., and Hawley, G.J. In press. Comparative growth trends of five northern hardwood and montane tree species reveal divergent trajectories and response to climate. Canadian Journal of Forest Research.

Kunkel, K.E., Stevens, L.E., Stevens, S.E., Sun, L., Janssen, E., Wuebbles, D., Hilberg, S., Timlin, M., Stoecker, L., and Westcott, N. 2013. Regional climate trends and scenarios for the US national climate assessment. Part 1. Climate of the Northeast U.S. NOAA Technical Report NESDIS 142-1.

Lawrence, G.B., Hazlett, P.W., Fernandez, I.J., Ouimet, R., Bailey, S.W., Shortle, W.C., Smith, K.T., and Antidormi, M.R. 2015. Declining Acidic Deposition Begins Reversal of Forest-Soil Acidification in the Northeastern U.S. and Eastern Canada. Environmental Science & Technology. doi: 10.1021/acs.est.5b02904.

Lawrence, G.B., Shortle, W.C., David, M.B., Smith, K.T., Warby, R.A.F., and Lapenis, A.G. 2012. Early Indications of Soil Recovery from Acidic Deposition in U.S. Red Spruce Forests. Soil Science Society of America Journal **76**(4): 1407-1417. doi: 10.2136/sssaj2011.0415.

Lazarus, B.E., Schaberg, P.G., DeHayes, D.H., and Hawley, G.J. 2004. Severe red spruce winter injury in 2003 creates unusual ecological event in the northeastern United States. Canadian journal of forest research **34**(8): 1784-1788.

Lazarus, B.E., Schaberg, P.G., Hawley, G.J., and DeHayes, D.H. 2006. Landscape-scale spatial patterns of winter injury to red spruce foliage in a year of heavy region-wide injury. Canadian Journal of Forest Research **36**(1): 142-152. doi: 10.1139/x05-236.

Lorimer, C.G., and Frelich, L.E. 1989. A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. Canadian Journal of Forest Research **19**(5): 651-663.

Miller, A.C., Woeste, K.E., Anagnostakis, S.L., and Jacobs, D.F. 2014. Exploration of a rare population of Chinese chestnut in North America: stand dynamics, health and genetic relationships. AoB Plants 6: plu065.

Martín-Benito, D., Cherubini, P., del Río, M., and Cañellas, I. 2008. Growth response to climate and drought in Pinus nigra Arn. trees of different crown classes. Trees **22**(3): 363-373. doi: 10.1007/s00468-007-0191-6.

McLaughlin, S.B., Downing, D.J., Blasing, T.J., Cook, E.R., and Adams, H.S. 1987. An analysis of climate and competition as contributors to decline of red spruce in high elevation Appalachian forests of the Eastern United states. Oecologia **72**(4): 487-501. doi: 10.1007/BF00378973.

National Atmospheric Deposition Program. 2016. NADP/NTN Monitoring. US Geological Survey [accessed 4 May 2016].

National Drought Mitigation Center. 2012. SPEI. University of Nebraska, Lincoln. http://droughtatlas.unl.edu/About.aspx [acessed 15 March 2015].

NOAA Earth System Research Laboratory Global Monitoring Division. 2016. Monthly Average Mauna Loa CO_2. http://www.esrl.noaa.gov/gmd/ccgg/trends/ [accessed 6 October 2016].

NOAA National Centers for Environmental Information. 2016. Monthly global summaries by station http://www.ncdc.noaa.gov/cdo-web/search [accessed 18 August 2016].

NOAA National Climatic Data Center. 2010. State of the Climate: National Overview. Available from http://www.ncdc.noaa.gov/sotc/national [accessed December 15, 2011.

NOAA National Weather Service. 2014. Monthly total growing degree days for Burlington, VT. http://www.weather.gov/btv/climo_gdd [Accessed 4/23/14].

NOAA Regional Climate Centers. 2016. DROUGHT-ACIS: Single station temperature and precipitation data http://drought.rcc-acis.org/ [acessed 14 August 2016].

Ollinger, S.V., Aber, J.D., Lovett, G.M., Millham, S.E., Lathrop, R.G., and Ellis, J.M. 1993. A spatial model of atmospheric deposition for the northeastern US. Ecological Applications **3**(3): 459-472.

Park, B.B., Yanai, R.D., Fahey, T.J., Bailey, S.W., Siccama, T.G., Shanley, J.B., and Cleavitt, N.L. 2008. Fine Root Dynamics and Forest Production Across a Calcium Gradient in Northern Hardwood and Conifer Ecosystems. Ecosystems **11**(2): 325-341. doi: 10.1007/s10021-008-9126-3.

Pederson, N., Bell, A.R., Cook, E.R., Lall, U., Devineni, N., Seager, R., Eggleston, K., and Vranes, K.J. 2013. Is an Epic Pluvial Masking the Water Insecurity of the Greater New York City Region? Journal of Climate. doi: 10.1175/jcli-d-11-00723.1.

Persson, H., Majdi, H., and Clemensson-Lindell, A. 1995. Effects of Acid Deposition on Tree Roots. Ecological Bulletins(44): 158-167.

Pontius, J., and Halman, J.M. 2012. Red spruce tree cores from the Bartlett Experimental Forest, NH. University of Vermont.

R Development Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rayback, S.A. 2012. Red spruce tree cores from sites in Vermont, New Hampshire, and Maine. University of Vermont.

Reich, P.B., Stroo, H.F., Schoettle, A.W., and Amundson, R.G. 1986. Acid rain and ozone influence mycorrhizal infection in tree seedlings. Journal of the Air Pollution Control Association **36**(6): 724-726.

Rennenberg, H., Loreto, F., Polle, A., Brilli, F., Fares, S., Beniwal, R., and Gessler, A. 2006. Physiological responses of forest trees to heat and drought. Plant Biology **8**(05): 556-571.

Salzer, M.W., Hughes, M.K., Bunn, A.G., and Kipfmueller, K.F. 2009. Recent unprecedented tree-ring growth in bristlecone pine at the highest elevations and possible causes. Proceedings of the National Academy of Sciences **106**(48): 20348-20353. doi: 10.1073/pnas.0903029106.

Saurer, M., Spahni, R., Frank, D.C., Joos, F., Leuenberger, M., Loader, N.J., McCarroll, D., Gagen, M., Poulter, B., Siegwolf, R.T.W., Andreu-Hayles, L., Boettger, T., Dorado Liñán, I., Fairchild, I.J., Friedrich, M., Gutierrez, E., Haupt, M., Hilasvuori, E., Heinrich, I., Helle, G., Grudd, H., Jalkanen, R., Levanič, T., Linderholm, H.W., Robertson, I., Sonninen, E., Treydte, K., Waterhouse, J.S., Woodley, E.J., Wynn, P.M., and Young, G.H.F. 2014. Spatial variability and temporal trends in water-use efficiency of European forests. Global Change Biology: n/a-n/a. doi: 10.1111/gcb.12717.

Schaberg, P.G., and DeHayes, D.H. 2000. Physiological and envrionmental causes of freezing injury to red spruce. *In* Responses of Northern U.S. Forests to Environmental Change. *Edited by* R.A. Mickler and R.A. Birdsey and J.L. Hom. Springer-Verlag, New York. pp. 181-227.

Schaberg, P.G., DeHayes, D.H., and Hawley, G.J. 2001. Anthropogenic Calcium Depletion: A Unique Threat to Forest Ecosystem Health? Ecosystem Health **7**(4): 214-228. doi: 10.1046/j.1526-0992.2001.01046.x.

Schaberg, P.G., DeHayes, D.H., Hawley, G.J., Strimbeck, G.R., Cumming, J., Murakami, P.F., and Borer, C.H. 2000. Acid mist, soil Ca and Al alter the mineral nutrition and physiology of red spruce. Tree Physiology **20**: 73-85.

Schaberg, P.G., Lazarus, B.E., Hawley, G.J., Halman, J.M., Borer, C.H., and Hansen, C.F. 2011. Assessment of weather-associated causes of red spruce winter injury and consequences to aboveground carbon sequestration. Canadian journal of forest research **41**(2): 359-369.

Schaberg, P.G., Shane, J.B., Cali, P.F., Donnelly, J.R., and Strimbeck, G.R. 1998. Photosynthetic capacity of red spruce during winter. Tree Physiology **18**(4): 271-276. doi: 10.1093/treephys/18.4.271.

Schaberg, P.G., Wilkinson, R.C., Shane, J.B., Donnelly, J.R., and Cali, P.F. 1995. Winter photosynthesis of red spruce from three Vermont seed sources. Tree Physiology **15**: 345-350.

Schwarz, P.A., Fahey, T.J., and Dawson, T.E. 1997. Seasonal air and soil temperature effects on photosynthesis in red spruce (*Picea rubens*) saplings. Tree Physiology **17**(3): 187-194. doi: 10.1093/treephys/17.3.187.

Scott, J.T., Siccama, T.G., Johnson, A.H., and Breisch, A.R. 1984. Decline of Red Spruce in the Adirondacks, New York. Bulletin of the Torrey Botanical Club **111**(4): 438-444.

Soule, P.T., and Knapp, P.A. 2006. Radial growth rate increases in naturally occurring ponderosa pine trees: a late-20th century CO2 fertilization effect? The New phytologist **171**(2): 379-390. doi: 10.1111/j.1469-8137.2006.01746.x.

Speer, J.H. 2010. Fundamentals of Tree-Ring Research. University of Arizona Press.

Stokes, M., and Smiley, T. 1996. An Introduction to Tree-Ring Dating. University of Chicago Press.

U.S. Geological Survey. 2016. Digital Representations of Tree Species Range Maps from "Atlas of United States Trees" by Elbert L. Little, Jr. (and other publications). U.S. Department of the Interior.

van Doorn, N.S., Battles, J.J., Fahey, T.J., Siccama, T.G., and Schwarz, P.A. 2011. Links between biomass and tree demography in a northern hardwood forest: a decade of stability and change in Hubbard Brook Valley, New Hampshire. Canadian Journal of Forest Research **41**(7): 1369-1379. doi: 10.1139/x11-063.

Vicente-Serrano, S.M., Beguería, S., and López-Moreno, J.I. 2010. A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. Journal of Climate **23**(7): 1696-1718.

Wason, J.W., Dovciak, M., Bier, C.M., and Battles, J. 2012. Red spruce tree cores from Dial Mountain, NY. SUNY-EFS.

Wason, J.W., Dovciak, M., Bier, C.M., and Battles, J.J. 2014. Responses of tree populations to recent climatic trends in northeastern mountain forests: Thinking beyond range margins. *In* Ecological Society of America Annual Meeting, Sacramento, CA.

Weverka, A.S. 2012. Remote sensing of productivity in northeastern forests. MS Thesis. Rubenstein School of Envrionment and Natural Resources, University of Vermont.

Wigley, T.M., Briffa, K.R., and Jones, P.D. 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. Bulletin of the American Meteorological Society **23**: 201-213.

World Data Center for Paleoclimatology and NOAA Paleoclimatology Program. Law Dome ice core data.

Yamaguchi, D.K. 1991. A simple method for cross-dating increment cores from living trees. Canadian Journal of Forest Research **21**(3): 414-416. doi: 10.1139/x91-053.

3.8 Supplementary Materials
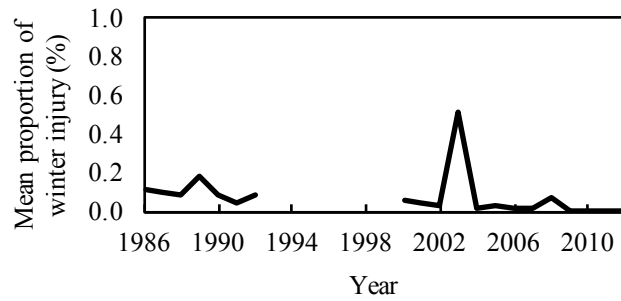
Figure S3.1: Foliar winter injury assessment at a red spruce (*Picea rubens* Sarg) plantation in Colebrook, NH, USA. Winter injury was quantified for each year of data following snow melt (e.g., late April or early May) by a team of two researchers using binoculars. Values are the percentage of previous season's (youngest) foliage showing visible damage, evident as reddish-brown needles, and quantified in 5% increments.
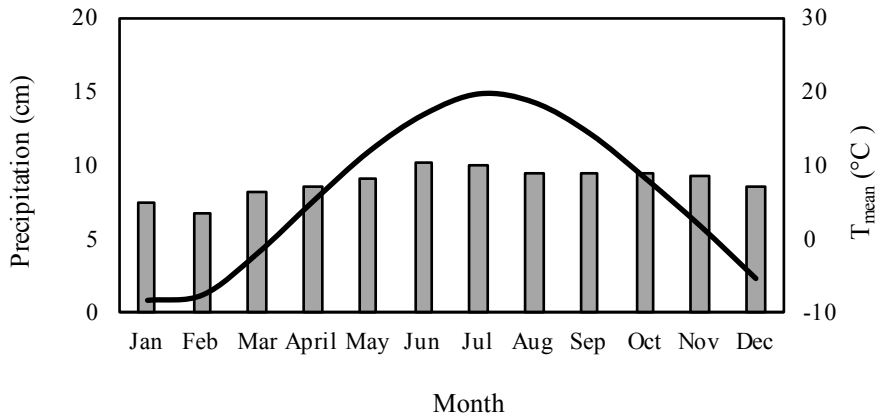
Figure S3.2: Mean monthly temperature (T_{mean}, °C) and total precipitation (cm) for the study area (42.67-45.04°N, 73.79-68.63°W) (NOAA Regional Climate Centers 2016).
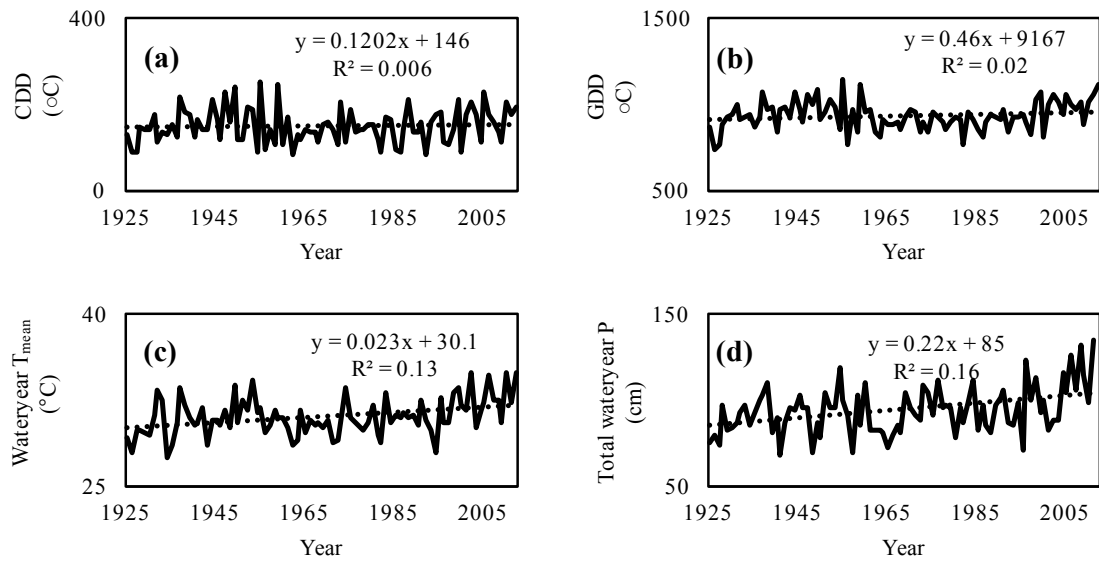
Figure S3.3: Climate variables from the study area (42.67-45.04°N, 73.79-68.63°W; solid line) with trend lines (dashed): (a) total cooling degree days (CDD, degree days >18.3°C), (b) total growing degree days (GDD, degree days >5°C), (c) mean water year (previous Oct-current Sept) temperature (°C), and (d) total water year precipitation (cm). See methods for data sources and descriptions (NOAA National Centers for Environmental Information 2016; NOAA Regional Climate Centers 2016)
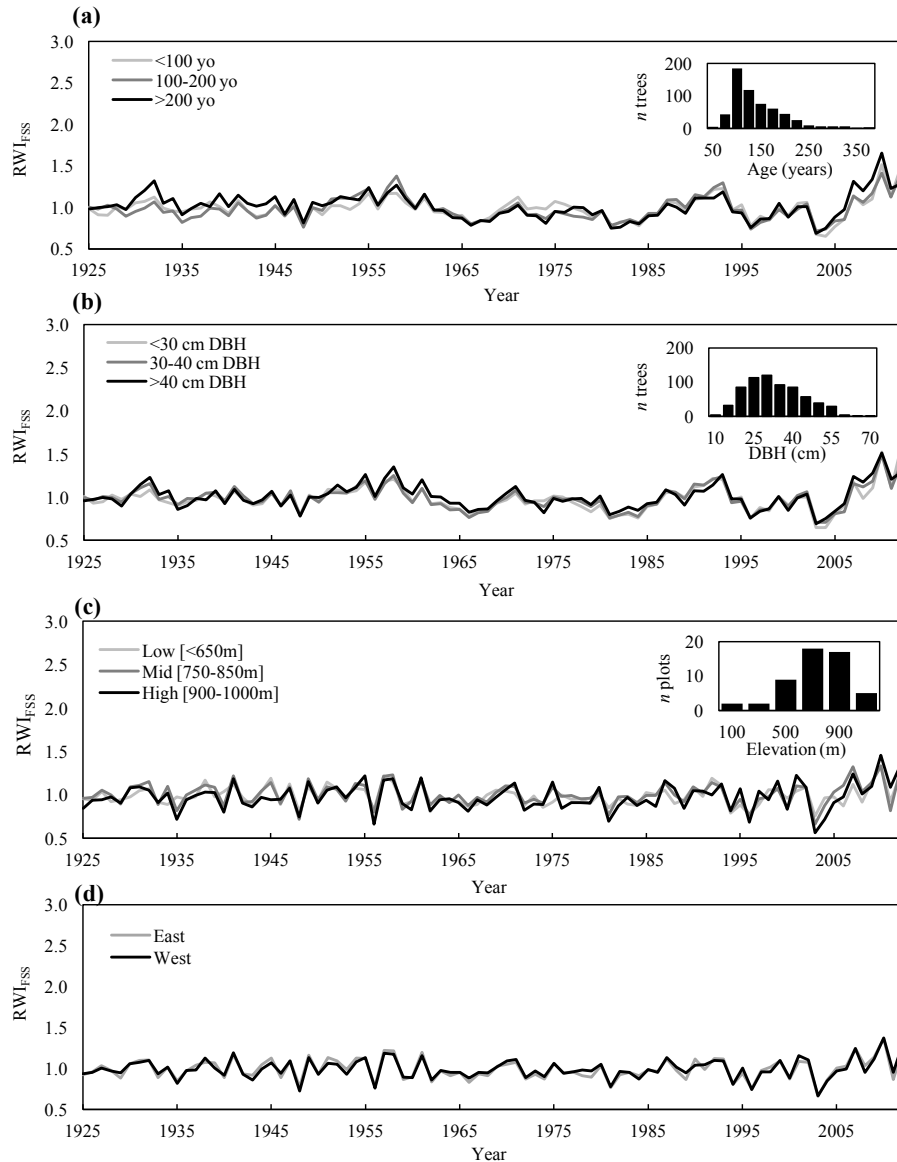
Figure S3.4: Red spruce tree ring chronologies classified by (a) estimated age (in years) at breast height (see methods for details), (b) diameter at breast height (DBH; cm), (c) plot elevation (Low<650m, Mid 750-850m, High 900-1000m), and (d) by regional groupings: east or west. RWI) chronologies (detrended with Friedman's Super Smoother) for age and DBH class were created with a Tukey's biweight mean of individual tree series, while the elevation class chronology was created as a mean of plot chronologies. There were no significant differences between the chronologies based on age, DBH, elevation class, or region (East, West) ($P = 0.37$, $P = 0.55$, $P = 0.34$, and $P = 0.92$, respectively). Inset to the right of chronologies (a-c) displays the parameter distribution.

$$y = -0.09x + 0.16$$
$$R^2 = 0.012$$
NS

Mortality assessment (% of trees dead in 2010)
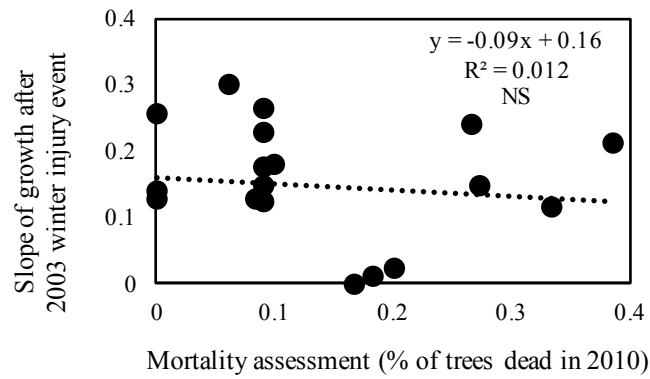
Figure S3.5: Mortality following the 2003 winter injury event (assessed in 2010) compared to growth of surviving trees following the event; the relationship was not significant.
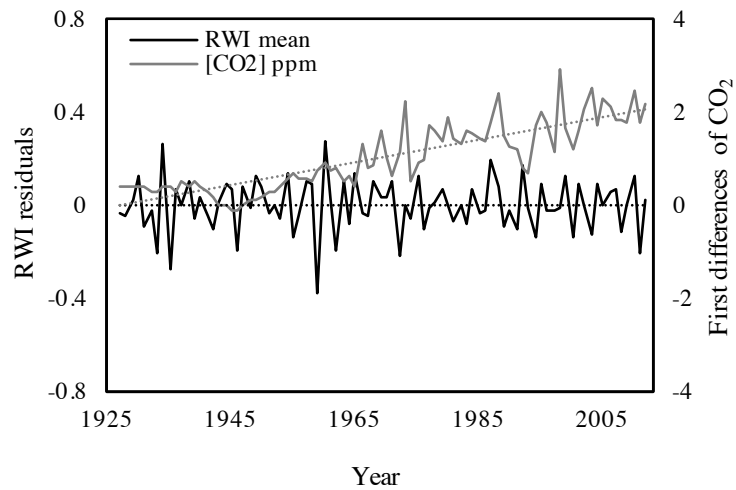
Figure S3.6: Residuals of best fit climate model for RWI (see Table 1; black line) and first differences of atmospheric CO_2 concentration (grey line) (NOAA Earth System Research Laboratory Global Monitoring Division 2016; World Data Center for Paleoclimatology and NOAA Paleoclimatology Program). Once climate had been accounted, the residuals of RWI for did not have a trend and were unrelated to changes in CO_2 over time (P=0.98).

115

Table S3.1: Chronology statistics for the 52 red spruce (*Picea rubens* Sarg.) plots used in this study.

Location	State	Elev. Cat.[a]	Aspect	Slope	Chron. Span	Mean Age ±SD (yrs)	Mean DBH ± SD (cm)	SI[b]	MS[b]	RW± SD (cm)	AC[b]	*n* cores	*n* trees	R-bar[c]	EPS[c]	SNR[c]	Slope of recent growth[d]
Bald Mountain	VT	Mid	SE	30%	1912-2012	97±16	25.2±2.6	0.65	0.25	1.17±0.53	0.79	24	12	0.44	0.89	7.9	4%
Bartlett Exp. For.	NH	Mid	N	20%	1759-2010	NA	31.5±6.5	0.61	0.28	1.10±0.61	0.75	18	9	0.37	0.84	5.2	2%
Bartlett Exp. For.	NH	Mid	SE	20%	1859-2010	138±26	34.2±7.5	0.62	0.24	1.14±0.56	0.81	20	10	0.43	0.95	18.5	1%
Bartlett Exp. For.	NH	Mid	E	20%	1781-2012	174±53	47.3±12.7	0.51	0.24	1.90±0.85	0.80	20	10	0.37	0.84	5.1	2%
Bartlett Exp. For.	NH	Mid	NE	10%	1799-2012	204±27	51.3±9.1	0.58	0.24	1.51±0.98	0.86	17	9	0.43	0.92	11.4	0%
Bartlett Exp. For.	NH	Mid	NE	20%	1855-2012	154±17	38.2±6.8	0.56	0.23	1.21±0.62	0.80	49	25	0.36	0.83	4.8	2%
Darling SF	VT	Low	N	10%	1913-2010	90±6	26.5±3.6	0.50	0.24	1.24±0.81	0.89	20	10	0.42	0.92	11.3	1%
Darling SF	VT	Mid	NW	40%	1765-2010	135±77	38.2±14.0	0.56	0.27	1.05±0.59	0.82	20	10	0.34	0.83	4.8	6%
Mt. Mansfield SF	VT	High	SW	30%	1922-2012	83±7	20.2±3.4	0.62	0.24	1.03±0.74	0.90	33	17	0.50	0.92	12.0	6%
Mt. Mansfield SF	VT	Low	SW	30%	1894-2012	104±20	29.6±5.4	0.51	0.23	1.24±0.64	0.82	15	9	0.40	0.87	6.7	1%
Mt. Mansfield SF	VT	Mid	NW	30%	1744-2012	173±58	44.1±8.4	0.56	0.25	1.32±0.70	0.83	31	16	0.45	0.88	7.5	1%
Burnt Mtn.	VT	Low	NE	10%	1891-2010	103±17	31.1±3.0	0.52	0.24	1.36±0.78	0.90	17	10	0.44	0.89	7.9	5%
Bristol Cliffs Wild.	VT	Low	W	80%	1713-2010	121±73	17.7±3.5	0.53	0.26	0.67±0.34	0.73	19	10	0.30	0.82	4.7	2%
Mt. Carmel	VT	High	SW	50%	1905-2010	90±9	19.9±3.7	0.56	0.34	0.97±0.74	0.89	22	11	0.46	0.93	12.7	7%
Mt. Carmel	VT	Mid	S	30%	1795-2010	170±29	40.7±8.8	0.59	0.26	1.15±0.75	0.89	20	10	0.44	0.94	16.7	7%
Dial Mtn.	NY	High	NA	NA	1772-2012	NA	34.3±8.3	0.51	0.24	0.92±0.51	0.83	17	9	0.40	0.85	5.7	5%
Mt. Ellen	VT	High	NE	40%	1824-2010	107±42	32.9±6.9	0.60	0.24	1.40±0.75	0.85	22	11	0.31	0.86	5.9	10%
Elephant Mtn.	ME	Mid	SE	20%	1650-2012	254±72	51.9±6.3	0.59	0.23	0.85±0.43	0.81	22	11	0.42	0.89	7.8	1%

Mt. Equinox	VT	High	SE	20%	1920-2010	83±15	26.9±4.7	0.67	0.31	1.31±0.91	0.83	21	11	0.26	0.80	3.9	2%
Mt. Equinox	VT	High	W	50%	1857-2010	111±40	28.3±6.1	0.55	0.28	1.07±0.87	0.92	24	12	0.50	0.92	10.8	3%
Mt. Equinox	VT	Low	SE	30%	1879-2010	97±20	31.8±7.3	0.48	0.31	1.41±1.25	0.92	19	10	0.25	0.80	3.1	-3%
Great Gulf Wild.	NH	Mid	SE	40%	1697-2012	171±62	48.1±7.3	0.56	0.23	1.35±0.69	0.80	39	21	0.51	0.91	10.0	1%
Goshen Mtn.	VT	High	NE	20%	1826-2012	104±30	39.3±6.1	0.53	0.25	1.66±0.87	0.80	39	22	0.37	0.84	5.1	0%
Weston Mtn.	VT	Low	NE	10%	1862-2012	145±11	42.9±5.3	0.58	0.21	1.31±0.68	0.86	20	11	0.47	0.90	8.6	3%
Weston Mtn.	VT	Low	NE	40%	1866-2012	116±14	39.2±7.8	0.62	0.21	1.36±1.07	0.91	23	12	0.41	0.87	6.8	4%
Mt. Greylock	MA	Low	NE	20%	1911-2010	86±9	30.5±4.0	0.59	0.27	1.60±1.03	0.86	23	12	0.42	0.88	7.4	-4%
Hedgehog Mtn.	NH	Mid	N	20%	1852-2010	104±27	29.7±6.1	0.67	0.21	1.36±0.58	0.77	24	12	0.40	0.88	7.4	2%
Killington Mtn.	VT	Mid	NE	80%	1815-2010	154±36	41.9±6.8	0.50	0.25	1.38±0.83	0.86	21	11	0.49	0.91	10.6	5%
Killington Mtn.	VT	High	NE	40%	1742-2010	172±61	40.1±8.1	0.53	0.29	1.07±0.76	0.87	20	11	0.55	0.93	14.2	6%
Killington Mtn.	VT	Mid	NE	20%	1793-2010	154±34	38.9±9.3	0.49	0.26	1.26±0.78	0.84	25	13	0.42	0.89	8.3	3%
Killington Mtn.	VT	High	NE	20%	1817-2010	97±34	30.4±7.5	0.65	0.26	1.37±0.93	0.88	22	11	0.56	0.92	11.4	3%
Killington Mtn.	VT	High	NW	40%	1861-2010	106±23	34.4±9.1	0.61	0.27	1.49±0.84	0.82	20	10	0.61	0.95	17.5	3%
Lord's Hill	VT	Low	W	30%	1772-2010	135±37	46.2±6.9	0.54	0.23	1.49±0.89	0.86	36	20	0.59	0.94	16.7	6%
Little Pond	VT	Mid	SW	0%	1897-2012	101±10	35.4±7.1	0.57	0.22	1.58±0.73	0.80	21	12	0.51	0.90	9.3	0%
Middlebury Gap	VT	Mid	SE	20%	1860-2010	94±31	32.4±8.9	0.60	0.25	1.60±0.70	0.74	20	10	0.46	0.90	8.6	2%
Mt. Moosilauke	NH	H	SE	10%	1760-2010	113±55	28.8±4.8	0.50	0.27	1.23±0.73	0.86	20	10	0.54	0.92	11.4	1%
Nancy Brook	NH	Mid	E	10%	1650-2012	253±68	48.5±6.6	0.57	0.21	1.20±0.64	0.85	38	21	0.59	0.94	14.6	1%
Penobscot Exp. For.	ME	Low	SW	0%	1837-2014	142±18	36.7±7.1	0.57	0.21	1.17±0.61	0.86	30	15	0.42	0.88	7.5	3%
Proctor-Piper SF	VT	Low	SW	50%	1897-2012	89±19	30.1±5.5	0.67	0.22	1.34±0.60	0.78	20	10	0.45	0.89	8.2	1%
Sugarloaf Mtn.	ME	High	SW	0%	1809-2012	142±42	43.7±11.2	0.52	0.25	1.29±0.64	0.77	23	16	0.44	0.89	8.1	0%

Mt. Mansfield SF	VT	High	SE	50%	1841-2012	90±44	24.0±4.8	0.55	0.24	1.31±0.70	0.81	23	12	0.31	0.81	4.2	2%
Mt. Mansfield SF	VT	Low	SE	20%	1737-2012	162±77	37.1±8.9	0.54	0.27	1.08±0.82	0.90	21	11	0.40	0.86	6.3	1%
Mt. Mansfield SF	VT	Mid	SE	50%	1772-2012	185±37	44.2±8.1	0.61	0.26	1.23±0.75	0.86	24	12	0.50	0.90	9.2	3%
Sterling-Whiteface Mtn.	VT	High	N	10%	1825-2012	100±41	26.0±7.5	0.61	0.27	1.14±0.68	0.81	22	12	0.50	0.91	10.2	4%
Sterling-Whiteface Mtn.	VT	High	SW	50%	1899-2012	90±22	29.3±11.0	0.58	0.26	1.42±0.63	0.73	19	11	0.32	0.82	4.4	5%
Sterling-Whiteface Mtn.	VT	Low	SE	10%	1910-2012	100±6	31.5±4.5	0.59	0.23	1.41±0.68	0.79	19	10	0.49	0.91	10.6	2%
Stratton Mtn.	VT	Mid	NW	10%	1906-2012	93±14	35.9±8.1	0.58	0.19	1.72±0.83	0.88	21	11	0.31	0.87	6.9	1%
Stratton Mtn.	VT	Mid	W	10%	1912-2012	94±13	34.0±6.7	0.56	0.20	1.65±0.74	0.82	21	12	0.38	0.93	12.8	0%
Mt. Mansfield SF	VT	High	W	40%	1837-2012	89±33	27.7±8.9	0.56	0.24	1.37±0.72	0.82	22	12	0.42	0.94	15.4	2%
Mt. Mansfield SF	VT	Low	SW	20%	1788-2012	166±35	36.3±6.9	0.51	0.27	1.01±0.74	0.87	20	11	0.32	0.91	9.8	4%
Mt. Mansfield SF	VT	Mid	W	20%	1850-2012	140±46	35.3±9.9	0.51	0.26	1.20±0.78	0.87	23	11	0.31	0.90	8.7	6%
Hubbard Brook Exp. For.	NH	Mid	SE	20%	1885-2010	97±20	28.6±9.2	0.28	87	0.80±0.84	0.84	45	24	0.44	0.89	7.9	5%

[a] Elevation categories: Low<650m, Mid 700-900m, High<950m
[b] SI= series intercorrelation, MS = mean sensitivity, AC = autocorrelation. From raw ring width (RWW) chronologies.
[c] EPS = expressed population signal, SNR = signal to noise ratio, R-bar = average correlation between the tree-ring series. From detrended, standardized (Friedman's Super Smoother, tweeter=5) and prewhitened chronologies
[d] The slope of recent growth was calculated from 2001 to the end of the chronology.

Table S3.2: Locations and data collected from NOAA weather (NOAA National Centers for Environmental Information 2016; NOAA Regional Climate Centers 2016) and NADP deposition monitoring stations (National Atmospheric Deposition Program 2016).

Station Name, State	Coordinates	Elevation (m)	Data Collated[a]
Acadia National Park, ME	44.38° N, 68.26° W	150	Monthly deposition of SO_4^{2-}, NO_3^-, cation:anion, pH of rainfall
Bennington, VT	42.88° N, 73.16° W	305	Monthly deposition of SO_4^{2-}, NO_3^-, cation:anion, pH of rainfall
Bridgton, ME	44.11° N, 70.73° W	222	Monthly deposition of SO_4^{2-}, NO_3^-, cation:anion, pH of rainfall
Burlington, VT	44.47° N, 73.15° W	102	Mean, min, max monthly T, total monthly P
Durham, NH	43.14° N, 70.95° W	23	Mean, min, max monthly T, total monthly P; Climate indices
Farmington, ME	44.69° N, 70.16° W	128	Mean, min, max monthly T, total monthly P; Climate indices
Hubbard Brook, NH	43.94° N, 71.70° W	250	Monthly deposition of SO_4^{2-}, NO_3^-, cation:anion, pH of rainfall
Huntington Wildlife, NY	43.97° N, 74.22° W	500	Monthly deposition of SO_4^{2-}, NO_3^-, cation:anion, pH of rainfall
Lake Placid 2 S, NY	44.39° N, 74.20° W	549	Mean, min, max monthly T, total monthly P
Madison, ME	44.79° N, 69.89° W	79	Mean, min, max monthly T, total monthly P; Climate indices
Pinkham Notch, NH	44.26° N, 71.25° W	617	Mean, min, max monthly T, total monthly P; Climate indices
Rutland, VT	43.63° N, 72.98° W	189	Mean, min, max monthly T, total monthly P; Climate indices
St. Johnsbury, VT	44.42° N, 72.02° W	213	Climate indices
Trenton Falls, NY	43.28° N, 75.16° W	244	Climate indices
Tupper Lake, NY	44.23° N, 74.44° W	512	Mean, min, max monthly T, total monthly P; Climate indices
Underhill, VT	44.53° N, 72.87° W	399	Monthly deposition of SO_4^{2-}, NO_3^-, cation:anion, pH of rainfall
Whiteface Mountain, NY	44.39° N, 73.86° W	610	Monthly deposition of SO_4^{2-}, NO_3^-, cation:anion, pH of rainfall

[a]T = temperature, P = precipitation, Min = minimum, Max = maximum, NO_3^-: nitrate deposition, SO_4^{2-}: sulfate deposition. For more details on climate indices, see Materials and Methods.

CHAPTER 4: SAPLING RESPONSE TO EXPERIMENTAL HEATING AND REDUCED SNOW DEPTH VARIES AMONG SPECIES AND BY SOIL TYPE

Alexandra M. Kosiba[a*], Paul G. Schaberg[b], E. Carol Adair [a], Gary J. Hawley[a], Carl Waite [a], Stephanie M. Juice[a], and Deane Wang[a]

[a] The University of Vermont, Rubenstein School of Environment and Natural Resources, Burlington, VT 05405, USA, akosiba@uvm.edu, cadair@uvm.edu, ghawley@uvm.edu, cwaite@uvm.edu, sjuice@uvm.edu, dwang@uvm.edu

[b] Forest Service, U.S. Department of Agriculture, Northern Research Station, Burlington, VT 05405, USA, pschaberg@fs.fed.us

[*] Corresponding author. akosiba@uvm.edu (A.M. Kosiba).

4.1. Abstract

Increased annual temperature is predicted to have varied effects on tree physiology, with some species likely benefitting from change, while others may suffer reductions in growth and vigor. Changes in temperature are projected to decrease the onset and depth of winter snow cover, alter water fluxes, and lengthen the effective growing season – all of which could strongly affect tree carbon capture. To further explore tree responses to a changing climate, we examined how species with differing physiological characteristics (e.g., characteristic rooting depth) and adaptations to climate (e.g., native latitudinal range) interact with site characteristics (e.g., soil nutrient status, water flux) and experimental heating and snow exclusion treatments to influence sapling physiology and growth. We examined these responses using a replicated 3-factor split plot design imposed on in-ground micro-catchments. We tested the effects of three treatments (infrared heating, snow exclusion, and control), and two soil types on the resulting physiology of four ecologically and economically important deciduous tree species native to the northeastern United States: paper birch (*Betula papyrifera* Marshall), quaking aspen (*Populus tremuloides* Michx.), American chestnut (*Castanea dentata* (Marshall) Borkh.), and black cherry (*Prunus serotina* Ehrh). While we found a variety of effects, soil type, and species characteristics most strongly influenced response. Additionally, highly variable natural weather patterns during the treatment period muted or exacerbated some responses. Overall, heating resulted in an extended potential photosynthetic period in the fall and was associated with increased biomass accumulation. Characteristic rooting depth had a stronger influence on spring leaf expansion and increased biomass ratios than extent of native latitudinal range. One of the northern species, quaking aspen, was strongly, negatively affected by a reduced early winter snowpack. Another, American chestnut, suffered high winter injury damage during both winters, possibly complicating the restoration efforts of this species in the northern limits of its native range. Our results demonstrate the variability in sapling response to a changing climate, as well as the complex interactions that occur with soil factors, water flux, and weather patterns.

Key words: *climate change, paper birch, American chestnut, quaking aspen, black cherry, soil texture, soil moisture*

4.2 Introduction

With climate change, tree species with different physiological traits or adaptations may be able to thrive under novel conditions that cause another species to decline. Although several reports have suggested that elevated temperature will alter tree physiology to enhance productivity and carbon (C) and nutrient uptake (Briffa et al. 2008; Jarvis and Linder 2000; Pregitzer et al. 2000; Vitasse et al. 2009), it is unclear how different tree species will respond depending on their native latitudinal range, physiological characteristics, and interconnections with site characteristics, like soil nutrient status and water flux. Differential physiological responses among species are critical to determining interspecific competition, which governs forest community structure and function, as well as species range limits that have broad influences on C, water, and nutrient fluxes. To date, it has been shown that tree species respond differently to reduced snowpack (Fitzhugh et al. 2003), elevated temperatures (Vitasse et al. 2009), and soil nutrient availability (e.g., calcium [Ca]:aluminum [Al]) (Kobe et al. 2002), but it remains unclear how these factors interrelate. Three potentially critical factors that have not been fully considered are how (1) tree rooting depth, (2) native range limits (i.e., adaptation to local climate), and (3) site factors (soil texture and nutrition, water flux) may interact to affect tree response to increased temperature and reduced snow depth.

In the northeastern United States (US), changes to the climate have been observed and models predict continued increases in annual temperature of up to 3.5°C by 2035 (Kunkel et al. 2013; USGCRP et al. 2014). Elevated temperatures have been shown to

increase the length of the frost-free season, intensify the frequency of soil freeze-thaw cycles, and decrease the amount, duration, and the onset of winter snowpack (Ahmed et al. 2013; Frumhoff et al. 2007; Groffman et al. 2012; Hodgkins and Dudley 2006; Northeast Climate Impacts Assessment Synthesis Team 2007). Snow insulates the soil from severe freezing and minimizes the frequency and extent of freeze-thaw cycles (Decker et al. 2003). Thus, reduced snowpack can lead to greater soil freezing that can damage roots, disrupt nutrient cycles, and alter plant C relations (Comerford et al. 2013; Decker et al. 2003; Fitzhugh et al. 2001; Groffman et al. 2001). In contrast, an extension of the growing season may trigger early bud break and leaf expansion in the spring, or delay leaf senescence in the fall for deciduous trees (add references here e.g., Groffman et al. 2012 and others?). Warming temperatures could also lead to substantial changes to water budgets through increased evapotranspiration, which could reduce fine root biomass and, consequently lower water and nutrient uptake (Pregitzer et al. 2000).

Such changes will likely alter both C and nutrient storage by trees; however, the magnitude and directionality of these changes remain uncertain. In forested ecosystems, trees control much of the influx of C into soils and can store C in woody biomass for centuries or longer; therefore, even a minor change in this C sequestration could affect global C budgets (Melillo et al. 2011).

Thus, we tested the response of four tree species, with different physiological characteristics and adaptations, to simulated climate change scenarios, which were operationally defined by two treatments: increased temperature (2-4°C above control via

123

infrared heating [hereafter, heating]) and reduced snow depth for the first six weeks of winter [hereafter, snow exclusion]. We also tested how soil characteristics affected sapling response. Specifically, we examined how soil nutrient status (notably Ca content), tree species (differing by characteristic rooting depth [hereafter, rooting depth] and extent of native latitudinal range [hereafter, native range]), and climate treatment influenced sapling growth, biomass, mortality, winter injury, spring and fall phenology, and insect and disease occurrence. To examine these effects, we used replicated, in-field micro-catchments with climate manipulation treatments (heating, snow exclusion, and control) imposed on deciduous sapling species growing in two types of mineral soil. Specifically, we hypothesized:

H_1 Heating will lengthen the effective growing season, increase sapling C uptake and storage, which will be evident by earlier spring leaf expansion, delayed leaf senescence, and an increase in woody growth and biomass.

H_2 Heating will more negatively affect species at the southern latitudinal limit of their range at the experimental site (Northern species) than species at the northern latitudinal limit of their range (Southern species).

H_3 Heating will alter water budgets by increasing evapotranspiration, evident via reduced water flux, increased root to shoot biomass ratio (root:shoot), and amplified negative effects to characteristically shallow-rooted species.

H_4 Snow exclusion will cause deeper soil freezing, evident as a delayed onset of spring bud break, lower woody growth, and decreased fine root biomass.

124

H₅ Soil type, specifically nutrient content, will amplify the effects of both heating and snow exclusion.

4.3 Materials and Methods

4.3.1 Study site

We used 24 previously established (see Beard et al. 2005) in-ground polyethylene micro-catchments situated in an open, flat field in South Burlington, VT (44.27' N, 73.12' W; 60 m a.s.l.; Fig. 4.1, 4.2a). The annual mean temperature is 7.3°C; January is the coldest month (mean temperature 1950-2015: -7.8°C) and July the warmest (21.3°C) (Burlington International Airport, S. Burlington, VT; elevation 100 m; ~ 5.9 km from study site) (NOAA National Weather Service 2017). The tanks were initially installed in 1995; they measure 2.44 m in diameter and hold approximately 4.7 m³ (3,600 L) of soil (Beard et al. 2005). A conical section at the bottom of each tank is filled with coarse granite covered with a geotextile cloth (~48 cm deep), which allows for the collection and measurement of micro-catchment water loss (Fig. 4.2a). A polyvinylchloride pipe in the center of each tank is connected to a vacuum extraction system for water removal and volume measurement. The micro-catchments do not have an underground outlet. Micro-catchments contain one of two unweathered glacial deposit substrates. The largest differences between these soils are particle size (i.e., proportion of gravel and sand), Ca content, and cation exchange capacity (CEC) (Table 1) and were initially chosen to reflect relatively poor and rich soil nutrient status (Beard et al. 2005).

Table 4.1: Soil physical and chemical properties of the two mineral soils in the micro-catchments: Kullman (K) and Milton (M) from a previous study (Beard et al. 2005) and during the initiation of this study (2013).

	K		M	
	2004	2013	2004	2013
Clay (%)[a]	1.15		0.95	
Silt (%)[a]	0.56		0.66	
Sand (%)[a]	63.92		81.17	
Gravel (%)[a]	34.26		17.3	
Bulk density (g cm^{-3})	1.61	1.72	1.46	1.49
Organic matter (%)	0.12		0.11	
CEC (meq 100 g^{-1})[a]	18.2		0.9	
pH±SD[b]	6.8	7.6± 0.7	5.6	6.2±0.7
Ca (mg Kg^{-1})	3,088	1,770	130	700
Mg (mg Kg^{-1})	40	34.7	22	10.7
K (mg Kg^{-1})	10	4.3	10	4.8

[a]Percent (%) clay, silt, sand, and gravel, and cation exchange capacity (CEC, meq 100 g^{-1}) were measured during micro-catchment installation (1995).
[a]pH values are from 2015.

4.3.2 Study design

A completely randomized three-factor split-plot design was imposed on six in-field micro-catchments, replicated four times ($n = 24$ micro-catchments). The whole-plot treatments were soil type (2 levels: Milton [M] and Kullman [K]) and climate change treatment (hereafter, "treatment"; 3 levels: heating, snow exclusion, and control). The within-plot treatment was tree species (4 levels, see below for species). The statistical model for this design was:

$$y_{ijkl} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + d_{ijk} + \Delta_l + (\alpha\Delta)_{il} + (\beta\Delta)_{jl} + (\alpha\beta\Delta)_{ijl} + e_{ijkl}$$

where:
$_i$ = treatment
$_j$ = soil type
$_k$ = rep
$_l$ = species
α_i = fixed effect of climate treatment
β_j = fixed effect of soil type
d_{ijk} ~ N (0, σ_{abr}^2) iid, random effect of whole plot error

Δ_{ijkl} = fixed effect of species

$e_{ijkl} \sim N\ (0,\ \sigma_{abrc}^{2})$ iid, random effect of subplot error

4.3.3 Treatments

To prepare the micro-catchments, all plant material was removed, the top 5 cm tilled, and 0.5 L Osmocote fertilizer (16-5-10; The Scotts Company, Marysville, OH) incorporated into the top 10 cm of soil. In May 2013, micro-catchments were planted with 20 nuts or seedlings per each of four tree species (n=480 seedlings per species) that were randomly distributed within each micro-catchment (Fig. 4.2b): paper birch (*Betula papyrifera* Marshall), quaking aspen (*Populus tremuloides* Michx.), American chestnut (*Castanea dentata* (Marshall) Borkh.), and black cherry (*Prunus serotina* Ehrh). These species were chosen because they are either at the northern or southern edge of their native latitudinal range in S. Burlington, VT (Fig. 4.1) and have different rooting strategies (Burns and Honkala 1990). All species are either economically or ecologically important in the region. The native range of paper birch, a shallow rooted species, and quaking aspen, deep rooted, extend much further north from Vermont (hereafter, Northern species) (Burns and Honkala 1990). Conversely, black cherry, a shallow rooted species, and American chestnut, considered a deep-rooted species by most sources (Wang et al. 2013), have native ranges that extend southward (hereafter, Southern species) (Burns and Honkala 1990) (Fig. 4.1). Although American chestnut is not a prominent species within eastern forests due to widespread mortality from the non-native chestnut blight fungus (*Cryphonectria parasitica* (Murr.) Barr*)* (Wang et al. 2013), it was once an ecologically and economically important species, and is now the subject of an

127

extensive restoration effort (Clark et al. 2014). Therefore, we included it in this study to assess how the impacts of climate change may affect its growth and vigor in the northern limits of its native range (Fig. 4.1).
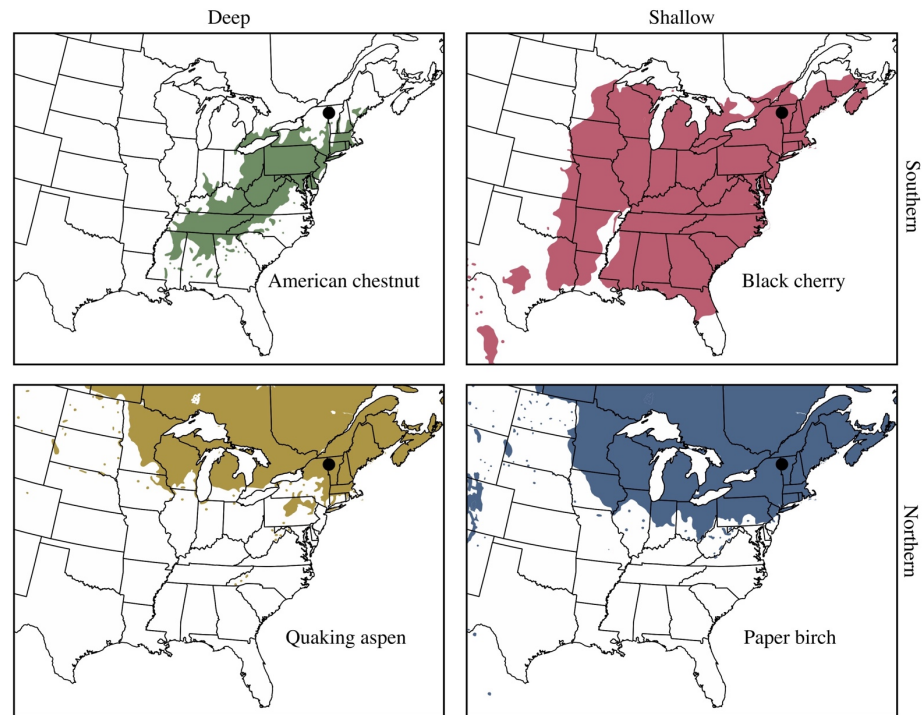
Figure 4.1: Map of study location in South Burlington, VT (black dot) along with the native ranges of the four study species: American chestnut (*Castanea dentata* (Marshall) Borkh.), black cherry (*Prunus serotina* Ehrh), paper birch (*Betula papyrifera* Marshall), and quaking aspen (*Populus tremuloides* Michx.) (U.S. Geological Survey 2016). Species were selected to contrast the extent of native latitudinal range limit relative to the study location (Southern vs. Northern) and characteristic rooting depth (deeper vs. shallower rooting tendencies) (Burns and Honkala 1990).

Paper birch, quaking aspen, and black cherry were purchased as 1+ year old bare-root seedlings from a commercial nursery (Porcupine Hollow Farm, Central Lake, MI). American chestnut nuts were obtained through the American Chestnut Foundation from a site in northeastern Pennsylvania (Haun, PA). American chestnut is barely cold tolerant

to withstand average minimum temperatures in Vermont (Gurney et al. 2011), which has restricted the northern limit of its native range to the Champlain and Connecticut River Valleys, VT (Fig. 4.1). However, this specific seed source was selected for this study because it was shown to be more cold tolerant than others (Saielli et al. 2012; Saielli et al. 2014).

To reduce moisture loss, provide nutrients and mimic forest floor conditions for seedling establishment, leaves of the four species were collected from mature trees in the area, including an American chestnut plantation located nearby. These leaves were air-dried and chopped using an electronic leaf mulcher and applied to a depth of 2.2 cm per micro-catchment in fall 2013. During the first growing season (May-Sept 2013), seedlings were equally watered within micro-catchment when needed using a drip irrigation system (Fig. 4.2b). We permitted six months for seedling establishment before treatment imposition and recorded height, diameter, and mortality during this phase. Micro-catchments were weeded for undesirable plant species and all excised biomass was left on the soil surface. During seedling establishment, the quaking aspen seedlings were infected by the Shepherd's crook fungus (*Venturia tremulae*) (Hunt 1978). To combat it, we applied copper sulfate fungicide (Hunt 1978) (Bonide Products Inc., Oriskany, NY, 7.00% basic copper sulfate) to all seedlings and micro-catchments at a rate of 35 mL L^{-1} every two weeks for 8 weeks during summer 2013.
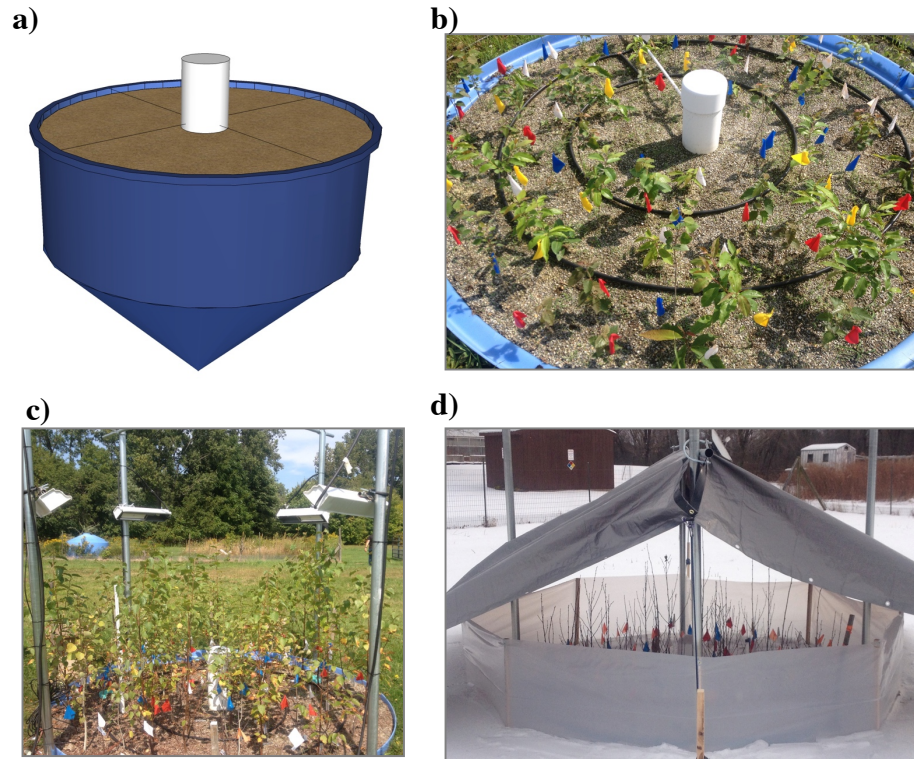
Figure 4.2: Examples of study infrastructure: (a) diagram of the in-ground micro-catchment, (b) seedling spacing and drip tube irrigation (only used during seedling establishment phase) around the micro-catchment, (c) infrared heater arrangement along edge of micro-catchment, and (d) snow exclusion tarps installed over the micro-catchment during a snow storm, shown with plastic knee wall to moderate the effects of wind.

Beginning in December 2013, the whole-plot treatments (control, heating, or snow exclusion) were imposed upon the micro-catchments. To produce the heating treatment, four Salamander ceramic infrared (IR) heater elements each housed within an ALEX (Aluminum Extrusion) reflector (Mor Electric Heating, Comstock Park, MI) and attached to vertical 5 cm diameter, aluminum conduit posts were positioned at the perimeter of micro-catchments. Modifying the methods of Kimball et al. (2008), heaters were placed ~1.5 m high, at ~45° (Fig. 4.2c) to obtain the most uniform heating across

the micro-catchment surface, as determined by preliminary testing using thermal imaging equipment. In order to prevent water infiltration into heaters, the seams on the heater covers were waterproofed with high temperature silicon and heaters were protected with covers fabricated from aluminum rain gutters (Fig. 4.2c) (Kimball et al. 2008). We also installed gutter covers to conduit posts following the same layout for both control and snow exclusion treatments to equalize the effects of shading across treatments. Using suspended (1.5 m) radiometers (SI-111 Infrared Radiometer, Apogee Instruments, Logan, UT) to assess micro-catchment temperature, we sought to raise the soil surface temperature of the heating treatment 2-4°C throughout the year relative to the control treatment. Radiometers were programmed to measure temperature every 30 seconds, although this was lengthened to 60 seconds in fall 2014. We paired a heating and control treatment micro-catchment for comparison and averaged data per 5-minute intervals.

For the snow exclusion treatment, we suspended tarps over each snow exclusion micro-catchment just before a snow event began, and removed them immediately afterward (Fig. 4.2d). The first 5 cm of snowfall was allowed to accrue to maintain albedo (Comerford et al. 2013). Following this, the snow exclusion treatment was maintained for the first 6 weeks of winter and then allowed to accumulate following previously established methods (Comerford et al. 2013). To moderate the effects of wind and attain more uniform heating within plots, we installed knee walls (0.6 m tall) around the perimeter of each micro-catchment using clear plastic sheeting and grade stakes for support (Fig. 4.2d); these were removed during the growing season.

131

Treatments were validated with thermocouples, radiometers, frost tubes, and snow stakes. Micro-catchments were equipped with in-ground soil thermocouples to monitor soil temperature at five depths: 0 cm (soil surface) and 5, 10, 30, and 60 cm below the soil surface. To monitor soil freezing, we installed a frost tube in each micro-catchment. Frost tubes were made from flexible PVC tubes filled with methylene blue dye which changes color when frozen (Ricard et al. 1976). Frost tubes were inserted into rigid polyethylene casings (Ricard et al. 1976) to a soil depth of 0.6 m. We measured the length of frozen dye weekly from late December until completely thawed in spring. Snow depth was measured three times a week using a permanently fixed meter stick within each micro-catchment. Because they did not have an underground outlet, we could monitor water flux through assessment of standing water at the conical base of each micro-catchment (Fig. 4.2a). We used a wooden dowel inserted into the central pipe and measured the length of the saturated dowel surface as a proxy for water flux. Micro-catchments were also pumped of excess water periodically during the freeze-free season to prevent the water table from saturating the sapling root zone.

4.3.4 Measures of sapling physiology

Sapling responses to treatments were assessed using a variety of measures, including: (1) diameter and height growth, (2) shoot winter injury damage, (3) mortality, (4) spring leaf expansion, (5) fall leaf senescence, (6) occurrence of visible disease or insect herbivory, and (7) above- and belowground biomass. Sapling heights were

measured at the higher of the tallest terminal leader (to nearest 0.5 cm) in late fall of 2013 and 2014. At this same time, diameters were measured with calipers just above the root collar (to the nearest 0.5 mm). Values were averaged by species per micro-catchment. Height and diameter growth during the treatment period were computed by subtracting measurements taken in 2013 (i.e., before treatment began) from subsequent measurements. Winter injury was identified in 2014 and 2015 after leaf-out as visible dieback (dark-colored and sunken portions of the stems) on terminal shoots. Winter injury was quantified by measuring the length (cm) of damaged terminal shoots and expressed as a percentage of the total height for each seedling (percent shoot dieback) following previously established methods (Saielli et al. 2014).

Twice per week from start of leaf expansion to near completion (day-of-year ~100-160), we visually assessed spring bud break and leaf expansion (2014 and 2015) following the methods of West and Wein (1971). Buds and expanding leaves were visually rated by two researchers to expansion stage (0-5; Table S4.1) and combined with the percentage (to the nearest 10%) of foliar tissue on the sapling that had developed to that stage; for example, a score of 2.5 indicated that 50% of the buds were at stage 2. In spring 2014, each sapling per micro-catchment was scored for leaf expansion, but in 2015 we pre-selected four saplings per species per micro-catchment (one per each cardinal quadrant) prior to bud break to reduce workload and account for uneven sapling mortality among the species. Leaf expansion scores were averaged by species per micro-catchment. We then fit a sigmoidal curve to each leaf expansion chronology by species and micro-

catchment using JMP 10 (Cary, NC) to extract the slope (k), midpoint (LE_m), and maximum value (Y_{max}) of the leaf expansion curve. During summer 2014, we also tallied the number of saplings per species‾ and micro-catchment with visible leaf discoloration or herbivory, and classified them into broad categories (insect herbivory, chlorosis, necrosis, and discoloration [spotting]).

Fall phenology of leaf area was assessed in 2014 using digital photographs. For two months (day-of-year 254-317), we took four photographs per micro-catchment of the areal portions of saplings - one per cardinal direction. Successive photos were taken from the same point and angle. We used the software ImageJ (Rasband 2016) to quantify the pixels per image that represented distinct spectra: green, yellow, and red. Custom macros were coded to batch process the images using the ImageJ "color thresholder" with the hue, saturation, and brightness (HSB) color space. In this process, threshold ranges (HSB) were defined as: background (0-255, 0-255, 0-255), green (50-141, 0-255, 0-255) and yellow (30-49, 0-255, 110-255). There was no overlap between green and yellow. Defining red was more complicated because red to light brown leaves needed to be distinguished from plastic flagging, stems, leaf litter, and soil surfaces. The three-dimensional LAB color space model was used where the threshold ranges were defined as: 122-209, 126-255, and 163-201 for the red class. There was minor overlap between yellow and red classes, but this was unavoidable considering the complex discrimination required for the red color class. The four images were then averaged by date per micro-catchment. Green pixels were considered a proxy for photosynthetic foliage, yellow

pixels were considered recently senescing (yet potentially still productive) foliage, and red were considered senescing foliage. Together green and yellow foliage were combined to provide a metric of potentially active leaf area. Total leaf area was quantified per micro-catchment by summing green, yellow, and red pixels. Pixel sums were converted to percentage of total pixels, and then to an area basis (m^2) per micro-catchment.

4.3.5 Statistical analyses

We performed all statistical analyses in the R programming environment (Version 3.3.2) (R Development Core Team 2016) using a split-plot ANOVA model, with repeated measures when time was a factor. Soil temperature, water levels, frost depth, spring leaf expansion, fall leaf area, insect and disease occurrences, height and diameter, mortality, and biomass values were transformed with a logarithm or tangent function prior to analysis to meet the assumptions of ANOVA. If significant, Tukey HSD post hoc tests were utilized to test for differences among factors. Lastly, we constructed orthogonal contrasts to examine if Northern species (paper birch, quaking aspen) differed significantly from Southern species (American chestnut, black cherry), as well as by rooting depth (deep: American chestnut, quaking aspen; shallow: paper birch, black cherry) (Fig. 4.1). Results were considered significant if $P<0.1$.

4.4 Results

4.4.1 Treatment effects on soil temperature, snowpack, and water flux

While we were aiming for a 2-4 °C temperature difference between the heating and control treatment micro-catchment pairs, this was hard to achieve with our system, particularly in the winter and spring (Fig. 4.3). In winter, the heating treatment tended to be <2°C, while in the spring, temperatures were often >4°C. Soil temperature varied by depth in soil and by time of year (Fig. S4.1), but none of the study factors (e.g., treatment or soil) were significant (Table S4.2). There was a trend for treatments to show the biggest soil temperature differences in the spring (Fig. S4.1).
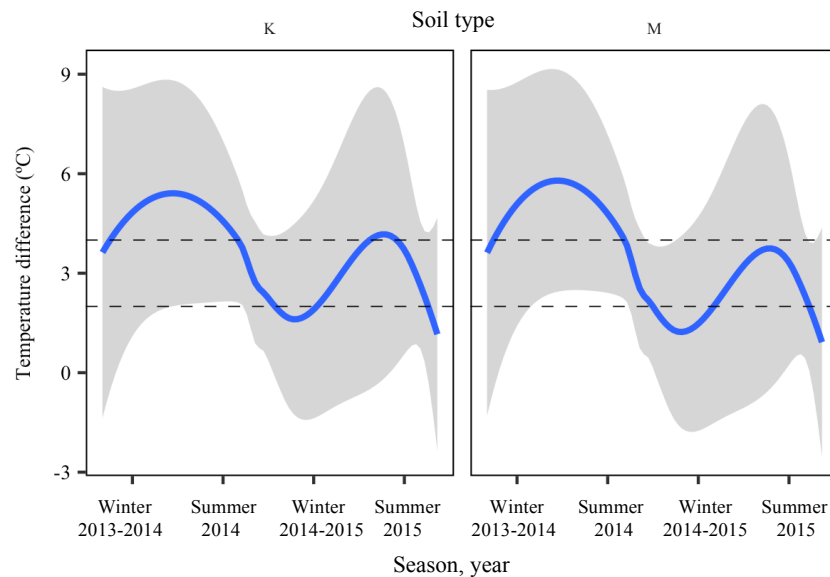
Figure 4.3: Mean difference in temperature (blue line, °C, ± minimum, maximum [smoothed by loess estimation]) between infrared heating and control treatment micro-catchment pairs over the study period: Winter 2013-2014 until early Fall 2015. Horizontal dotted lines indicate the 2-4°C increase compared to the control treatment we were attempting to meet.

There was high variability in snow depth by time (both by day and year) (Fig. 4.4). During winter 2013-2014 (day-of-year 360-100; hereafter, 2014), we found a significant effect of treatment on snow depth ($P<0.0001$), with the control having

136

significantly more snow then both snow exclusion and heating treatments (P=0.0004 and P<0.0001, respectively), and snow exclusion having more snow than heating (P<0.0001) (Fig. 4.4). There was also a significant soil type x day interaction on snow depth in both years (2014 P=0.005, 2015 P=0.057) (Table S4.2). Despite less variability in snow depth in winter 2014-2015 (day-of-year 360-100, hereafter, 2015), we detected a significant treatment effect (P=0.001), with control plots having deeper snow than heating (P=0.001).
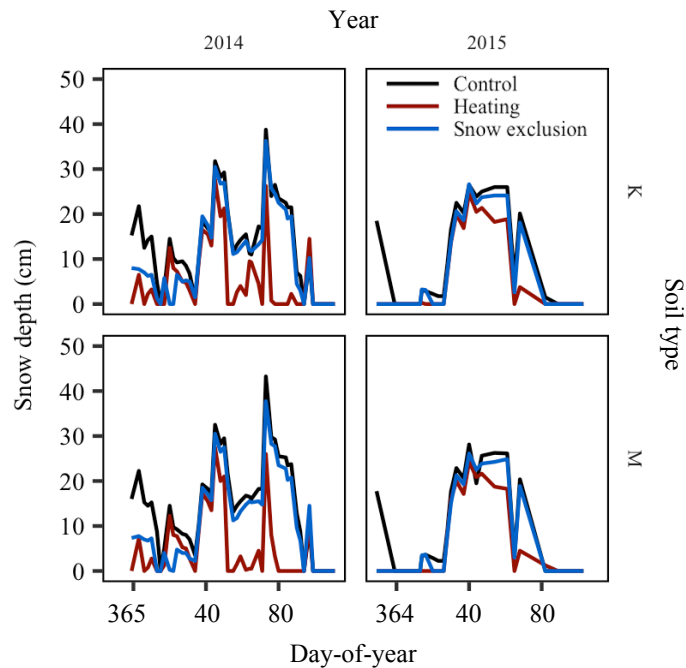
Figure 4.4: **Mean snow depth (cm) by day-of-year per treatment (control, heating, and snow exclusion [snow excluded for first six weeks of winter]) and soil type (K: Kullman; M: Milton), over two witners (2013-2014 [2014] and 2014-2015 [2015]). During both winters, there was a significant effect of treatment on snow depth (2014 P<0.0001 and 2015 P=0.001), as well as a treatment x day effect in 2014 (P<0.0001). The following differences were found using Tukey HSD post hoc tests, with different letters denoting significant differences (P<0.1). 2014: Control[a], heating[c], snow exclusion[b]; 2015: Control[a], heating[b], snow exclusion[ab]. There were no significant differences by soil type.**

Like snow depth, we measured higher variability in soil freezing depth in 2014 compared to 2015. In 2014, we found a significant treatment x day interaction on the depth of soil freezing ($P<0.0001$) (Fig. 4.5, Table S4.2). However, in 2015 (a year of low natural snow accumulation: reference?), depth of soil freezing was indistinguishable between the treatments (Fig. 4.5). While there appeared to be differences in water depth at the base of the micro-catchments by treatment and soil type, differences were not significant, even when we assessed it directly prior to the pumping of micro-catchments (indicated by the synchronous dips in water levels) (Fig. 4.6). However, there was a trend for the heating treatment and soil M to have less water percolate to the base of the micro-catchments, particularly in 2014.
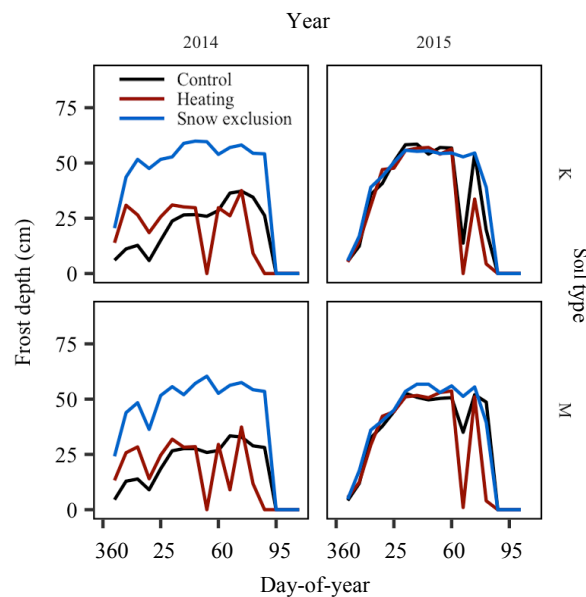
Figure 4.5: Mean depth of soil freezing (cm) by day-of-year per treatment (control, heating, and snow exclusion [snow excluded for first six weeks of winter]) and soil type (K: Kullman; M: Milton), over two winters (2013-2014 [2014] and 2014-2015 [2015]). There was a significant day x treatment interaction on the depth of surface frost (*P*<0.0001) in 2014, but no significant differences in 2015.

138
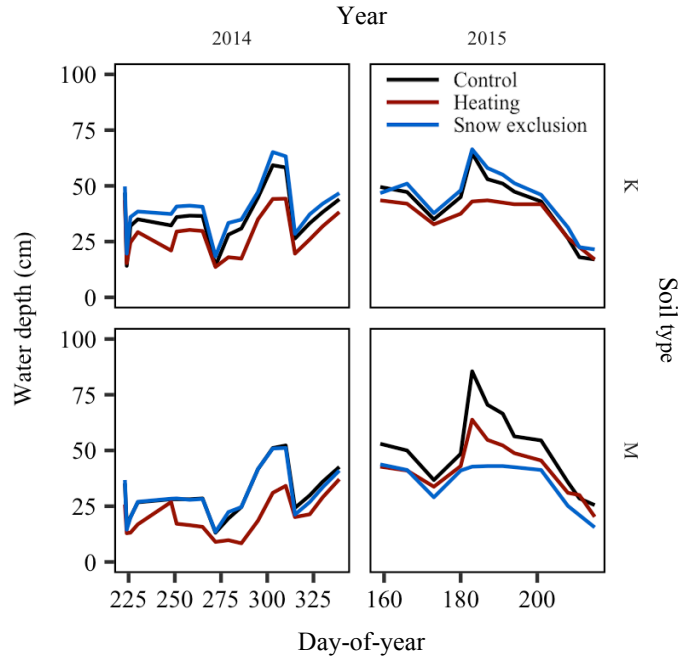
Figure 4.6: Mean water depth (cm) measured at the bottom of each micro-catchment as a proxy for water flux by day-of-year. Data are aggregated by treatment (control, heating, and snow exclusion [snow excluded for first six weeks of winter]), soil type (K: Kullman; M: Milton) over two years (2014, 2015). Water depth assessment began mid 2014 (day-of-year ~200) after the treatments had begun. Synchronous declines in water depth indicate when the micro-catchments were pumped of excess water. There were no significant differences in water depth by any study factor.

4.4.2 Factor effects on sapling leaf expansion progression

During spring leaf expansion in 2014, we found significant day x treatment x soil type (P=0.001) and treatment x soil type x species (P=0.004) interactions on the progression of leaf expansion (Fig. 4.7a, Table S4.2). In 2015, we found a significant treatment x soil type interaction (P=0.04), and while not significant in a post hoc test, the trend was for snow exclusion treatment applied to soil K to have the lowest leaf expansion score.

When we fit a sigmoidal curve to the 2014 leaf expansion data, Y_{max} showed significant effects of treatment (P=0.10), soil type (P=0.08), species (P=0.07), and a three-way interaction of treatment x species x soil type (P=0.07) (Table S4.2). However, in post hoc tests, we did not detect significant differences among the treatments or species pairs; orthogonal contrasts also showed no differences by species groupings (rooting depth or native range). For soil type, we found that seedlings growing in soil M exhibited more advanced leaf expansion (Y_{max}; P=0.10) compared to those in soil K.

The slope (k) of leaf expansion curves in 2014 differed significantly by species only (P=0.022), with quaking aspen exhibiting a significantly faster rate of leaf expansion compared to paper birch (P=0.0004) and black cherry (P=0.01) but not American chestnut. While paper birch was not significantly different from black cherry, both paper birch and black cherry had a shallower rate of progression than American chestnut (P<0.0001 and P=0.002, respectively). Using orthogonal contrasts, we detected species differences by rooting depth grouping (P<0.0001) – with deeper rooting species having faster leaf expansion – but not by species native range.

For LE_m (day of the midpoint of the leaf expansion curve) in 2014, we found significant effects of treatment (P=0.056), soil type (P=0.0008), species (P<0.0001) and a soil type x species interaction (P=0.06) (Table S4.2). Post hoc testing failed to detect differences among the treatment pairs, although the trend was for snow exclusion to have a later LE_m than the other two treatments. In terms of soil type effects, K had a significantly later LE_m than M (P=0.0008) and all species were significantly different

from each other ($P<0.0001$), except paper birch and black cherry. We did not detect

differences based on native range or rooting depth. Perhaps because of more limited

s ~~Control~~ ~~Heating~~ ~~Snow exclusion~~ find significant effects of any factor on Y_{max}, k, or LE_m in 2015.

(a) 2014
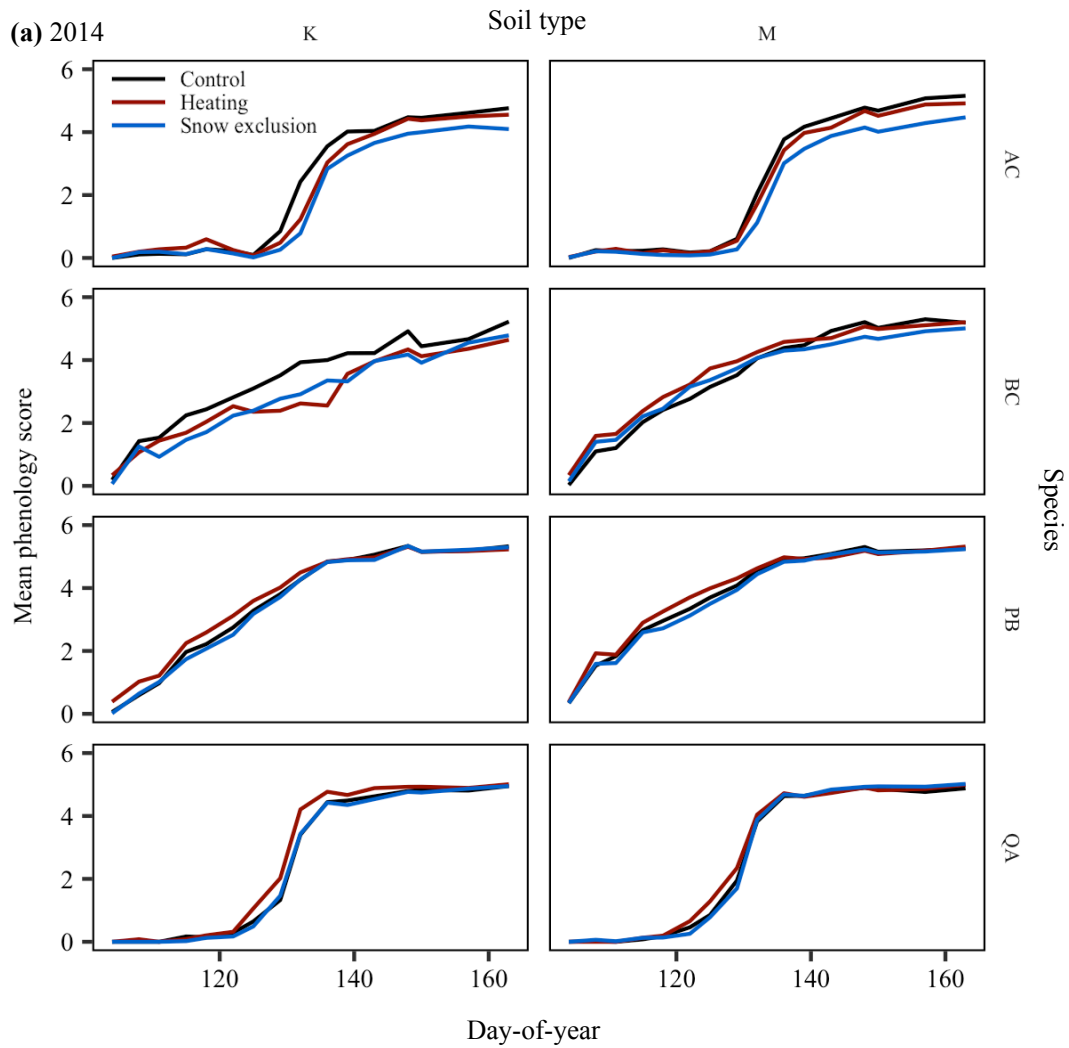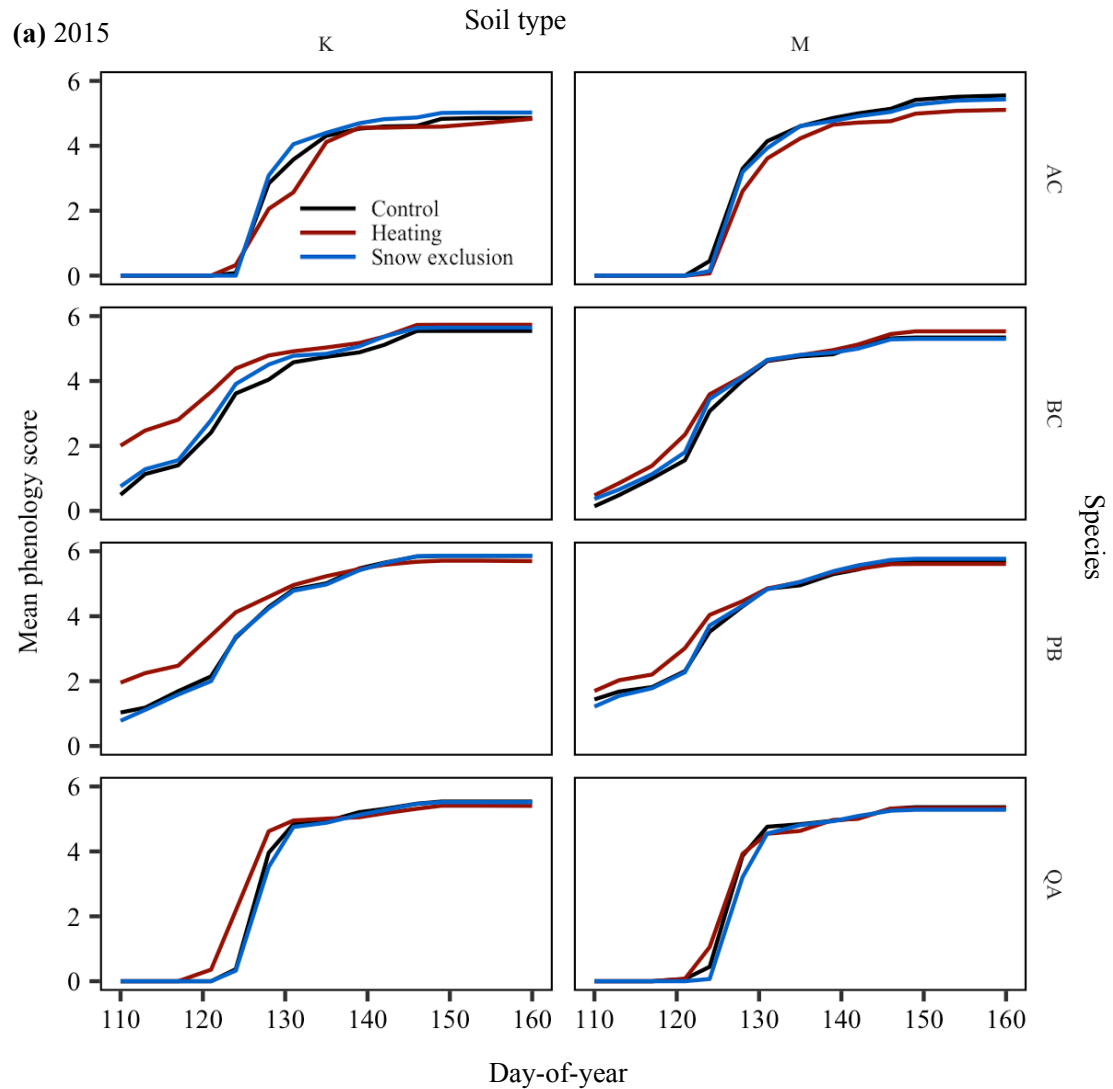
Figure 4.7: Mean spring leaf expansion progression scores (visual assessment of leaf expansion stage, see Table S1) by day-of-year. Results are displayed per treatment (control, heating, and snow exclusion [snow excluded for first six weeks of winter]), soil type (K: Kullman; M: Milton), and species (AC: American chestnut, BC: black cherry, PB: Paper birch, QA: quaking aspen), over two years: (a) 2014 and (b) 2015. There were significant day x treatment x soil type (P=0.001) and treatment x soil type x species (P=0.004) interactions on leaf expansion in 2014. There were significant effects of treatment (P=0.10), soil type (P=0.08), species (P=0.07), and a three-way interaction of treatment x species x soil type (P=0.07) on the maximum leaf expansion score (Y_{max}). In 2015, there was a significant treatment x soil type (P=0.04) interaction on leaf expansion progression score.

4.4.3 Factor effects on sapling biomass

We failed to detect any influence of the treatment and soil factors on height or diameter growth after one year of treatment (Fig. S4.2). However, at peak foliar biomass (day-of-year 261; Fig. 4.8) we found that total leaf area differed significantly by treatment (P=0.029), with snow exclusion having less photosynthetically active leaf area than both control and heating treatments (P=0.018 and P=0.08, respectively). On this day, soil M had a significantly greater amount of senesced leaf area than soil K (P=0.0002). Overall, total leaf area (green+yellow+red spectra) measured during leaf senescence (fall 2014) varied significantly by treatment (P<0.0001), soil type (P<0.0001), day x soil type (P=0.00016), and day x treatment (P=0.09). In post hoc tests, soil M had significantly more total leaf area than K (P<0.0001) and heating had accumulated more than the snow exclusion treatment (P=0.002). There were no significant differences in amount of photosynthetically active (green, and green+yellow spectra) or senescing (yellow spectrum) leaf area. There was a difference, however, in the senesced (red spectrum) leaf area by a treatment x day interaction (P=0.058).

To assess the longevity of active foliage by treatment and soil type, we looked at differences on the penultimate day of sampling (day-of-year 300). We avoided assessing the final sampling date as nearly all foliage had completely senesced (Fig. 4.8). On day 300, there were significant differences in all leaf area spectral categories due to treatment (green+yellow P=0.0005; green P=0.009; yellow P=0.001; red P=0.001; and total

143

P=0.0001). Saplings growing in heating plots had significantly more leaf area of all four spectral categories compared to saplings growing on control (green+yellow *P*=0.0005, green *P*=0.007, yellow *P*=0.003, red *P*=0.005, and total *P*<0.0001) and snow exclusion (green+yellow *P*=0.007, green *P*=0.07, yellow *P*=0.004, red *P*=0.001, and total *P*=0.007) plots. However, leaf areas between the control and snow exclusion treatments were indistinguishable. We also found soil M had greater amounts of all spectral categories of leaf area (green+yellow, *P*<0.0001, green *P*<0.0001, red *P*=0.036, total *P*=0.007), except for yellow (*P*=0.7), than soil K.
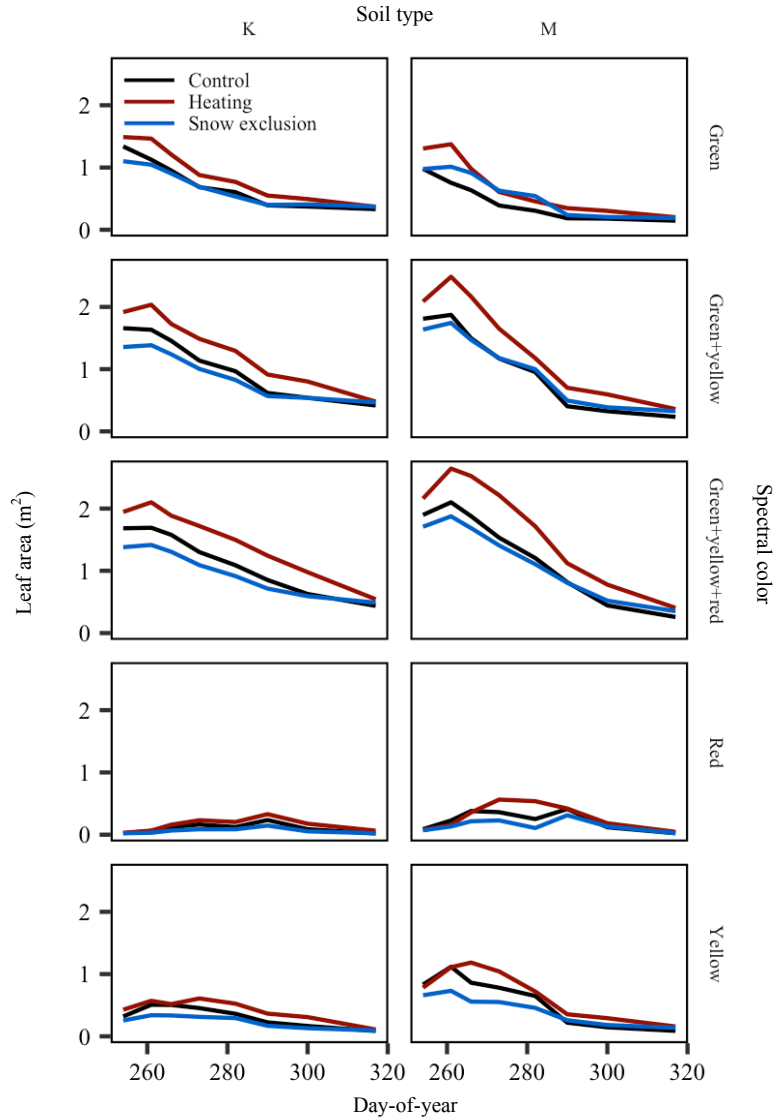
Figure 4.8: Mean spectral composition of amount of fall leaf area assessed using digital photographs, by treatment (control, heating, snow exclusion [snow excluded for first six weeks of winter]), day-of-year, and soil type (Kullman (K) and Milton (M)). We found significant differences by treatment ($P<0.0001$), soil type ($P<0.0001$), day ($P<0.0001$), day x soil type ($P=0.00016$), and day x treatment ($P=0.09$) on total leaf area. The following differences were found using Tukey HSD post hoc tests, with different letters denoting significant differences ($P<0.1$). Control[ab], heating[a], snow exclusion[b]; soil M[a], soil K[b] . We also found a significant treatment x day ($P=0.058$) interaction for sensed leaf area (red).

At the end of the experiment (fall 2015), but prior to leaf senescence, we harvested all above and belowground plant tissues (stems, leaves, fine and coarse roots). We found that total foliar biomass differed significantly by species (P=0.001), as well as by treatment x species x and soil type (P=0.07) (Fig. 4.9, Table S4.2). However, none of the species pairs were significantly different from each other in post hoc tests and we did not detect differences by species groupings (native range or rooting depth). Similarly, we found a significant effect of species on coarse root biomass (P=0.01), but specific differences could not be distinguished using post hoc tests. Fine root biomass differed by treatment (P=0.088), with control plots having more fine roots than heating plots (P=0.068). Overall, stem biomass, total above- and belowground biomass, and the ratio of above- to belowground biomass (aboveground:belowground) did not significantly differ by any factor.

We found a significant effect of soil type (P=0.023), species (P=0.0029), and a soil type x species interaction (P=0.037) on the root:shoot ratio (Fig. 4.9, Table S4.2). Soil K had a higher amount of root biomass relative to shoot biomass compared to soil M (P=0.06). By species, we found that American chestnut had a significantly lower root:shoot than the three other species (black cherry P=0.068; paper birch P=0.0002; and quaking aspen P=0.0008). Further, American chestnut growing in soil M had a significantly lower root:shoot than every other species and soil type combination (P<0.001). We found significant differences by species groupings (native range,

P>0.0001; rooting depth *P*=0.046), with Southern species and deep rooted species having

a lower root:shoot biomass ratio.
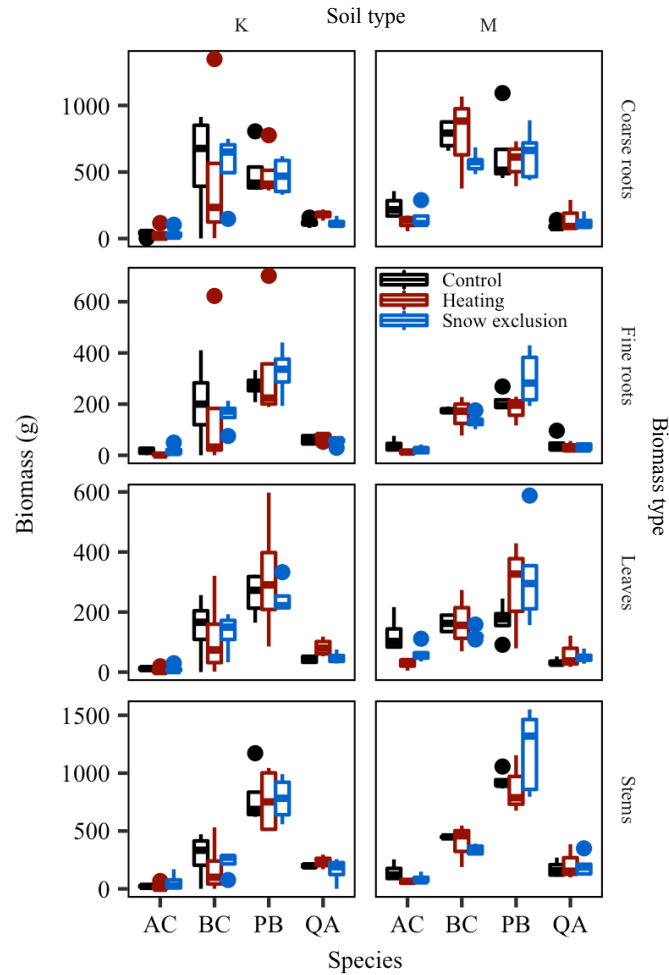
Figure 4.9: Mean biomass per type: coarse roots (>2 mm diameter), fine roots (<2 mm diameter), leaves, stems. Data is aggregated by species (AC: American chestnut, BC: black cherry, PB: Paper birch, QA: quaking aspen), soil type (Kullman (K) and Milton (M)) and treatment (control, heating, and snow exclusion [snow excluded for first six weeks of winter]). Boxplots shown with median (horizontal line within box), upper and lower whiskers (1.5*inter-quartile range; 75% and 25% percentile, respectively), and outliers (points). Coarse root biomass differed by species (*P*=0.01), and fine root biomass differed by treatment (*P*=0.088; Tukey HSD different letters signify significant differences (*P*<0.1): control[a], heating[b], snow exclusion[ab]). Leaf biomass differed significantly by species (*P*=0.001), and treatment x species x soil interaction (*P*=0.07). There were no differences among study factors for stems.

4.4.4 Factor effects on sapling stress, injury, and mortality

The number of saplings with visible insect herbivory varied significantly with species ($P<0.0001$), as well as by several complex interactions: treatment x soil type ($P=0.015$), treatment x species ($P=0.0086$), soil type x species ($P=0.0088$), and treatment x soil type x species ($P=0.04$) (data not shown). However, in post hoc tests we failed to detect significant differences among species pairs. Leaf necrosis showed a significant effect of species ($P<0.0001$) with American chestnut having a higher occurrence than paper birch and quaking aspen ($P<0.0001$ for both), but not black cherry. Paper birch had significantly more leaf necrosis than black cherry and quaking aspen ($P<0.0001$ for both), which had significantly more than black cherry ($P=0.0048$). Discoloration of leaves (visible as leaf spotting) was significantly different based on treatment ($P=0.0007$) and species ($P<0.0001$). While none of the treatment pairs were significantly different in post hoc tests, all the species pairs were significantly different from each other (aside from paper birch and black cherry) ($P<0.0001$). There were no significant effects of any factor on the number of saplings with chlorotic leaves.

In both 2014 and 2015, we found significant effects of species on percentage of winter injury damage ($P<0.001$ and $P=0.024$, respectively) (Fig. 4.10). In 2014, both Southern species (American chestnut and black cherry) suffered significantly more winter injury than the Northern species (paper birch and quaking aspen) ($P<0.0001$ for all comparisons). Within the Northern species, quaking aspen experienced more winter injury than paper birch ($P=0.006$) and within the Southern species, winter injury to black

cherry and American chestnut was indistinguishable. We saw also significant differences in 2014 winter injury damage based on species rooting depth grouping, with deep-rooted species (e.g., American chestnut and quaking aspen) having more severe winter injury ($P<0.0001$).

There were also significant interaction effects for our winter injury results: treatment x soil type ($P=0.05$), treatment x species ($P=0.06$), and soil type x species ($P=0.0004$) (Table S4.2), which together explained 36% of the total model variance. While the post hoc tests between treatment and soil type pairs was not significant for any comparison, there were significant pairwise comparisons between treatment and species as well as for soil type and species. While winter injury damage for the two Northern species was similar among treatments, for the two Southern species, treatment differences in winter injury showed contrasting responses. For example, American chestnut winter injury damage was most extreme in the heating and snow exclusion treatments, while for black cherry, it was most severe in the control treatment (Fig. 4.11).
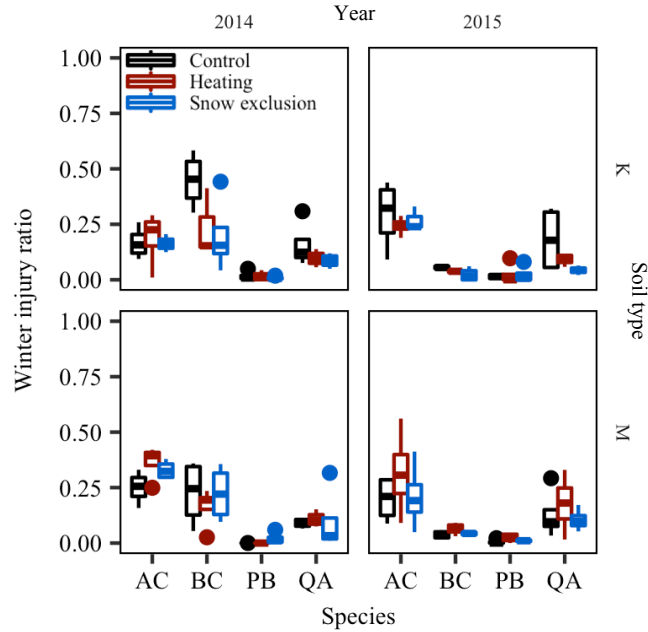
Figure 4.10: Mean percent winter injury (measured as a ratio of injury to total height) per species, soil type (Kullman (K) and Milton (M)), and treatment (control, heating, and snow exclusion [snow excluded for first six weeks of winter]) assessed over two winters (2014, 2015). Species abbreviations: AC: American chestnut, BC: black cherry, PB: Paper birch, QA: quaking aspen. Boxplots shown with median (horizontal line within box), upper and lower whiskers (1.5*inter-quartile range; 75% and 25% percentile, respectively), and outliers (points).

For winter injury damage in 2015, American chestnut again suffered from elevated damage and had significantly more winter injury than the other species (black cherry P=0.00004; paper birch P=0.0009; and quaking aspen P=0.015) (Fig. 4.10). The other species did not significantly differ from each other. While we observed differences in winter injury, with deep-rooted species (e.g., American chestnut and quaking aspen) having more severe winter injury in 2015 (P<0.0001), this effect may be driven by the substantial winter injury suffered by American chestnut.
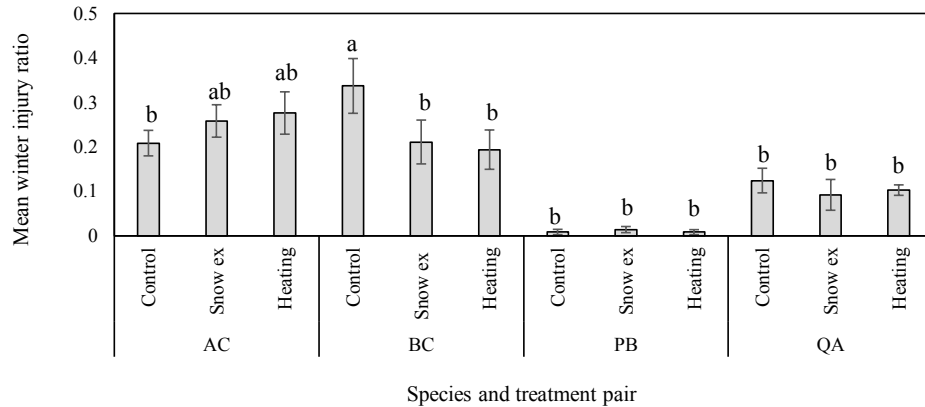
Figure 4.11: Mean percent winter injury in 2014 (measured as a ratio of injury to total height) per treatment (control, heating, and snow exclusion [here, "Snow ex" for brevity; snow excluded for first six weeks of winter]) and species (AC: American chestnut, BC: black cherry, PB: Paper birch, QA: quaking aspen) pair to examine interactions. Different letters above the treatment and species pairs indicate significant differences (Tukey HSD, $P<0.01$).

Total mortality (2014 + 2015) did not vary significantly based on any factor. However, we did find that 2014 mortality was significantly related to treatment ($P=0.059$), as well as treatment x soil type ($P=0.06$), treatment x species ($P=0.029$), soil type x species ($P=0.053$), and treatment x soil type x species ($P=0.014$) interactions (Fig. 4.12, Table S4.2). While the treatment pairs were not significantly different in a post hoc test, there was a trend for the snow exclusion treatment to suffer greater mortality rates than both control and heating, especially considering interactions with soil type. We found that among treatment and soil type pairs, soil K and snow exclusion had the highest mortality. By species, snow exclusion was most detrimental to quaking aspen, especially when paired with soil K (Fig. 4.12). We did not see any significant differences by species grouping (native range or rooting depth). In 2015, none of the factors significantly accounted for variations in mortality.
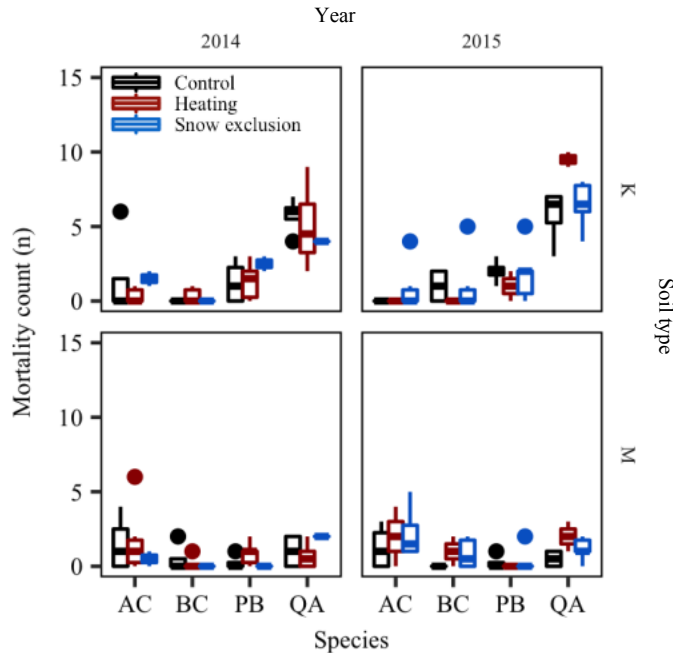
Figure 4.12: Mortality counts (*n* trees) by species, soil type (K:Kullman; M: Milton) treatment (control, heating, and snow exclusion [snow excluded for first six weeks of winter]), over two years (2014, 2015). Species abbreviations: AC: American chestnut, BC: black cherry, PB: Paper birch, QA: quaking aspen. Boxplots shown with median (horizontal line within box), upper and lower whiskers (1.5*inter-quartile range; 75% and 25% percentile, respectively), and outliers (points). Mortality in 2014 was significantly different among treatments (*P*=0.059), as were treatment x soil type (*P*=0.06), treatment x species (*P*=0.029), soil type x species (*P*=0.053), and treatment x soil type x and species (*P*=0.014) interactions. No significant differences were found for 2015.

4.5 Discussion

H_1: Heating will lengthen the effective growing season, increase sapling C uptake and storage, which will be evident by earlier spring leaf expansion, delayed leaf senescence, and an increase in woody growth and biomass.

While the heating treatment did not result in an earlier onset of spring leaf expansion (Fig. 4.7), there was a delaying effect on fall leaf senescence (Fig. 4.8). A lack of earlier onset of leaf expansion is likely related to the relative timing of soil thawing

152

(Campbell et al. 2005; Pregitzer et al. 2000) and accumulation of degree days (Richardson et al. 2006). All micro-catchments experienced soil thawing around the same day-of-year (~100), and leaf expansion slowly increased thereafter. While the soil in the heating treatment did thaw slightly sooner than the other treatments (Fig. 4.5), this difference must have been too subtle to alter treatment-related leaf expansion because all treatments showed a similar progression of leaf expansion (Fig. 4.7). Given the cold temperatures during both winters, perhaps even a 2-4°C increase in temperature in the heating treatment may not have been sufficient to increase the accumulation of degree days for earlier leaf expansion. For deciduous trees in the northeastern US, an earlier spring leaf expansion may be relatively riskier, compared to a delayed fall senescence, due to the potential for frost damage and resultant C losses (Saxe et al. 2001). Additionally, some evidence suggests that there may be physiological constraints on how early bud break and leaf expansion may occur – even when exposed to atypically mild temperatures (Groffman et al. 2012). Some of these contrary results may result from how winter temperature and spring bud break and leaf expansion interact; for example, elevated temperature during winter dormancy has been shown to delay leaf expansion the following spring for a number of deciduous species (Heide 2003; Westergaard and Eriksen 1997).

While we failed to detect treatment effects on height and diameter growth (Fig. S4.2), the heating treatment contained significantly more leaf area than both the control and snow exclusion, and foliage remained greener longer (Fig. 4.8), suggesting that

153

heating increased overall C uptake and led to an extended photosynthetic period. Heating did not increase tree mortality (Fig. 4.12) or alter the amount of winter injury (Fig. 4.10).

H₂: Heating will more negatively affect species at the southern latitudinal limit of their range at the experimental site (Northern species) than species at the northern latitudinal limit of their range (Southern species).

We detected no differences in height and diameter growth between Northern and Southern species (Fig. S4.2). Although heating decreased fine root biomass (Fig. 4.8), and we did note significant differences between root:shoot by species, we did not find differences based on native range limits; these results were likely driven by the low root:shoot for American chestnut, particularly when grown in combination with soil M. Additionally, we found no differences in spring leaf expansion between Southern compared to the Northern species. Indeed, species grouping by characteristic rooting depth appeared to be a more influential driver on the timing and rate of spring leaf expansion progression than native latitudinal range limits. Overall, the Southern species had a lower root:shoot than Northern species irrespective of treatment; we detected significantly greater winter injury damage (2014) for Southern compared to Northern species (Fig. 4.10). We also observed high winter injury damage to American chestnut saplings. The American chestnut seed source we used was previously noted to be cold hardy to Vermont winters (Saielli et al. 2012; Saielli et al. 2014). However, it was not cold tolerant enough for the two winters evaluated here. By chance, extreme cold was

prevalent during Jan-Feb 2015 (Fig. S4.3), which likely complicated the physiological response to imposed treatments. Nonetheless, there was generally less winter injury in 2015 than 2014, perhaps because there was greater treatment separation and saplings were younger and more vulnerable to injury or because snow depth was much more variable in 2014.

H_3 Heating will alter water budgets by increasing evapotranspiration, evident via reduced water flux, increased root to shoot biomass ratio (root:shoot), and amplified negative effects to characteristically shallow-rooted species.

Shallow rooted species did not show significant detrimental effects of heating on diameter and height growth (Fig. S4.2), nor did they suffer more mortality due to heating (Fig. 4.12). Yet, we did observe a divergent leaf expansion progression associated with rooting type. The two deeper rooted species displayed a sigmoidal curve-shaped progression of bud break, while the two shallower rooted species showed a more consistent and gradual progression (Fig. 4.7). However, this did not vary by treatment. Soil temperature and timing of thawing varied by depth (Fig. S4.1). Therefore, it is possible the later initiation of leaf expansion by the two characteristically deeper rooting species, American chestnut and quaking aspen, was related to frozen soils at deeper depths which may have limited water and nutrient uptake (Pregitzer et al. 2000). Another possibility is that in early spring, deeper rooted species divert more C towards root growth than to above ground processes like leaf expansion. While we found that

155

root:shoot did not vary by treatment, it was significantly related to rooting depth, with shallower-rooted species diverting more C allocation to root growth. Interestingly, at the termination of the study we also found that the heating treatment resulted in an overall reduction of fine root biomass (Fig. 4.9), aligning with other findings (Way and Oren 2010). This conclusion not only discredits our hypothesis that heating will result in more root growth, but poses the possibility of reduced water uptake and drought tolerance with warmer temperatures (Way and Oren 2010).

H_4: *Snow exclusion will cause deeper soil freezing, evident as a delayed onset of spring bud break, lower woody growth, and decreased fine root biomass.*

We measured deeper soil freezing in 2014 for the snow exclusion treatment (Fig. 4.5). We found that the heating treatment, which reduced the snow depth more than the snow exclusion treatment, had more variability in freezing depth than snow exclusion (Fig. 4.5). In both years, but particularly in 2014, the heating treatment experienced large fluctuations in frost depth (Fig. 4.5). The snow exclusion treatment did not result in significantly different height and diameter growth for any of the species (Fig. S4.2), even for shallow-rooted species. Yet, we did note that snow exclusion delayed the progression of leaf expansion as predicted (Fig. 4.7). Consequently, saplings in the snow exclusion treatment had significantly less overall biomass (Fig. 4.9). We did find a trend toward greater mortality with snow exclusion treatment, particularly for quaking aspen (Fig. 4.12), contrary to other findings of positive growth responses of western quaking aspen

156

populations with decreased snowpack (Brown et al. 2006). However, in other parts of its native range, there have been reports of widespread quaking aspen decline and mortality (Michaelian et al. 2011; Worrall et al. 2008) suspected to be due to extreme temperature and drought; this topic may warrant further study in the northeastern US. While the snow exclusion treatment did increase the depth and duration of soil frost, the heating treatment experienced a greater number of freeze-thaw cycles, particularly in 2014 (Fig. 4.5). Indeed, the heating treatment was associated with a reduction in fine root biomass (Fig. 4.9), possibly due to the increased frequency of freeze-thaw cycles (Fig. 4.5), which has been shown to cause root damage and mortality (Comerford et al. 2013).

Snow exclusion was particularly consequential to quaking aspen. This was not related to changes in shoot winter injury (Fig. 4.10, 4.11), although spring leaf expansion and overall mortality was disproportionately affected by snow exclusion (Fig. 4.7, 4.12). It is understood that changes in winter snowpack and associated soil freezing can impact spring phenology (Groffman et al. 2012), but how this might be associated with increased mortality is unclear. The missing link here could be freeze-induced root damage (e.g., Comerford et al. 2013), but incipient root damage was not assessed in our study. Whatever the mechanism, our findings raise the interesting possibility that deep-rooted Northern species that typically grow in locations with a steady winter snowpack may be surprisingly susceptible to even temporary (here six weeks of snow exclusion) alterations of snow depth protection.

In addition, this experiment clearly demonstrates the year-to-year variability in local weather conditions that can affect outcomes. Both 2014 and 2015 were cold winters in Vermont (Fig. S4.3). Winter 2015 was cold without typical freeze-thaw cycles. Thus, all treatments had soil freezing that was indistinguishable and deep (Fig. 4.5); in some micro-catchments, freezing occurred to the maximum depth of our measurement capability (0.6 m). Thus, our snow exclusion treatment did not result in greater soil freezing depth in 2015 as it did in 2014.

H5: Soil type, specifically nutrient content, will amplify the effects of both heating and snow exclusion.

The two soils, K and M, differed in particle size as well as cation concentration (Table 4.1), and we detected a large effect of soil type on water flux through the micro-catchments, with the coarser soil (K) tending to retain less water (Fig. 4.6), particularly in 2014. Soil type was associated with differences in many of the sapling-based measures we assessed. For example, spring leaf expansion and fall senescence varied with soil type (Fig. 4.7, 4.8). Generally, soil M (the soil with lower Ca) was more favorable for the saplings. We found that plants growing on soil M proceeded more quickly through spring leaf expansion stages than those on K, and had a larger total leaf area (Fig. 4.8). These results may be related to greater water retention in this soil type (adequate leaf turgor pressures drive leaf expansion), rather than its nutrient content. Soil type also had a strong effect on biomass, especially root:shoot, with K having a higher ratio than M (Fig. 4.9).

Thus, saplings growing in soil K directed more C to root biomass, rather than shoot growth, likely due to the lower water holding capacity of this soil (Fig. 4.6). Additionally, we detected higher overall biomass for saplings growing in soil M, including a greater amount of photosynthetic biomass (Fig. 4.8). However, both soils had similar total sapling biomass. We also observed higher mortality (Fig. 4.12) and other signs of stress (e.g., herbivory) on soil K.

4.6 Conclusions

Overall, our findings highlight the basic importance of biological (e.g., associated with species) and ecological (e.g., associated with soil type) factors in affecting sapling performance independent of climate treatment. Despite this predominance, climate treatment was associated with differences in leaf expansion, fall leaf area, fine root biomass, leaf spotting, and sapling mortality in 2014. Treatments generally had a greater impact on spring and fall measures than growing season or winter measures. However, the apparently greater impact on spring and fall physiology may reflect the difficulty of getting treatment impositions that can overcome winter and summer temperature extremes. This may be particularly evident for the winter warming treatment. Here our 2-4°C increase in temperature appeared insufficient to overcome the dominating effects of the unusually low ambient air temperatures that prevailed over the course of this study (Fig. S4.3). Consequently, American chestnut (a species with limited cold hardiness; Gurney et al. 2013) experienced significant winter injury despite supplemental heating.

159

And this may also explain the high mortality suffered by quaking aspen on the snow exclusion treatment. Both outcomes complicate predictions of species response to changes in climate.

Perhaps most importantly, our work clearly demonstrated that the complex interaction of site and species characteristics with climate can be more important than climate factors alone. Whereas we found direct climate treatment impacts on five sapling performance parameters, we detected 14 interactions of climate treatment with species and/or soil factors. In many cases, these interactions explained >30% of the model variance. As such, our results suggest that a range of responses in tree performance (some perhaps even contradictory) are likely and may depend on myriad influences, including species' physiology and site factors. Indeed, this illustrates the problematic issue of inferring species responses based on the examination of just a few measurement variables (e.g., climate variables alone). In a forested setting, site characteristics may moderate or exacerbate tree responses to climate change, with certain tree species showing favorable responses, while others may not, depending on tree physiology, water and nutrient availability, and localized weather. While our research has addressed some fundamental questions about species response to potential climate change scenarios, it has also raised many additional questions, and points to the complex interplay of biological and environmental factors that influence species performance in a changing environment.

4.7 Acknowledgements

4.8 References

Ahmed, K.F., Wang, G., Silander, J., Wilson, A.M., Allen, J.M., Horton, R., and Anyah, R. 2013. Statistical downscaling and bias correction of climate model outputs for climate change impact assessment in the U.S. northeast. Global and Planetary Change **100**: 320-332. doi: http://dx.doi.org/10.1016/j.gloplacha.2012.11.003.

Beard, K., Wang, D., Waite, C., Decker, K., Hawley, G., DeHayes, D., Hughes, J., and Cumming, J. 2005. Quantifying Ecosystem Controlsand Their Contextual Interactionson Nutrient Export fromDeveloping Forest Mesocosms. Ecosystems **8**(2): 210-224. doi: 10.1007/s10021-004-0041-y.

Brown, K., Hansen, A.J., Keane, R.E., and Graumlich, L.J. 2006. Complex interactions shaping aspen dynamics in the Greater Yellowstone Ecosystem. Landscape Ecology **21**(6): 933-951. doi: 10.1007/s10980-005-6190-3.

Burns, R., and Honkala, B. 1990. Silvics of North America: 1. Conifers; 2. Hardwoods Agriculture Handbook 654. US Department of Agriculture, Forest Service, Washington, DC.

Campbell, J.L., Mitchell, M.J., Groffman, P.M., Christenson, L.M., and Hardy, J.P. 2005. Winter in northeastern North America: a critical period for ecological processes. Frontiers in Ecology and the Environment **3**(6): 314-322. doi: 10.1890/1540-9295(2005)003[0314:winnaa]2.0.co;2.

Clark, S.L., Schlarbaum, S.E., Pinchot, C.C., Anagnostakis, S.L., Saunders, M.R., Thomas-Van Gundy, M., Schaberg, P., McKenna, J., Bard, J.F., and Berrang, P.C. 2014. Reintroduction of American chestnut in the national forest system. Journal of Forestry **112**(5): 502-512.

Comerford, D.P., Schaberg, P.G., Templer, P.H., Socci, A.M., Campbell, J.L., and Wallin, K.F. 2013. Influence of experimental snow removal on root and canopy physiology of sugar maple trees in a northern hardwood forest. Oecologia **171**(1): 261-269. doi: 10.1007/s00442-012-2393-x.

Decker, K., Wang, D., Waite, C., and Scherbatskoy, T. 2003. Snow removal and ambient air temperature effects on forest soil temperatures in northern Vermont. Soil Science Society of America Journal **67**(4): 1234-1242.

Fitzhugh, R., Driscoll, C., Groffman, P., Tierney, G., Fahey, T., and Hardy, J. 2001. Effects of soil freezing disturbance on soil solution nitrogen, phosphorus, and carbon chemistry in a northern hardwood ecosystem. Biogeochemistry **56**(2): 215-238. doi: 10.1023/A:1013076609950.

Fitzhugh, R.D., Driscoll, C.T., Groffman, P.M., Tierney, G.L., Fahey, T.J., and Hardy, J.P. 2003. Soil freezing and the acid-base chemistry of soil solutions in a northern hardwood forest. Soil Science Society of America Journal **67**(6): 1897-1908.

Groffman, P., Driscoll, C., Fahey, T., Hardy, J., Fitzhugh, R., and Tierney, G. 2001. Colder soils in a warmer world: A snow manipulation study in a northern hardwood forest ecosystem. Biogeochemistry **56**(2): 135-150. doi: 10.1023/A:1013039830323.

Groffman, P.M., Rustad, L.E., Templer, P.H., Campbell, J.L., Christenson, L.M., Lany, N.K., Socci, A.M., Vadeboncoeur, M.A., Schaberg, P.G., Wilson, G.F., Driscoll, C.T., Fahey, T.J., Fisk, M.C., Goodale, C.L., Green, M.B., Hamburg, S.P., Johnson, C.E., Mitchell, M.J., Morse, J.L., Pardo, L.H., and Rodenhouse, N.L. 2012. Long-term integrated studies show complex and surprising effects of climate change in the northern hardwood forest. Bioscience **62**: 1056-1066.

Gurney, K.M., Schaberg, P.G., Hawley, G.J., and Shane, J.B. 2011. Inadequate Cold Tolerance as a Possible Limitation to American Chestnut Restoration in the Northeastern United States. Restor. Ecol. **19**(1): 55-63. doi: 10.1111/j.1526-100X.2009.00544.x.

Heide, O. 2003. High autumn temperature delays spring bud burst in boreal trees, counterbalancing the effect of climatic warming. Tree Physiology **23**(13): 931-936.

Hunt, R.S. 1978. Poplar shoot blight. Forestry Canada, Forest Insect and Disease Survey, Forest Pest Leaflet 42. p. 3.

Kimball, B.A., Conley, M.M., Wang, S., Lin, X., Luo, C., Morgan, J., and Smith, D. 2008. Infrared heater arrays for warming ecosystem field plots. Global Change Biology **14**(2): 309-320.

Kobe, R.K., Likens, G.E., and Eagar, C. 2002. Tree seedling growth and mortality responses to manipulations of calcium and aluminum in a northern hardwood forest. Canadian Journal of Forest Research **32**(6): 954-966.

Kunkel, K.E., Stevens, L., Stevens, S., Sun, L., Janssen, E., Wuebbles, D., Rennells, J., DeGaetano, A., and Dobson, J. 2013. NOAA Technical Report NESDIS. Regional climate trends and scenarios for the U.S. National Climate Assessment. Part 1: Climate of the Northeast U.S. .

Melillo, J.M., Butler, S., Johnson, J., Mohan, J., Steudler, P., Lux, H., Burrows, E., Bowles, F., Smith, R., Scott, L., Vario, C., Hill, T., Burton, A., Zhou, Y.-M., and Tang, J. 2011. Soil warming, carbon–nitrogen interactions, and forest carbon budgets. Proceedings of the National Academy of Sciences **108**(23): 9508-9512. doi: 10.1073/pnas.1018189108.

NOAA National Weather Service. 2017. Temperature records for Burlington International Airport, https://www.ncdc.noaa.gov/. [Accessed 1/28/17].

Northeast Climate Impacts Assessment Synthesis Team. 2007. Confronting climate change in the U.S. Northeast. A report of the Northeast Climate Impacts Assessment.

Pregitzer, K.S., King, J.S., Burton, A.J., and Brown, S.E. 2000. Responses of tree fine roots to temperature. New Phytologist **147**(1): 105-115.

R Development Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rasband, W.S. 2016. ImageJ, U. S. National Institutes of Health, Bethesda, Maryland, USA, http://imagej.nih.gov/ij/.

Ricard, J.A., Tobiasson, W., and Greatorex, A. 1976. The field assembled frost gage. United States Army Cold Regions Research and Engineering Laboratory (CRREL), Hanover, NH.

Richardson, A.D., Bailey, A.S., Denny, E.G., Martin, C.W., and O'Keefe, J. 2006. Phenology of a northern hardwood forest canopy. Global Change Biology **12**(7): 1174-1188. doi: 10.1111/j.1365-2486.2006.01164.x.

Saielli, T.M., Schaberg, P.G., Hawley, G.J., Halman, J.M., and Gurney, K.M. 2012. Nut cold hardiness as a factor influencing the restoration of American chestnut in northern latitudes and high elevations. Canadian Journal of Forest Research **42**(5): 849-857. doi: 10.1139/x2012-033.

Saielli, T.M., Schaberg, P.G., Hawley, G.J., Halman, J.M., and Gurney, K.M. 2014. Genetics and silvicultural treatments influence the growth and shoot winter injury of american chestnut in Vermont. *In*. Society of American Foresters.

Saxe, H., Cannell, M.G.R., Johnsen, Ø., Ryan, M.G., and Vourlitis, G. 2001. Tree and forest functioning in response to global warming. New Phytologist **149**(3): 369-399. doi: 10.1046/j.1469-8137.2001.00057.x.

U.S. Geological Survey. 2016. Digital Representations of Tree Species Range Maps from "Atlas of United States Trees" by Elbert L. Little, Jr. (and other publications). U.S. Department of the Interior.

USGCRP, Horton, R., Yohe, G., Easterling, W., Kates, R., Ruth, M., Sussman, E., Whelchel, A., Wolfe, D., and Lipschultz, F. 2014. Ch. 16: Northeast. Climate Change Impacts in the United States: The Third National Climate Assessment. *Edited by* J.M. Melillo and T.C. Richmond and G.W. Yohe. U.S. Global Change Research Program.

Vitasse, Y., Delzon, S., Dufrêne, E., Pontailler, J.-Y., Louvet, J.-M., Kremer, A., and Michalet, R. 2009. Leaf phenology sensitivity to temperature in European trees: Do within-species populations exhibit similar responses? Agricultural and Forest Meteorology **149**(5): 735-744.

Wang, G.G., Knapp, B.O., Clark, S.L., and Mudder, B.T. 2013. The Silvics of *Castanea dentata* (Marsh.) Borkh., American chestnut, Fagaceae (Beech Family).

Way, D.A., and Oren, R. 2010. Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data. Tree Physiology **30**(6): 669-688.

West, N.E., and Wein, R.W. 1971. A plant phenological index technique. BioScience **21**(4): 116-117.

Westergaard, L., and Eriksen, E.N. 1997. Autumn temperature affects the induction of dormancy in first- year seedlings of acer platanoides L. Scandinavian Journal of Forest Research **12**(1): 11-16.

4.9 Supplementary Materials

Table S4.1: Bud break and leaf expansion progression score and descriptions of visual identifiers (West and Wein 1971).

Leaf expansion score	Description
0	Bud dormant, no sign of breaking
1	Bud is swollen or displays green tip
2	Bud green, but tight or separating slightly, no leaves unfolding
3	Bud expanding, leaves unfolding from bud
4	Internodes/petioles visible, leaves not enlarged
5	Internodes/petioles visible, leaves enlarged

Table S4.2: Significance values (*P*<F) from ANOVA models listed by response variable, factor and interactions among factors. Bold text indicates *P*<0.1 and bold, red text indicates *P*<0.05. Factor abbreviations are as follows. tmt: treatment (control, heating, snow exclusion [snow excluded for the first six weeks of winter]); day: day-of-year; soil: soil type (K: Kullman; M: Milton); sp: species (American chestnut, black cherry, paper birch, quaking aspen).

Response variable	Year	Trt	Soil	Sp	Day x trt	Day x soil	Day x sp	Trt x soil	Trt x sp	Sp x soil	Day x trt x soil	Day x trt x sp	Day x soil x sp	Trt x soil x sp	Day x trt x soil x sp
Soil temperature	All	0.555	0.124	0	0.470	0.197		0.539			0.554				
Snow depth	2014	**0.000**	0.449		0.440	**0.005**		0.881			0.949				
	2015	**0.002**	0.910		0.985	**0.057**		0.927			0.997				
Soil frost depth	2014	0.262	0.612		**0.000**	0.994		0.935			0.940				
	2015	0.143	0.275		0.983	0.955		0.234			0.904				
Water flux	2014	0.141	0.399		0.188	0.340		0.685			0.384				
	2015	0.487	0.715		0.335	0.376		0.828			0.581				
Leaf expansion score	2014	0.622	0.911	0.152	0.547	0.362	0.146	0.772	0.353	0.354	**0.001**	0.205	0.152	**0.004**	0.861
	2015	0.823	0.714	0.109	0.357	0.961	0.281	**0.044**	0.201	0.736	0.229	0.163	0.980	0.114	0.523
Max. leaf expansion (Y max)	2014	**0.097**	**0.076**	**0.073**				0.460	0.181	0.390				**0.069**	
	2015	0.347	0.401	0.188				0.449	0.383	0.514				0.587	
Slope of leaf expansion curve (k)	2014	0.923	**0.095**	**0.022**				0.633	0.370	0.749				0.642	
	2015	0.788	0.422	0.366				0.472	0.678	0.201				0.827	
Midpoint of leaf expansion curve (LE$_m$)	2014	0.383	0.346	0.835				0.470	0.548	0.500				0.531	
	2015	0.869	0.800	0.148				0.748	0.831	0.109				0.442	
Leaf are: green + yellow	2014	0.917	0.971		0.302	0.390		0.822			0.260				
Leaf area: yellow	2014	0.418	0.349		0.647	0.404		0.347			0.465				
Leaf area: green	2014	0.554	0.727		0.393	0.541		0.379			0.600				
Leaf area: red	2014	0.554	0.137		**0.058**	0.132		0.213			0.877				
Leaf area: total	2014	**0.000**	**0.000**		**0.090**	**0.000**		0.367			0.953				
Biomass: coarse roots	2015	0.651	0.203	**0.011**				0.781	0.294	0.420				0.736	
Biomass: fine roots	2015	**0.088**	0.316	0.732				0.827	0.505	0.591				0.375	
Biomass: coarse:fine	2015	0.484	0.368	0.989				0.586	0.632	0.569				0.752	
Biomass: leaves	2015	0.465	0.600	**0.001**				0.161	0.637	0.482				**0.072**	
Biomass: stems	2015	0.627	0.556	0.291				0.537	0.442	0.249				0.280	
Biomass: roots:shoots	2015	0.486	**0.023**	**0.003**				0.345	0.237	**0.037**				0.860	
Biomass: aboveground	2015	0.752	0.858	0.929				0.489	0.671	0.205				0.277	
Biomass: belowground	2015	0.330	0.229	0.970				0.676	0.642	0.678				0.587	
Biomass: above:below	2015	0.504	0.119	0.996				0.663	0.406	0.334				0.601	

Biomass: total	2015	0.246	0.410	0.892	0.529	0.342	0.355		0.573
Winter injury	2014	0.214	0.136	**0.000**	**0.066**	**0.072**	**0.020**		**0.034**
	2015	0.362	0.933	**0.000**	**0.076**	0.607	0.731		0.720
Mortality	2014	**0.059**	0.109	0.946	**0.063**	**0.029**	**0.053**		**0.014**
	2015	0.173	0.410	0.867	0.814	0.755	0.511		0.652
Diameter	2014	0.637	0.173	0.877	0.335	0.880	0.521		0.705
Height	2014	0.252	**0.062**	0.518	0.651	0.455	0.758		0.208
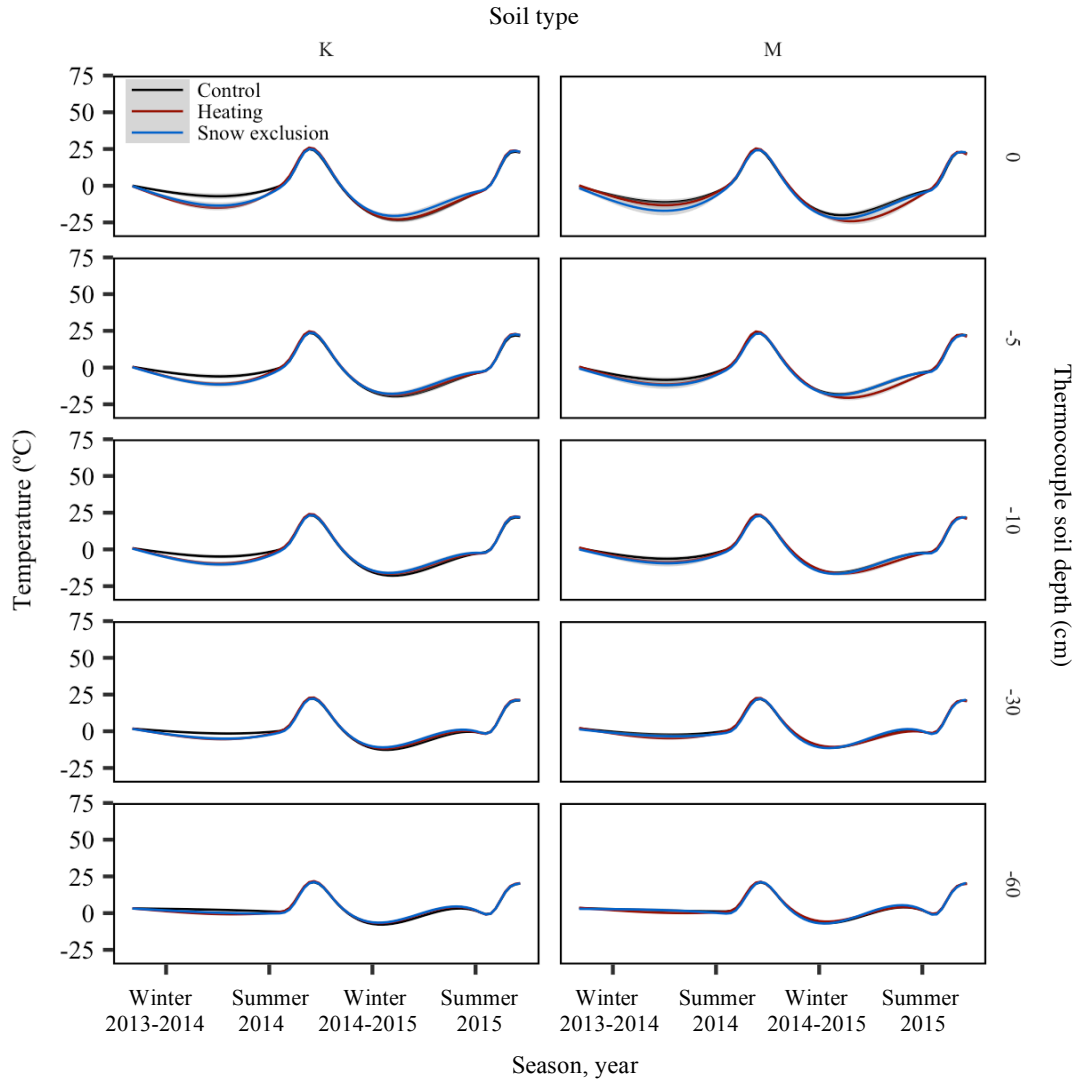
Figure S4.1: Mean soil temperature (°C) during the experimental period (Winter 2013-2014 to early Fall 2015) recorded by thermocouples placed at five soil depths: 0 (soils surface), and 5, 10, 30, and 60 cm below the soil surface. Temperatures are shown by treatment (control, heating, snow exclusion [snow excluded for the first six weeks of winter]) and soil type (K: Kullman; M: Milton). Values were smoothed with a loess function.

167
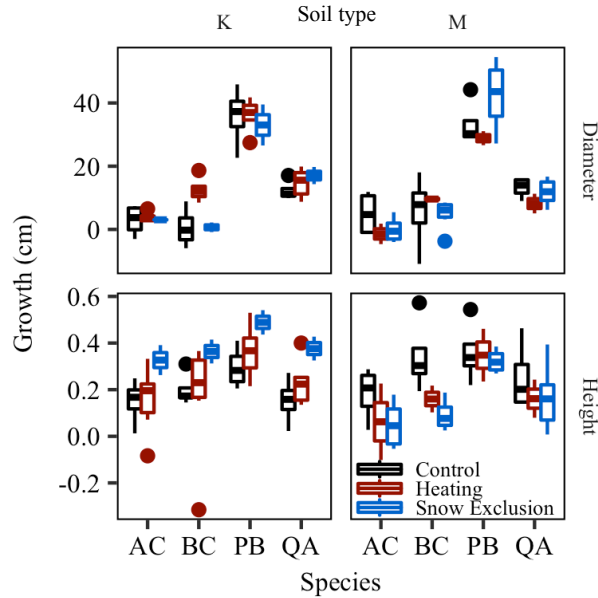
Figure S4.2: Mean height (cm) and diameter (cm) growth during treatment period by species, treatment (control, heating, snow exclusion), and soil type (K: Kullman; M: Milton) in 2014. Differences were not significant. Species abbreviations: AC: American chestnut, BC: black cherry, PB: paper birch, QA: quaking aspen. Boxplots shown with median (horizontal line within box), upper and lower whiskers (1.5*inter-quartile range; 75% and 25% percentile, respectively), and outliers (points).
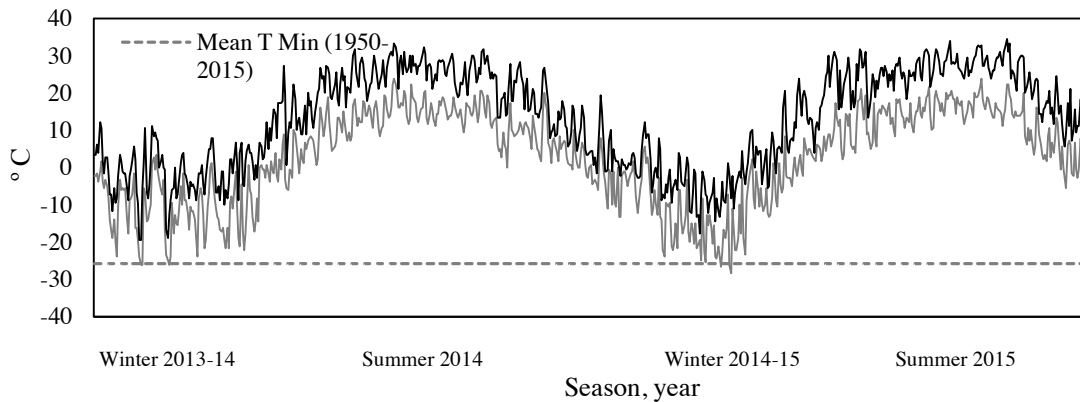
Figure S4.3: Maximum (max) and minimum (min, grey line) temperature (T; °C) and mean January minimum temperature (1950-2015; dashed horizontal grey line) for Burlington International Airport (S. Burlington, VT; elevation 100 m; ~ 5.9 km from study site) . (NOAA National Weather Service 2017)

168

COMPREHENSIVE BIBLIOGRAPHY

Aber, J., McDowell, W., Nadelhoffer, K., Alison, M., Berntson, G., Kamakea, M., McNulty, S., Currie, W., Rustad, L., and Fernandez, I. 1998. Nitrogen saturation in temperate forest ecosystems. BioScience **48**(11): 921-934.

Aber, J.D., Goodale, C.L., Ollinger, S.V., Smith, M.-L., Magill, A.H., Martin, M.E., Hallett, R.A., and Stoddard, J.L. 2003. Is nitrogen deposition altering the nitrogen status of northeastern forests? BioScience **53**(4): 375-389. doi: 10.1641/0006-3568(2003)053[0375:indatn]2.0.co;2.

Aber, J.D., Nadelhoffer, K.J., Steudler, P., and Melillo, J.M. 1989. Nitrogen saturation in northern forest ecosystems. BioScience **39**(6): 378-286.

Ahmed, K.F., Wang, G., Silander, J., Wilson, A.M., Allen, J.M., Horton, R., and Anyah, R. 2013. Statistical downscaling and bias correction of climate model outputs for climate change impact assessment in the U.S. northeast. Global and Planetary Change **100**: 320-332. doi: http://dx.doi.org/10.1016/j.gloplacha.2012.11.003.

Ainsworth, E.A., and Long, S.P. 2005. What have we learned from 15 years of free-air CO2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO2. New Phytologist **165**(2): 351-372.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A., and Cobb, N. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management **259**(4): 660-684. doi: http://dx.doi.org/10.1016/j.foreco.2009.09.001.

Allen, G.J., Chu, S.P., Harrington, C.L., Schumacher, K., Hoffmann, T., Tang, Y.Y., Grill, E., and Schroeder, J.I. 2001. A defined range of guard cell calcium oscillation parameters encodes stomatal movements. Nature **411**(6841): 1053-1057.

Bader, M.K.F., Leuzinger, S., Keel, S.G., Siegwolf, R.T.W., Hagedorn, F., Schleppi, P., and Körner, C. 2013. Central European hardwood trees in a high-CO2 future: synthesis of an 8-year forest canopy CO2 enrichment project. Journal of Ecology **101**(6): 1509-1519. doi: 10.1111/1365-2745.12149.

Bailey, S., Horsley, S., Long, R., and Hallett, R. 2004. Influence of edaphic factors on sugar maple nutrition and health on the Allegheny Plateau. Soil Science Society of America Journal **68**(1): 243-252.

Battipaglia, G., Saurer, M., Cherubini, P., Calfapietra, C., McCarthy, H.R., Norby, R.J., and Francesca Cotrufo, M. 2013. Elevated CO2 increases tree-level intrinsic water use efficiency: insights from carbon and oxygen isotope analyses in tree rings across three forest FACE sites. New Phytologist **197**(2): 544-554. doi: 10.1111/nph.12044.

Beard, K., Wang, D., Waite, C., Decker, K., Hawley, G., DeHayes, D., Hughes, J., and Cumming, J. 2005. Quantifying Ecosystem Controlsand Their Contextual Interactionson Nutrient Export fromDeveloping Forest Mesocosms. Ecosystems **8**(2): 210-224. doi: 10.1007/s10021-004-0041-y.

Beckage, B., Osborne, B., Gavin, D.G., Pucko, C., Siccama, T., and Perkins, T. 2008. A rapid upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont. Proceedings of the National Academy of Sciences **105**(11): 4197-4202. doi: 10.1073/pnas.0708921105.

Betts, A.K. 2011. Vermont climat change indicators. Weather, Climate, and Society **3**: 106-115.

Bigras, F., and Bertrand, A. 2006. Responses of Picea mariana to elevated CO2 concentration during growth, cold hardening and dehardening: phenology, cold tolerance, photosynthesis and growth. Tree Physiology **26**(7): 875-888.

Bishop, D.A., Beier, C.M., Pederson, N., Lawrence, G.B., Stella, J.C., and Sullivan, T.J. 2015. Regional growth decline of sugar maple (Acer saccharum) and its potential causes. Ecosphere **6**(10): art179. doi: 10.1890/ES15-00260.1.

Bonan, G.B. 2008. Forests and Climate Change: Forcings, Feedbacks, and the Climate Benefits of Forests. Science **320**(5882): 1444-1449. doi: 10.1126/science.1155121.

Borer, C.H., Schaberg, P.G., and DeHayes, D.H. 2005. Acidic mist reduces foliar membrane-associated calcium and impairs stomatal responsiveness in red spruce. Tree Physiology **25**(6): 673-680. doi: 10.1093/treephys/25.6.673.

Briffa, K.R., Shishov, V.V., Melvin, T.M., Vaganov, E.A., Grudd, H., Hantemirov, R.M., Eronen, M., and Naurzbaev, M.M. 2008. Trends in recent temperature and radial tree growth spanning 2000 years across northwest Eurasia. Philosophical Transactions of the Royal Society of London B: Biological Sciences **363**(1501): 2269-2282.

Brown, K., Hansen, A.J., Keane, R.E., and Graumlich, L.J. 2006. Complex interactions shaping aspen dynamics in the Greater Yellowstone Ecosystem. Landscape Ecology **21**(6): 933-951. doi: 10.1007/s10980-005-6190-3.

Bunn, A., Korpela, M., Biondi, F., Campelo, F., Merian, P., Qeadan, F., and Zang, C. 2015. dplR: Dendrochronology Program Library in R. R package version 1.6.3. http://r-forge.r-project.org/projects/dplr/.

Burns, D., Lynch, J., Cosby, B., Fenn, M., and Baron, J. 2011. National acid precipitation assessment program report to Congress 2011: an integrated assessment. US Environmental Protection Agency, Washington, DC, USA.

Burns, R., and Honkala, B. 1990. Silvics of North America: 1. Conifers; 2. Hardwoods Agriculture Handbook 654. US Department of Agriculture, Forest Service, Washington, DC.

Campbell, J.L., Mitchell, M.J., Groffman, P.M., Christenson, L.M., and Hardy, J.P. 2005. Winter in northeastern North America: a critical period for ecological processes. Frontiers in Ecology and the Environment **3**(6): 314-322. doi: 10.1890/1540-9295(2005)003[0314:winnaa]2.0.co;2.

Cape, J.N., Leith, I.D., Fowler, D., Murray, M.B., Sheppard, L.J., Eamus, D., and Wilson, R.H.F. 1991. Sulphate and ammonium in mist impair the frost hardening of red spruce seedlings. New Phytologist **118**(1): 119-126. doi: 10.1111/j.1469-8137.1991.tb00572.x.

Carnicer, J., Coll, M., Ninyerola, M., Pons, X., Sánchez, G., and Peñuelas, J. 2011. Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. Proceedings of the National Academy of Sciences **108**(4): 1474-1478.

Chmielewski, F.-M., and Rötzer, T. 2001. Response of tree phenology to climate change across Europe. Agricultural and Forest Meteorology **108**(2): 101-112.

Christensen, J.H., Hewitson, A., and Busuioc, A. 2007. Regional Climate Projections. Cambridge University Press, Cambridge, United Kingdom.

Clark, S.L., Schlarbaum, S.E., Pinchot, C.C., Anagnostakis, S.L., Saunders, M.R., Thomas-Van Gundy, M., Schaberg, P., McKenna, J., Bard, J.F., and Berrang, P.C. 2014. Reintroduction of American chestnut in the national forest system. Journal of Forestry **112**(5): 502-512.

Climatic Research Unit. 2016. University of East Anglia. Monthly CRU TS3.24 temperature [accessed 4 June 2016]

Cogbill, C.V. 1996. Historical ecology of the upper Stevensville Brook watershed, Underhill, Vermont. For Vermont Department of Forest, Parks and Recreation and Vermont Monitoring Cooperative.

Cogbill, C.V., and Likens, G.E. 1974. Acid precipitation in the northeastern United States. Water Resources Research **10**(6): 1133-1137. doi: 10.1029/WR010i006p01133.

Comerford, D.P., Schaberg, P.G., Templer, P.H., Socci, A.M., Campbell, J.L., and Wallin, K.F. 2013. Influence of experimental snow removal on root and canopy physiology of sugar maple trees in a northern hardwood forest. Oecologia **171**(1): 261-269. doi: 10.1007/s00442-012-2393-x.

Cook, E.R. 1985. A time series analysis approach to tree ring standardization (dendrochronology, forestry, dendroclimatology, autoregressive process). *In* Renewable Natural Resources. University of Arizona, Tucson, AZ.

Cook, E.R., Johnson, A.H., and Blasing, T.J. 1987. Forest decline: modeling the effect of climate in tree rings. Tree Physiology **3**(1): 27-40. doi: 10.1093/treephys/3.1.27.

Cook, E.R., and Kairiukstis, L.A. (eds). 1990. Methods of Dendrochronology: Applications in the Envrionmental Sciences. Kluwer Academic Publishers, Dordrecht.

Cook, E.R., and Pederson, N. 2011. Uncertainty, emergence, and statistics in dendrochronology. *In* Dendroclimatology. Springer. pp. 77-112.

Cook, E.R., and Peters, K. 1997. Calculating unbiased tree-ring indices for the study of climatic and environmental change. The Holocene **7**(3): 361-370.

Cunningham, S., and Read, J. 2002. Comparison of temperate and tropical rainforest tree species: photosynthetic responses to growth temperature. Oecologia **133**(2): 112-119.

Decker, K., Wang, D., Waite, C., and Scherbatskoy, T. 2003. Snow removal and ambient air temperature effects on forest soil temperatures in northern Vermont. Soil Science Society of America Journal **67**(4): 1234-1242.

DeHayes, D.H. 1992. Winter injury and developmental cold tolerance of red spruce. *In* The Ecology and Decline of Red Spruce in the Eastern United States. *Edited by* C. Eagar and M.B. Adams. Springer-Verlag New York Inc., New York, NY, USA. pp. 295-337.

DeHayes, D.H., Schaberg, P.G., Hawley, G.J., Borer, C.H., Cumming, J.R., and Strimbeck, G.R. 1997. Physiological implications of seasonal variation in membrane-associated calcium in red spruce mesophyll cells. Tree Physiology **17**(11): 687-695. doi: 10.1093/treephys/17.11.687.

DeHayes, D.H., Schaberg, P.G., Hawley, G.J., and Strimbeck, G.R. 1999. Acid rain impacts on calcium nutrition and forest health. BioScience **49**(10): 789-800.

DeHayes, D.H., Schaberg, P.G., and Strimbeck, G.R. 2001. Red spruce cold hardiness and freezing injury susceptibility. *In* Conifer Cold Hardiness. *Edited by* F. Bigras. Kluwer Academic Publishers, Dordrecht, the Netherlands.

DeHayes, D.H., Waite, C.E., Ingle, M.A., and Williams, M.W. 1990. Winter injury susceptibility and cold tolerance of current and year-old needles of red spruce trees from several provenances. Forest Science **36**: 982-994.

Dixon, R.K., Solomon, A.M., Brown, S., Houghton, R.A., Trexier, M.C., and Wisniewski, J. 1994. Carbon pools and flux of global forest ecosystems. Science **263**(5144): 185-190. doi: 10.1126/science.263.5144.185.

Doak, D.F., and Morris, W.F. 2010. Demographic compensation and tipping points in climate-induced range shifts. Nature **467**(7318): 959-962.

Driscoll, C.T., Lawrence, G.B., Bulger, A.J., Butler, T.J., Cronan, C.S., Eagar, C., Lambert, K.F., Likens, G.E., Stoddard, J.L., and Weathers, K.C. 2001. Acidic deposition in the northeastern United States: sources and inputs, ecosystem effects, and management strategies. BioScience **51**(3): 180-198. doi: 10.1641/0006-3568(2001)051[0180:aditnu]2.0.co;2.

Duchesne, L., Ouimet, R., and Morneau, C. 2003. Assessment of sugar maple health based on basal area growth pattern. Canadian Journal of Forest Research **33**(11): 2074-2080. doi: 10.1139/x03-141.

Dupigny-Giroux, L.-A. 2002. Climate variability and socioeconomic consequences of Vermont's natural hazards: a historical perspective. Vermont History **70**: 19-39.

Durán, J., Morse, J.L., Groffman, P.M., Campbell, J.L., Christenson, L.M., Driscoll, C.T., Fahey, T.J., Fisk, M.C., Mitchell, M.J., and Templer, P.H. 2014. Winter climate change affects growing-

season soil microbial biomass and activity in northern hardwood forests. Global Change Biology: n/a-n/a. doi: 10.1111/gcb.12624.

Eagar, C., and Adams, M.B. 1992. Ecology and decline of red spruce in the eastern United States. Springer-Verlag, New York.

Eamus, D., Leith, I., and Fowler, D. 1989. Water relations of red spruce seedlings treated with acid mist. Tree Physiology **5**(3): 387-397. doi: 10.1093/treephys/5.3.387.

Engel, B.J. 2013. Investigating the relationship between modeled calcium depletion and red spruce growth and response to environmental stress. MS Thesis, the University of Vermont. *In* Rubenstein School of Environment and Natural Resources.

Engel, B.J., Schaberg, P.G., Hawley, G.J., Rayback, S.A., Pontius, J., Kosiba, A.M., and Miller, E.K. 2016. Assessing relationships between red spruce radial growth and pollution critical load exceedence values. Forest Ecology and Management **359**: 83-91.

Fahey, T.J., Woodbury, P.B., Battles, J.J., Goodale, C.L., Hamburg, S.P., Ollinger, S.V., and Woodall, C.W. 2010. Forest carbon storage: ecology, management, and policy. Frontiers in Ecology and the Environment **8**(5): 245-252.

Field, C.B., Behrenfeld, M.J., Randerson, J.T., and Falkowski, P. 1998. Primary production of the biosphere: integrating terrestrial and oceanic components. Science **281**(5374): 237-240.

Fitzhugh, R., Driscoll, C., Groffman, P., Tierney, G., Fahey, T., and Hardy, J. 2001. Effects of soil freezing disturbance on soil solution nitrogen, phosphorus, and carbon chemistry in a northern hardwood ecosystem. Biogeochemistry **56**(2): 215-238. doi: 10.1023/A:1013076609950.

Fitzhugh, R.D., Driscoll, C.T., Groffman, P.M., Tierney, G.L., Fahey, T.J., and Hardy, J.P. 2003. Soil freezing and the acid-base chemistry of soil solutions in a northern hardwood forest. Soil Science Society of America Journal **67**(6): 1897-1908.

Flannigan, M.D., Stocks, B.J., and Wotton, B.M. 2000. Climate change and forest fires. Science of The Total Environment **262**(3): 221-229. doi: http://dx.doi.org/10.1016/S0048-9697(00)00524-6.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., and Snyder, P.K. 2005. Global Consequences of Land Use. Science **309**(5734): 570-574. doi: 10.1126/science.1111772.

Foley, J.A., Levis, S., Prentice, I.C., Pollard, D., and Thompson, S.L. 1998. Coupling dynamic models of climate and vegetation. Global Change Biology **4**(5): 561-579. doi: 10.1046/j.1365-2486.1998.t01-1-00168.x.

Foster, D.R. 1992. Land-Use History (1730-1990) and Vegetation Dynamics in Central New England, USA. Journal of Ecology **80**(4): 753-771.

Foster, J.R., and D'Amato, A.W. 2015. Montane forest ecotones moved downslope in northeastern US in spite of warming between 1984 and 2011. Global Change Biology: 4497-4507. doi: 10.1111/gcb.13046.

Fowler, D., Cape, J.N., Deans, J.D., Leith, I.D., Murray, M.B., Smith, R.I., Sheppard, L.J., and Unsworth, M.H. 1989. Effects of acid mist on the frost hardiness of red spruce seedlings. New Phytologist **113**(3): 321-335.

Fraver, S., White, A.S., and Seymour, R.S. 2009. Natural disturbance in an old-growth landscape of northern Maine, USA. Journal of Ecology **97**(2): 289-298. doi: 10.1111/j.1365-2745.2008.01474.x.

Friedman, J.H. 1984. A variable span smoother. DTIC Document.

Fritts, H.C. 1976. Tree Rings and Climate. Academic Press, New York.

Fromm, J. 2010. Wood formation of trees in relation to potassium and calcium nutrition. Tree Physiology. doi: 10.1093/treephys/tpq024.

Frumhoff, P.C., McCarthy, J.J., Melillo, J.M., Moser, S.C., and Wuebbles, D.J. 2007. Confronting climate change in the US Northeast. A report of the northeast climate impacts assessment. Union of Concerned Scientists, Cambridge, Massachusetts.

Gavin, D.G., and Peart, D.R. 1993. Effects of beech bark disease on the growth of American beech (Fagus grandifolia). Canadian Journal of Forest Research **23**(8): 1566-1575. doi: 10.1139/x93-197.

Girardin, M.P., Bouriaud, O., Hogg, E.H., Kurz, W., Zimmermann, N.E., Metsaranta, J.M., de Jong, R., Frank, D.C., Esper, J., Büntgen, U., Guo, X.J., and Bhatti, J. 2016. No growth stimulation of Canada's boreal forest under half-century of combined warming and CO2 fertilization. Proceedings of the National Academy of Sciences **113.52**: E8406-E8414. doi: 10.1073/pnas.1610156113.

Goulden, M.L., Munger, J.W., Fan, S.-M., Daube, B.C., and Wofsy, S.C. 1996. Exchange of carbon dioxide by a deciduous forest: response to interannual climate variability. Science **271**(5255).

Greaver, T.L., Sullivan, T.J., Herrick, J.D., Barber, M.C., Baron, J.S., Cosby, B.J., Deerhake, M.E., Dennis, R.L., Dubois, J.-J.B., Goodale, C.L., Herlihy, A.T., Lawrence, G.B., Liu, L., Lynch, J.A., and Novak, K.J. 2012. Ecological effects of nitrogen and sulfur air pollution in the US: what do we know? Frontiers in Ecology and the Environment **10**(7): 365-372. doi: 10.1890/110049.

Groffman, P., Driscoll, C., Fahey, T., Hardy, J., Fitzhugh, R., and Tierney, G. 2001. Colder soils in a warmer world: A snow manipulation study in a northern hardwood forest ecosystem. Biogeochemistry **56**(2): 135-150. doi: 10.1023/A:1013039830323.

Groffman, P., Hardy, J., Fisk, M., Fahey, T., and Driscoll, C. 2009. Climate Variation and Soil Carbon and Nitrogen Cycling Processes in a Northern Hardwood Forest. Ecosystems **12**(6): 927-943. doi: 10.1007/s10021-009-9268-y.

Groffman, P.M., Rustad, L.E., Templer, P.H., Campbell, J.L., Christenson, L.M., Lany, N.K., Socci, A.M., Vadeboncoeur, M.A., Schaberg, P.G., Wilson, G.F., Driscoll, C.T., Fahey, T.J., Fisk, M.C., Goodale, C.L., Green, M.B., Hamburg, S.P., Johnson, C.E., Mitchell, M.J., Morse, J.L., Pardo, L.H., and Rodenhouse, N.L. 2012. Long-term integrated studies show complex and surprising effects of climate change in the northern hardwood forest. Bioscience **62**: 1056-1066.

Groisman, P.Y., Knight, R.W., Zolina, O.G., and Pielke, R. 2013. Recent trends in regional and global intense precipitation patterns. Climate vulnerability **5**: 25-55.

Guilbert, J., Beckage, B., Winter, J.M., Horton, R.M., Perkins, T., and Bomblies, A. 2014. Impacts of projected climate change over the Lake Champlain basin in Vermont. Journal of Applied Meteorology and Climatology **53**(8): 1861-1875. doi: 10.1175/JAMC-D-13-0338.1.

Gurney, K.M., Schaberg, P.G., Hawley, G.J., and Shane, J.B. 2011. Inadequate Cold Tolerance as a Possible Limitation to American Chestnut Restoration in the Northeastern United States. Restor. Ecol. **19**(1): 55-63. doi: 10.1111/j.1526-100X.2009.00544.x.

Halman, J.M., Schaberg, P.G., Hawley, G.J., and Eagar, C. 2008. Calcium addition at the Hubbard Brook Experimental Forest increases sugar storage, antioxidant activity and cold tolerance in native red spruce (*Picea rubens*). Tree Physiology **28**(6): 855-862. doi: 10.1093/treephys/28.6.855.

Halman, J.M., Schaberg, P.G., Hawley, G.J., and Hansen, C.F. 2011. Potential role of soil calcium in recovery of paper birch following ice storm injury in Vermont, USA. Forest Ecology and Management **261**: 1539-1545.

Hamburg, S.P., Yanai, R.D., Arthur, M.A., Blum, J.D., and Siccama, T.G. 2003. Biotic control of calcium cycling in northern hardwood forests: acid rain and aging forests. Ecosystems **6**(4): 399-406.

Hansen, C.F. 2015. LiDAR remote sensing of forest canopy structure and integrity: Trophic interactions among forest health, productivity, insects and birds. MS Thesis, the University of Vermont.

173

Hawley, G.J., and DeHayes, D.H. 1994. Genetic diversity and population structure of red spruce (Picea rubens). Canadian Journal of Botany **72**(12): 1778-1786. doi: 10.1139/b94-219.

Hayhoe, K., Wake, C., Anderson, B., Liang, X.-Z., Maurer, E., Zhu, J., Bradbury, J., DeGaetano, A., Stoner, A., and Wuebbles, D. 2008. Regional climate change projections for the Northeast USA. Mitigation and Adaptation Strategies for Global Change **13**(5-6): 425-436. doi: 10.1007/s11027-007-9133-2.

Hayhoe, K., Wake, C., Huntington, T., Luo, L., Schwartz, M., Sheffield, J., Wood, E., Anderson, B., Bradbury, J., DeGaetano, A., Troy, T., and Wolfe, D. 2007. Past and future changes in climate and hydrological indicators in the US Northeast. Climate Dynamics **28**: 381-407.

Hedin, L.O., Granat, L., Likens, G.E., Buishan, T.A., Galloway, J.N., Butler, T.J., and Rodhe, H. 1994. Steep declines in atmospheric base cations in regions of Europe and North America. Nature **367**: 351-354.

Heide, O. 2003. High autumn temperature delays spring bud burst in boreal trees, counterbalancing the effect of climatic warming. Tree Physiology **23**(13): 931-936.

Hodgkins, G.A., and Dudley, R.W. 2006. Changes in late-winter snowpack depth, water equivalent, and density in Maine, 1926–2004. Hydrological Processes **20**(4): 741-751.

Holmes, R.L. 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-ring Bulletin **43**: 69-78.

Hornbeck, J.W., Smith, R.B., and Federer, C.A. 1987. Growth decline in red spruce and balsam fir relative to natural processes. Water Air Soil Pollut **31**(1-2): 425-430. doi: 10.1007/BF00630860.

Hornbeck, J.W., and Smith, R.L. 1985. Documentation of red spruce growth decline. Canadian Journal of Forest Research **15**: 1199-1201.

Hufkens, K., Friedl, M.A., Keenan, T.F., Sonnentag, O., Bailey, A., O'Keefe, J., and Richardson, A.D. 2012. Ecological impacts of a widespread frost event following early spring leaf-out. Global Change Biology **18**(7): 2365-2377. doi: 10.1111/j.1365-2486.2012.02712.x.

Huggett, B.A., Schaberg, P.G., Hawley, G.J., and Eagar, C. 2007. Long-term calcium addition increases growth release, wound closure, and health of sugar maple (Acer saccharum) trees at the Hubbard Brook Experimental Forest. Canadian Journal of Forest Research **37**(9): 1692-1700. doi: 10.1139/X07-042.

Hunt, R.S. 1978. Poplar shoot blight. Forestry Canada, Forest Insect and Disease Survey, Forest Pest Leaflet 42. p. 3.

Huntington, T.G., Richardson, A.D., McGuire, K.J., and Hayhoe, K. 2009. Climate and hydrological changes in the northeastern United States: recent trends and implications for forested and aquatic ecosystemsThis article is one of a selection of papers from NE Forests 2100: A Synthesis of Climate Change Impacts on Forests of the Northeastern US and Eastern Canada. Canadian Journal of Forest Research **39**(2): 199-212. doi: 10.1139/X08-116.

IPCC. 2014. Executive summary of the Intergovernmental Panel on Climate Change.

Iverson, L.R., Prasad, A.M., Matthews, S.N., and Peters, M. 2008. Estimating potential habitat for 134 eastern US tree species under six climate scenarios. Forest Ecology and Management **254**(3): 390-406.

Jacobson, J.S., Heller, L.I., Yamada, K.E., Osmeloski, J.F., Bethard, T., and Lassoie, J.P. 1990. Foliar injury and growth response of red spruce to sulfate and nitrate acidic mist. Canadian Journal of Forest Research **20**(1): 58-65. doi: 10.1139/x90-009.

Jarvis, P., and Linder, S. 2000. Botany: Constraints to growth of boreal forests. Nature **405**(6789): 904-905.

Johnson, A., Cook, E., and Siccama, T. 1988. Climate and red spruce growth and decline in the northern Appalachians. Proceedings of the National Academy of Sciences **85**(15): 5369-5373.

Johnson, A.H., Friedland, A.J., and Dushoff, J.G. 1986. Recent and historic red spruce mortality: Evidence of climatic influencee. Water, Air, & Soil Pollution **30**(1): 319-330. doi: 10.1007/bf00305203.

Johnson, A.H., and Siccama, T.G. 1983. Acid deposition and forest decline. Environmental Science & Technology **17**(7): 294A-305A. doi: 10.1021/es00113a001.

Johnson, D.W., and Fernandez, I.J. 1992. Soil-mediated effects of atmospheric deposition on eastern U.S. spruce-fir forests. Ecological Studies: Analysis and Synthesis **96**: 235-270.

Johnson, S.E., and Abrams, M.D. 2009. Age class, longevity and growth rate relationships: protracted growth increases in old trees in the eastern United States. Tree Physiology **29**(11): 1317-1328. doi: 10.1093/treephys/tpp068.

Joslin, J., and Wolfe, M. 1992. Red spruce soil solution chemistry and root distribution across a cloud water deposition gradient. Canadian Journal of Forest Research **22**(6): 893-904.

Juice, S.M., Fahey, T.J., Siccama, T.G., Driscoll, C.T., Denny, E.G., Eagar, C., Cleavitt, N.L., Minocha, R., and Richardson, A.D. 2006. Response of sugar maple to calcium addition to northern hardwood forest. Ecology **87**(5): 1267-1280.

Kelly, A.E., and Goulden, M.L. 2008. Rapid shifts in plant distribution with recent climate change. Proceedings of the National Academy of Sciences **105**(33): 11823-11826.

Kenefic, L. 2015. Red spruce tree cores from the Penobscott Experimental Forest, Maine. USDA Forest Service.

Kimball, B.A., Conley, M.M., Wang, S., Lin, X., Luo, C., Morgan, J., and Smith, D. 2008. Infrared heater arrays for warming ecosystem field plots. Global Change Biology **14**(2): 309-320.

Kobe, R.K., Likens, G.E., and Eagar, C. 2002. Tree seedling growth and mortality responses to manipulations of calcium and aluminum in a northern hardwood forest. Canadian Journal of Forest Research **32**(6): 954-966.

Körner, C. 2003. Carbon limitation in trees. Journal of Ecology **91**(1): 4-17. doi: 10.1046/j.1365-2745.2003.00742.x.

Körner, C., Asshoff, R., Bignucolo, O., Hättenschwiler, S., Keel, S.G., Peláez-Riedl, S., Pepin, S., Siegwolf, R.T.W., and Zotz, G. 2005. Carbon flux and growth in mature deciduous forest trees exposed to elevated CO_2. Science **309**(5739): 1360-1362. doi: 10.1126/science.1113977.

Kosiba, A.M., Schaberg, P.G., Hawley, G.J., and Hansen, C.F. 2013. Quantifying the legacy of foliar winter injury on woody aboveground carbon sequestration of red spruce trees. Forest Ecology and Management **302**: 363-371.

Kosiba, A.M., Schaberg, P.G., Hawley, G.J., and Rayback, S.A. 2014. Using dendroecological techniques to interpret the response of trees to environmental change at Vermont Monitoring Cooperative's Mount Mansfield study site. Vermont Monitoring Cooperative.

Kosiba, A.M., Schaberg, P.G., Rayback, S.A., and Hawley, G.J. In press. Comparative growth trends of five northern hardwood and montane tree species reveal divergent trajectories and response to climate. Canadian Journal of Forest Research.

Kunkel, K.E., Bromirski, P.D., Brooks, H.E., Cavazos, T., Douglas, A.V., Easterling, D.R., Emanuel, K.A., Groisman, P.Y., Holland, G.J., Knutson, T.R., Kossin, J.P., Komar, P.D., Levinson, D.H., and Smith, R.L. 2008. Observed changes in weather and climate extremes. *In* Weather and Climate Extremes in a Changing Climate: Regions of Focus: North America, Hawaii, Caribbean, and U.S. Pacific Islands. *Edited by* T.R. Karl and G.A. Meehl and C.D. Miller and S.J. Hassol and A.M. Waple and W.L. Murray. Synthesis and Assessment Product 3.3. U.S. Climate Change Science Program Washington, DC. pp. 35-80.

Kunkel, K.E., Stevens, L.E., Stevens, S.E., Sun, L., Janssen, E., Wuebbles, D., Hilberg, S., Timlin, M., Stoecker, L., and Westcott, N. 2013. Regional climate trends and scenarios for the US national

climate assessment. Part 1. Climate of the Northeast U.S. NOAA Technical Report NESDIS 142-1.

Lawrence, G.B., Hazlett, P.W., Fernandez, I.J., Ouimet, R., Bailey, S.W., Shortle, W.C., Smith, K.T., and Antidormi, M.R. 2015. Declining Acidic Deposition Begins Reversal of Forest-Soil Acidification in the Northeastern U.S. and Eastern Canada. Environmental Science & Technology. doi: 10.1021/acs.est.5b02904.

Lawrence, G.B., Shortle, W.C., David, M.B., Smith, K.T., Warby, R.A.F., and Lapenis, A.G. 2012. Early Indications of Soil Recovery from Acidic Deposition in U.S. Red Spruce Forests. Soil Science Society of America Journal **76**(4): 1407-1417. doi: 10.2136/sssaj2011.0415.

Lazarus, B.E., Schaberg, P.G., DeHayes, D.H., and Hawley, G.J. 2004. Severe red spruce winter injury in 2003 creates unusual ecological event in the northeastern United States. Canadian journal of forest research **34**(8): 1784-1788.

Lazarus, B.E., Schaberg, P.G., Hawley, G.J., and DeHayes, D.H. 2006. Landscape-scale spatial patterns of winter injury to red spruce foliage in a year of heavy region-wide injury. Canadian Journal of Forest Research **36**(1): 142-152. doi: 10.1139/x05-236.

Leakey, A.D.B., Ainsworth, E.A., Bernacchi, C.J., Rogers, A., Long, S.P., and Ort, D.R. 2009. Elevated CO2 effects on plant carbon, nitrogen, and water relations: six important lessons from FACE. Journal of Experimental Botany **60**(10): 2859-2876. doi: 10.1093/jxb/erp096.

LeBlanc, D.C. 1992. Spatial and temporal variation in the prevalence of growth decline in red spruce populations of the northeastern United States. Can. J. For. Res. **22**: 1351–1363.

Likens, G. 2010. Chemistry of Steamwater at HBEF WS-1. http://www.hubbardbrook.org/data/dataset.php?id=3 [Acessed 10/14/14].

Likens, G.E., and Bormann, F.H. 1974. Acid rain: a serious regional environmental problem. Science **184**(4142): 1176-1179. doi: 10.1126/science.184.4142.1176.

Likens, G.E., Driscoll, C.T., and Buso, D.C. 1996. Long-term effects of acid rain: response and recovery of a forest ecosystem. Science **272**(5259): 244-246. doi: 10.1126/science.272.5259.244.

Long, R.P., Horsley, S.B., Hallett, R.A., and Bailey, S.W. 2009. Sugar maple growth in relation to nutrition and stress in the northeastern United States. Ecological Applications **19**(6): 1454-1466. doi: 10.1890/08-1535.1.

Lorimer, C.G., and Frelich, L.E. 1989. A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. Canadian Journal of Forest Research **19**(5): 651-663.

Lovett, G.M., Canham, C.D., Arthur, M.A., Weathers, K.C., and Fitzhugh, R.D. 2006. Forest Ecosystem Responses to Exotic Pests and Pathogens in Eastern North America. BioScience **56**(5): 395-405. doi: 10.1641/0006-3568(2006)056[0395:FERTEP]2.0.CO;2.

Luo, Y. 2007. Terrestrial carbon-cycle feedback to climate warming. Annual Review of Ecology, Evolution, and Systematics **38**: 683-712. doi: 10.2307/30033876.

Marschner, H. 2002. Mineral Nutrition of Higher Plants. 2nd ed. Academic Press, Boston.

Martín-Benito, D., Cherubini, P., del Río, M., and Cañellas, I. 2008. Growth response to climate and drought in Pinus nigra Arn. trees of different crown classes. Trees **22**(3): 363-373. doi: 10.1007/s00468-007-0191-6.

Martinez-Vilalta, J., Lopez, B.C., Adell, N., Badiella, L., and Ninyerola, M. 2008. Twentieth century increase of Scots pine radial growth in NE Spain shows strong climate interactions. Global Change Biology **14**(12): 2868-2881. doi: 10.1111/j.1365-2486.2008.01685.x.

McLaughlin, S.B., Andersen, C.P., Hanson, P.J., Tjoelker, M.G., and Roy, W.K. 1991. Increased dark respiration and calcium deficiency of red spruce in relation to acidic deposition at high-elevation southern Appalachian Mountain sites. Canadian Journal of Forest Research **21**(8): 1234-1244. doi: 10.1139/x91-172.

McLaughlin, S.B., Downing, D.J., Blasing, T.J., Cook, E.R., and Adams, H.S. 1987. An analysis of climate and competition as contributors to decline of red spruce in high elevation Appalachian forests of the Eastern United states. Oecologia **72**(4): 487-501. doi: 10.1007/BF00378973.

McLaughlin, S.B., and Wimmer, R. 1999. Tansley Review No. 104: Calcium physiology and terrestrial ecosystem processes. New Phytologist **142**(3): 373-417. doi: 10.1046/j.1469-8137.1999.00420.x.

McMahon, S.M., Parker, G.G., and Miller, D.R. 2010. Evidence for a recent increase in forest growth. Proceedings of the National Academy of Sciences **107**(8): 3611-3615.

Meehl, G.A., and Tebaldi, C. 2004. More intense, more frequent, and longer lasting heat waves in the 21st Century. Science **305**(5686): 994-997. doi: 10.1126/science.1098704.

Melillo, J.M., Butler, S., Johnson, J., Mohan, J., Steudler, P., Lux, H., Burrows, E., Bowles, F., Smith, R., Scott, L., Vario, C., Hill, T., Burton, A., Zhou, Y.-M., and Tang, J. 2011. Soil warming, carbon–nitrogen interactions, and forest carbon budgets. Proceedings of the National Academy of Sciences **108**(23): 9508-9512. doi: 10.1073/pnas.1018189108.

Menzel, A., and Fabian, P. 1999. Growing season extended in Europe. Nature **397**(6721): 659-659.

Michaelian, M., Hogg, E.H., Hall, R.J., and Arsenault, E. 2011. Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest. Global Change Biology **17**(6): 2084-2094.

Miller, A.C., Woeste, K.E., Anagnostakis, S.L., and Jacobs, D.F. 2014. Exploration of a rare population of Chinese chestnut in North America: stand dynamics, health and genetic relationships. AoB Plants 6: plu065.

Minocha, R., Long, S., Thangavel, P., Minocha, S.C., Eagar, C., and Driscoll, C.T. 2010. Elevation dependent sensitivity of northern hardwoods to Ca addition at Hubbard Brook Experimental Forest, NH, USA. Forest Ecology and Management **260**(12): 2115-2124. doi: http://dx.doi.org/10.1016/j.foreco.2010.09.002.

Myneni, R.B., Keeling, C., Tucker, C., Asrar, G., and Nemani, R. 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. Nature **386**(6626): 698-702.

NAPAP. 2005. National Acid Precipitation Assessment Program Report to Congress National Acid Precipitation Assessment Program, Washington, D.C.

National Atmospheric Deposition Program. 2016. NADP/NTN Monitoring. US Geological Survey [accessed 4 May 2016].

National Drought Mitigation Center. 2012. SPEI. University of Nebraska, Lincoln. http://droughtatlas.unl.edu/About.aspx [acessed 15 March 2015].

National Drought Mitigation Center. 2014. Drought Risk Atlas. http://droughtatlas.unl.edu/Data.aspx [Accessed 10/10/13].

NOAA Earth System Research Laboratory Global Monitoring Division. 2016. Monthly Average Mauna Loa CO_2. http://www.esrl.noaa.gov/gmd/ccgg/trends/ [accessed 6 October 2016].

NOAA National Centers for Environmental Information. 2016. Monthly global summaries by station http://www.ncdc.noaa.gov/cdo-web/search [accessed 18 August 2016].

NOAA National Climatic Data Center. 2010. State of the Climate: National Overview. Available from http://www.ncdc.noaa.gov/sotc/national [accessed December 15, 2011.

NOAA National Weather Service. 2014. Monthly total growing degree days for Burlington, VT. http://www.weather.gov/btv/climo_gdd [Accessed 4/23/14].

NOAA National Weather Service. 2017. Temperature records for Burlington International Airport, https://www.ncdc.noaa.gov/. [Accessed 1/28/17].

NOAA Regional Climate Centers. 2016. DROUGHT-ACIS: Single station temperature and precipitation data http://drought.rcc-acis.org/ [acessed 14 August 2016].

Northeast Climate Impacts Assessment Synthesis Team. 2007. Confronting climate change in the U.S. Northeast. A report of the Northeast Climate Impacts Assessment.

Ollinger, S.V., Aber, J.D., Lovett, G.M., Millham, S.E., Lathrop, R.G., and Ellis, J.M. 1993. A spatial model of atmospheric deposition for the northeastern US. Ecological Applications **3**(3): 459-472.

Oren, R., Ellsworth, D.S., Johnsen, K.H., Phillips, N., Ewers, B.E., Maier, C., Schäfer, K.V., McCarthy, H., Hendrey, G., and McNulty, S.G. 2001. Soil fertility limits carbon sequestration by forest ecosystems in a CO2-enriched atmosphere. Nature **411**(6836): 469-472.

Pallardy, S.G. 2010. Physiology of woody plants. Academic Press.

Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S., and Hayes, D. 2011. A Large and Persistent Carbon Sink in the World's Forests. Science **333**(6045): 988-993. doi: 10.1126/science.1201609.

Park, B.B., Yanai, R.D., Fahey, T.J., Bailey, S.W., Siccama, T.G., Shanley, J.B., and Cleavitt, N.L. 2008. Fine Root Dynamics and Forest Production Across a Calcium Gradient in Northern Hardwood and Conifer Ecosystems. Ecosystems **11**(2): 325-341. doi: 10.1007/s10021-008-9126-3.

Pederson, N., Bell, A.R., Cook, E.R., Lall, U., Devineni, N., Seager, R., Eggleston, K., and Vranes, K.J. 2013. Is an Epic Pluvial Masking the Water Insecurity of the Greater New York City Region? Journal of Climate. doi: 10.1175/jcli-d-11-00723.1.

Peltola, H., Kilpeläinen, A., and Kellomäki, S. 2002. Diameter growth of Scots pine (Pinus sylvestris) trees grown at elevated temperature and carbon dioxide concentration under boreal conditions. Tree physiology **22**(14): 963-972.

Persson, H., Majdi, H., and Clemensson-Lindell, A. 1995. Effects of Acid Deposition on Tree Roots. Ecological Bulletins(44): 158-167.

Peters, G.P., Andrew, R.M., Boden, T., Canadell, J.G., Ciais, P., Le Quéré, C., Marland, G., Raupach, M.R., and Wilson, C. 2013. The challenge to keep global warming below 2 C. Nature Climate Change **3**(1): 4-6.

Pontius, J., and Halman, J.M. 2012. Red spruce tree cores from the Bartlett Experimental Forest, NH. University of Vermont.

Pregitzer, K.S., King, J.S., Burton, A.J., and Brown, S.E. 2000. Responses of tree fine roots to temperature. New Phytologist **147**(1): 105-115.

PRISM Climate Group. 2004. Available from http://prism.oregonstate.edu/ [accessed 5/10/14 2014].

R Development Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Radoglou, K., and Jarvis, P. 1990. Effects of CO2 enrichment on four poplar clones. I. Growth and leaf anatomy. Annals of Botany **65**(6): 617-626.

Rasband, W.S. 2016. ImageJ, U. S. National Institutes of Health, Bethesda, Maryland, USA, http://imagej.nih.gov/ij/.

Rayback, S.A. 2012. Red spruce tree cores from sites in Vermont, New Hampshire, and Maine. University of Vermont.

Reich, P.B., Stroo, H.F., Schoettle, A.W., and Amundson, R.G. 1986. Acid rain and ozone influence mycorrhizal infection in tree seedlings. Journal of the Air Pollution Control Association **36**(6): 724-726.

Rennenberg, H., Loreto, F., Polle, A., Brilli, F., Fares, S., Beniwal, R., and Gessler, A. 2006. Physiological responses of forest trees to heat and drought. Plant Biology **8**(05): 556-571.

Repo, T., Hanninen, H., and Kellomaki, S. 1996. The effects of long-term elevation of air temperature and CO$_2$ on the frost hardiness of Scots pine. Plant, Cell & Environment **19**(2): 209-216. doi: 10.1111/j.1365-3040.1996.tb00242.x.

Rhoads, A.G., Hamburg, S.P., Fahey, T.J., Siccama, T.G., Hane, E.N., Battles, J., Cogbill, C., Randall, J., and Wilson, G. 2002. Effects of an intense ice storm on the structure of a northern hardwood forest. Canadian Journal of Forest Research **32**(10): 1763-1775. doi: 10.1139/x02-089.

Ricard, J.A., Tobiasson, W., and Greatorex, A. 1976. The field assembled frost gage. United States Army Cold Regions Research and Engineering Laboratory (CRREL), Hanover, NH.

Richardson, A.D., Bailey, A.S., Denny, E.G., Martin, C.W., and O'Keefe, J. 2006. Phenology of a northern hardwood forest canopy. Global Change Biology **12**(7): 1174-1188. doi: 10.1111/j.1365-2486.2006.01164.x.

Saielli, T.M., Schaberg, P.G., Hawley, G.J., Halman, J.M., and Gurney, K.M. 2012. Nut cold hardiness as a factor influencing the restoration of American chestnut in northern latitudes and high elevations. Canadian Journal of Forest Research **42**(5): 849-857. doi: 10.1139/x2012-033.

Saielli, T.M., Schaberg, P.G., Hawley, G.J., Halman, J.M., and Gurney, K.M. 2014. Genetics and silvicultural treatments influence the growth and shoot winter injury of american chestnut in Vermont. *In*. Society of American Foresters.

Salzer, M.W., Hughes, M.K., Bunn, A.G., and Kipfmueller, K.F. 2009. Recent unprecedented tree-ring growth in bristlecone pine at the highest elevations and possible causes. Proceedings of the National Academy of Sciences **106**(48): 20348-20353. doi: 10.1073/pnas.0903029106.

Saurer, M., Spahni, R., Frank, D.C., Joos, F., Leuenberger, M., Loader, N.J., McCarroll, D., Gagen, M., Poulter, B., Siegwolf, R.T.W., Andreu-Hayles, L., Boettger, T., Dorado Liñán, I., Fairchild, I.J., Friedrich, M., Gutierrez, E., Haupt, M., Hilasvuori, E., Heinrich, I., Helle, G., Grudd, H., Jalkanen, R., Levanič, T., Linderholm, H.W., Robertson, I., Sonninen, E., Treydte, K., Waterhouse, J.S., Woodley, E.J., Wynn, P.M., and Young, G.H.F. 2014. Spatial variability and temporal trends in water-use efficiency of European forests. Global Change Biology: n/a-n/a. doi: 10.1111/gcb.12717.

Saxe, H., Cannell, M.G.R., Johnsen, Ø., Ryan, M.G., and Vourlitis, G. 2001. Tree and forest functioning in response to global warming. New Phytologist **149**(3): 369-399. doi: 10.1046/j.1469-8137.2001.00057.x.

Saxe, H., Ellsworth, D.S., and Heath, J. 1998. Tree and forest functioning in an enriched CO2 atmosphere. New Phytologist **139**(3): 395-436.

Schaberg, P.G., and DeHayes, D.H. 2000. Physiological and environmental causes of freezing injury to red spruce. *In* Responses of Northern U.S. Forests to Environmental Change. *Edited by* R.A. Mickler and R.A. Birdsey and J.L. Hom. Springer-Verlag, New York. pp. 181-227.

Schaberg, P.G., DeHayes, D.H., and Hawley, G.J. 2001. Anthropogenic Calcium Depletion: A Unique Threat to Forest Ecosystem Health? Ecosystem Health **7**(4): 214-228. doi: 10.1046/j.1526-0992.2001.01046.x.

Schaberg, P.G., DeHayes, D.H., Hawley, G.J., Strimbeck, G.R., Cumming, J., Murakami, P.F., and Borer, C.H. 2000. Acid mist, soil Ca and Al alter the mineral nutrition and physiology of red spruce. Tree Physiology **20**: 73-85.

Schaberg, P.G., Lazarus, B.E., Hawley, G.J., Halman, J.M., Borer, C.H., and Hansen, C.F. 2011. Assessment of weather-associated causes of red spruce winter injury and consequences to aboveground carbon sequestration. Canadian journal of forest research **41**(2): 359-369.

Schaberg, P.G., Shane, J.B., Cali, P.F., Donnelly, J.R., and Strimbeck, G.R. 1998. Photosynthetic capacity of red spruce during winter. Tree Physiology **18**(4): 271-276. doi: 10.1093/treephys/18.4.271.

Schaberg, P.G., Tilley, J.W., Hawley, G.J., DeHayes, D.H., and Bailey, S.W. 2006. Associations of calcium and aluminum with the growth and health of sugar maple trees in Vermont. Forest Ecology and Management **223**(1–3): 159-169. doi: http://dx.doi.org/10.1016/j.foreco.2005.10.067.

Schaberg, P.G., Wilkinson, R.C., Shane, J.B., Donnelly, J.R., and Cali, P.F. 1995. Winter photosynthesis of red spruce from three Vermont seed sources. Tree Physiology **15**: 345-350.

Schwartz, M.D., and Reiter, B.E. 2000. Changes in north American spring. International Journal of climatology **20**(8): 929-932.

Schwarz, P.A., Fahey, T.J., and Dawson, T.E. 1997. Seasonal air and soil temperature effects on photosynthesis in red spruce (*Picea rubens*) saplings. Tree Physiology **17**(3): 187-194. doi: 10.1093/treephys/17.3.187.

Scott, J.T., Siccama, T.G., Johnson, A.H., and Breisch, A.R. 1984. Decline of Red Spruce in the Adirondacks, New York. Bulletin of the Torrey Botanical Club **111**(4): 438-444.

Sheppard, L.J. 1994. Causal mechanisms by which sulphate, nitrate and acidity influence frost hardiness in red spruce: review and hypothesis. New Phytologist **127**(1): 69-82.

Shortle, W.C., Smith, K.T., Minocha, R., Lawrence, G.B., and David, M.B. 1997. Acidic deposition, cation mobilization, and biochemical indicators of stress in healthy red spruce. Journal of Envrionmental Quality **26**: 871-876.

Siccama, T.G. 1971. Presettlement and Present Forest Vegetation in Northern Vermont with Special Reference to Chittenden County. American Midland Naturalist **85**(1): 153-172.

Siccama, T.G., Bliss, M., and Vogelmann, H.W. 1982. Decline of Red Spruce in the Green Mountains of Vermont. Bulletin of the Torrey Botanical Club **109**(2): 162-168. doi: 10.2307/2996256.

Silva, L.C.R., and Anand, M. 2013. Probing for the influence of atmospheric CO2 and climate change on forest ecosystems across biomes. Global Ecology and Biogeography **22**(1): 83-92. doi: 10.1111/j.1466-8238.2012.00783.x.

Silva, L.C.R., Anand, M., and Leithead, M.D. 2010. Recent widespread tree growth decline despite increasing atmospheric CO_2. PLoS ONE **5**(7): e11543. doi: 10.1371/journal.pone.0011543.

Soil Survey Staff. 2015. Natural Resources Conservation Service, United States Department of Agriculture. Web Soil Survey. http://websoilsurvey.nrcs.usda.gov/ [Accessed 08/15/2015].

Soule, P.T., and Knapp, P.A. 2006. Radial growth rate increases in naturally occurring ponderosa pine trees: a late-20th century CO2 fertilization effect? The New phytologist **171**(2): 379-390. doi: 10.1111/j.1469-8137.2006.01746.x.

Speer, J.H. 2010. Fundamentals of Tree-Ring Research. University of Arizona Press.

Stokes, M., and Smiley, T. 1996. An Introduction to Tree-Ring Dating. University of Chicago Press.

Tjoelker, M., Reich, P., and Oleksyn, J. 1999. Changes in leaf nitrogen and carbohydrates underlie temperature and CO2 acclimation of dark respiration in five boreal tree species. Plant, Cell & Environment **22**(7): 767-778.

Tritton, L.M., Martin, C.W., Hornbeck, J.W., and Pierce, R.S. 1987. Biomass and nutrient removals from commercial thinning and whole-tree clearcutting of central hardwoods. Environmental Management **11**: 659-666.

U.S. Geological Survey. 2016. Digital Representations of Tree Species Range Maps from "Atlas of United States Trees" by Elbert L. Little, Jr. (and other publications). U.S. Department of the Interior.

USGCRP, Horton, R., Yohe, G., Easterling, W., Kates, R., Ruth, M., Sussman, E., Whelchel, A., Wolfe, D., and Lipschultz, F. 2014. Ch. 16: Northeast. Climate Change Impacts in the United States: The Third National Climate Assessment. *Edited by* J.M. Melillo and T.C. Richmond and G.W. Yohe. U.S. Global Change Research Program.

van der Maaten-Theunissen, M., and Bouriaud, O. 2012. Climate–growth relationships at different stem heights in silver fir and Norway spruce. Canadian Journal of Forest Research **42**(5): 958-969. doi: 10.1139/x2012-046.

van Doorn, N.S., Battles, J.J., Fahey, T.J., Siccama, T.G., and Schwarz, P.A. 2011. Links between biomass and tree demography in a northern hardwood forest: a decade of stability and change in Hubbard Brook Valley, New Hampshire. Canadian Journal of Forest Research **41**(7): 1369-1379. doi: 10.1139/x11-063.

Vann, D.R., Strimbeck, G.R., and Johnson, A.H. 1992. Effects of ambient levels of airborne chemicals on freezing resistance of red spruce foliage. Forest Ecology and Management **51**: 69-79.

Vermont Agency of Natural Resources Department of Forest Parks & Recreation. 2010. Forest insects and disease conditions in Vermont 2010. Waterbury, VT.

Vermont Agency of Natural Resources Department of Forest Parks & Recreation. 2013. Combined Master Dataset of Aerial Defoliation Surveys, 1985 to 2013 [downloaded July 25, 2014, http://www.uvm.edu/vmc/research/data.php?id=66]. Hosted by Vermont Monitoring Cooperative.

Vicente-Serrano, S.M., Beguería, S., and López-Moreno, J.I. 2010. A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. Journal of Climate **23**(7): 1696-1718.

Vitasse, Y., Delzon, S., Dufrêne, E., Pontailler, J.-Y., Louvet, J.-M., Kremer, A., and Michalet, R. 2009. Leaf phenology sensitivity to temperature in European trees: Do within-species populations exhibit similar responses? Agricultural and Forest Meteorology **149**(5): 735-744.

Wang, G.G., Knapp, B.O., Clark, S.L., and Mudder, B.T. 2013. The Silvics of *Castanea dentata* (Marsh.) Borkh., American chestnut, Fagaceae (Beech Family).

Wason, J.W., Dovciak, M., Bier, C.M., and Battles, J. 2012. Red spruce tree cores from Dial Mountain, NY. SUNY-EFS.

Wason, J.W., Dovciak, M., Bier, C.M., and Battles, J.J. 2014. Responses of tree populations to recent climatic trends in northeastern mountain forests: Thinking beyond range margins. *In* Ecological Society of America Annual Meeting, Sacramento, CA.

Way, D.A., and Oren, R. 2010. Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data. Tree Physiology **30**(6): 669-688.

Webb, A.A.R., McAinsh, M.R., Mansfield, T.A., and Hetherington, A.M. 1996. Carbon dioxide induces increases in guard cell cytosolic free calcium. The Plant Journal **9**(3): 297-304. doi: 10.1046/j.1365-313X.1996.09030297.x.

West, N.E., and Wein, R.W. 1971. A plant phenological index technique. BioScience **21**(4): 116-117.

West, P.W. 1980. Use of diameter increment and basal area increment in tree growth studies. Canadian Journal of Forest Research **10**(1): 71-77. doi: doi:10.1139/x80-012.

Westergaard, L., and Eriksen, E.N. 1997. Autumn temperature affects the induction of dormancy in first-year seedlings of acer platanoides L. Scandinavian Journal of Forest Research **12**(1): 11-16.

Westing, A.H. 1966. Sugar Maple Decline: An Evaluation. Economic Botany **20**(2): 196-212. doi: 10.2307/4252732.

Weverka, A.S. 2012. Remote sensing of productivity in northeastern forests. MS Thesis. Rubenstein School of Envrionent and Natural Resources, University of Vermont.

Whitney, G. 1994. From coastal wilderness to fruited plain: An environmental history of the eastern US. 1500 to present. Cambridge University, Cambridge, MA.

Wigley, T.M., Briffa, K.R., and Jones, P.D. 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. Bulletin of the American Meteorological Society **23**: 201-213.

Wofsy, S.C., Goulden, M.L., Munger, J.W., Fan, S.-M., Bakwin, P.S., Daube, B.C., Bassow, S.L., and Bazzaz, F.A. 1993. Net exchange of CO_2 in a mid-latitude forest. Science **260**(5112): 1314-1317. doi: 10.1126/science.260.5112.1314.

World Data Center for Paleoclimatology and NOAA Paleoclimatology Program. Law Dome ice core data.

World Data Center for Paleoclimatology and NOAA Paleoclimatology Program. Law Dome ice core data. ftp://ftp.ncdc.noaa.gov/pub/data/paleo/icecore/antarctica/law/law2006.txt [Access date: 10 October 2016].

Worrall, J.J., Egeland, L., Eager, T., Mask, R.A., Johnson, E.W., Kemp, P.A., and Shepperd, W.D. 2008. Rapid mortality of Populus tremuloides in southwestern Colorado, USA. Forest Ecology and Management **255**(3–4): 686-696. doi: http://dx.doi.org/10.1016/j.foreco.2007.09.071.

Yamaguchi, D.K. 1991. A simple method for cross-dating increment cores from living trees. Canadian Journal of Forest Research **21**(3): 414-416. doi: 10.1139/x91-053.

Zang, C., and Biondi, F. 2015. treeclim: an R package for the numerical calibration of proxy-climate relationships. Ecography **38**(4): 431-436. doi: 10.1111/ecog.01335.