THE IMPACTS OF MULTIPLE ANTHROPOGENIC DISTURBANCES ON THE MONTANE FORESTS OF THE GREEN MOUNTAINS, VERMONT, USA

A Dissertation Presented

by

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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 Plant Biology

October 2014

Accepted by the Faculty of the Graduate College, The University of Vermont, in partial fulfillment of the requirements for the degree of Doctor of Philosophy, specializing in Plant Biology.

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ABSTRACT

How and why species' ranges shift has long been a focus of ecology but is now becoming increasingly important given the current rate of climatic and environmental change. In response to global warming, species will need to migrate northward or upward to stay within their climatic tolerances. The ability of species to migrate will determine their fate and affect the community compositions of the future. However, to more accurately predict the future extent of species, we must identify and understand their responses to past and current climatic and environmental changes. The first place change is expected to occur is within ecotones where the ranges of many species converge and individuals exist at the limits of their environmental tolerances. In montane regions, these boundaries are compressed, creating a situation in which even relatively small changes in conditions can lead to shifts in the elevational ranges of species.

In this dissertation, I examine the responses of forests in the Green Mountains of Vermont to recent climatic and environmental change in an attempt to understand how future climate change will affect their location and composition. I focus on the Boreal-Deciduous Ecotone (BDE), where the high elevation spruce-fir forests converge with the lower elevation northern hardwoods. In addition to investigating adult trees within the BDE, I also examine the responses of understory herbs and tree seedlings to changes in environmental and climatic factors. Factors considered in these investigations include temperature, soil environment, light environment, invasive species, competition, disturbance and many others. I will examine the complex range of responses in forest species that results from prolonged exposure to these forces alone and in combination.

I have attempted to identify the responses of forest species to environmental changes by resurveying historic vegetation plots (Chapter 2), experimentally manipulating the growing environment of tree seedlings (Chapter 3) and performing dendrochronological analyses on tree rings (Chapter 4). Through my resurvey of historic vegetation plots, I determined the degree to which understory species have shifted as individuals or as groups. I also identified a set of novel understory communities that have developed since the 1960's in response to recent climate change, acid deposition and invasive species (Chapter 2). By transplanting and artificially warming tree seedlings, I identified factors responsible for limiting the growth and survival of northern hardwood species above the BDE. Temperature was the primary factor limiting sugar maple (*Acer saccharum*) at high elevations, while yellow birch (*Betula alleghaniensis*) was limited almost exclusively by light (Chapter 3). Dendrochronological studies of sugar maples indicated that prolonged exposure to acidified soils has only recently caused growth declines and has altered their relationship to climate (Chapter 4). Together, these studies have produced a cohesive picture of how northeastern montane forests have responded to recent climate change and other anthropogenic impacts. These findings can be used to help predict future species' ranges and identify species that may not be capable of migrating fast enough on their own to keep pace with changes in climatic conditions.

CITATIONS

Material from this dissertation has been published in the following form:

Pucko, C, B. Beckage, T. Perkins and W.S. Keeton..(2011). Species shifts in response to climate change: Individual or shared responses? *The Journal of the Torrey Botanical Society*. 138(2). 156 – 176.

ACKNOWLEDGEMENTS

I would like to sincerely thank my advisor Dr. Brian Beckage, my committee Drs. Lesley-Ann Dupigny-Giroux, Bill Keeton, Tim Perkins and Paul Schaberg. You all helped guide me and made me think hard about what it was I was doing which ultimately made me a better scientist. I also need to thank the rest of the Plant Biology Department at the University of Vermont for your tireless support, as well as for your scientific insight. Specifically, I would like to thank Drs. Mary Tierney, Laura Hill, Shelly Rayback and Dave Barrington for all your advice and encouragement. You all gave me the opportunity to grow and always had your doors open for a nervous or frustrated graduate student and offered invaluable suggestions. I greatly appreciate it.

I would also like to thank all of the graduate students in the Plant Biology Department including most importantly, the other members of the Beckage Lab and the Molofsky Lab: Dr. Jens Stevens, Kimmie Beal, Dr. Robin Collins, Dr. Matt Kaproth and Dr. Gabriela Bucini. You became my family and were always there to laugh with, vent with, celebrate with and sometimes cry with. I cannot thank you all enough and I miss you all terribly.

Lastly and most importantly, I would like to thank my actual family. My husband Jamie, you always supported me and never let me give up. You were sympathetic when I needed you to be and tough when I needed you to be, but most impressively, you were patient with me when this process took much longer than either of us anticipated. I love you always and forever. Mom, dad, Kyle and Nathan, thank you for always believing in me and supporting me and never letting me lose perspective of what it was I was trying to accomplish. I truly could not have done it without you.

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CHAPTER 1: INTRODUCTION

Ecosystems worldwide are responding to unprecedented changes in climate caused primarily by increasing anthropogenic production of CO_2. In 2013, the global atmospheric concentration of CO_2 exceeded 400 ppm for the first time in recorded history, representing a 40% increase since 1750 and the highest concentration of atmospheric carbon in at least the last 800,000 years. This increase in atmospheric carbon has increased average global temperatures by at least 0.85 °C since industrialization (IPCC 2013). The IPCC has projected further increases in global temperatures of between 1 and 7 °C by 2100, depending on the quantity of global emissions over the next century (IPCC 2013). Regardless of future emissions, the amount of warming we are currently committed to is enough to cause enormous change to human and natural communities in the decades and centuries to come (IPCC 2014). In addition to warming, climate change also brings changes in precipitation patterns and increased climatic unpredictability. As a result, many regions may experience more prolonged droughts and more unpredictable and intense storms. In many places, these changes will lead to altered disturbance regimes, such as increased fire frequency, that can further influence ecosystems (IPCC 2014).

Climate change has already altered countless aspects of the natural environment and has caused species around the world to respond in a variety of ways. When faced with a rapidly warming environment, or one in which the soil moisture is rapidly changing, species must either migrate, adapt or risk extinction (Aitken et al. 2008). Examples of each of these responses have been observed in recent decades (Parmesan 2006, Gerlach 2007, Beckage et al. 2008, Wake and Vredenburg 2008). Forests, for example, have been migrating poleward (Leithead et al. 2010) or upward (Svenning and Skov 2007, Beckage et al. 2008, Pucko et al. 2011, Lenoir and Svenning 2013) in response to warming in order to stay within their optimal climatic range. Other species have behaviorally or genetically adapted in order to take advantage of changes in their environments (Walther et al. 2002, Parmesan 2006). Behavioral adaptations may include changing the timing or route of migration, or shifting blooming time (Walther et al. 2002, Jenni and Kery 2003). However, species that have not been able to respond to climatic or environmental changes fast enough, or have seen their suitable habitat reduced or eliminated, have become locally or entirely extinct (Thomas et al. 2006, Gerlach 2007, Aitken et al. 2008). Species with long generation times, low mobility, specialists and those that are topographically or are otherwise geographically range limited are most vulnerable to extinction as a result of climate change (Walther et al. 2002, Walther 2010, Dirnbock et al. 2011, IPCC 2014). Among the groups most vulnerable to long-term climate change are trees (IPCC 2014). At this time, most analyses suggest that trees are unlikely to be able to keep pace with climate change because of their natural dispersal constraints (McLachlan et al. 2005, Aitken et al. 2008, IPCC 2014).

1.1 Forest Responses to Historic Climate Change

In order to identify species, communities, ecosystems or regions that are at risk of rapid and permanent change as a result of global change, it is imperative that we first understand how species have responded to climatic changes in the past. Climate has always influenced species distributions and our landscape today is in large part, a product of climatic changes that have taken place since the start of the last ice age. During this time, many species died out that were not able to migrate south fast enough to escape the ice or find suitable habitats in the cooling climate. Some species found southern refugia where they sustained small populations until they were able to repopulate areas vacated by ice after it began to melt (Webb III et al. 2003, Barnes 2009). However, these species often experienced a reduction in their genetic variability, leaving them susceptible to future changes in environmental conditions or disease (e.g. red pine)(Fowler and Morris 1977, Pautasso 2009). Still, other species thrived and expanded geographically in the cooler climate (Davis and Shaw 2001, Davis et al. 2003, Webb III et al. 2003). While questions persist regarding the mechanisms by which species rapidly migrated both before and after the glacial maximum, progress has been made in reconciling observed migration and dispersal rates (Cain et al. 1998, Clark 1998, Higgins et al. 2003b, Zhu et al. 2012). Determining how species migrated in response to past climatic change and identifying the factors that promoted or limited migration may help us identify species' migration potential and identify species that will be more likely to migrate quickly with changing climates in the future.

As species continue to adapt or shift with current climate change, we are likely to see echoes of the patterns exhibited by past species migrations. This underscores the need to understand how past climate influenced species migration, survival and extinction. While the paleo-record has been invaluable to the study of current species migrations, we also have data on how species have responded to recent and ongoing climatic changes, which may better foretell how species will react in the future given the current rate of warming (Thomas 2010, Lenoir and Svenning 2013)

In the northeastern United States, changes in climate since the 1960's have led to the upslope or northward migration of many species and forest types. In Vermont, average annual temperatures at low elevations have warmed by 1.66 °C between 1963 and the 2003 (Beckage et al. 2008). Additionally, winters have warmed significantly faster than summers at rates of 0.78 °C and 0.32°C per decade between 1965 and 2007, respectively (Pucko et al. 2011). Migration rates in response to this warming are determined by many factors including disturbance patterns (Leithead et al. 2010), interspecific competition, edaphic and topographic conditions (Barnes 2009) and dispersal mechanisms (Cain et al. 1998, Clark 1998). The relative importance of these factors may be different for each species. As a result, predicting the migration potential of a species requires in-depth understanding of each species' life history and environmental tolerances.

Species' responses to climate change are expected to appear first and occur most dramatically at the margins of their ranges, where individuals are living at the limits of their climatic tolerances. Within the Green Mountains, this means that we expect some of the greatest changes in forest composition to occur within the Boreal-Deciduous Ecotone (BDE) (Beckage et al. 2008). The BDE is defined as the narrow band of mixed forest that occurs between the lower elevation northern hardwood deciduous forests and the upper elevation boreal forests. Lower elevation northern hardwood forests are characterized by a canopy of sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*) and yellow birch (*Betula alleghaniensis*). High elevation boreal forest canopies are dominated by red spruce (*Piecea rubens*), balsam fir (*Abies balsamea*) and mountain paper birch (*Betula papyrifera var. cordifolia*). This ecotone has historically been located between 600 and 800 m.a.s.l. (Siccama 1974), however, recent climate change has caused northern hardwoods to migrate upslope by as much as 110 m into elevations previously occupied exclusively by boreal forest (Beckage et al. 2008). This displacement of high elevation forests by low elevation forests is not unique to this region (Kullman 2002, De Frenne et al. 2013, Lenoir and Svenning 2013), but the rate at which the transition zone is advancing upslope is of interest not only for its commercial importance, but for its ecological importance as well. While changes in overstory tree composition may be one of the most obvious indicators of forest shift, we also expect changes within the seedling and understory herbaceous plant communities (Lenoir et al. 2008, Lenoir et al. 2009).

Despite the focus by most research on canopy species, measuring elevational shifts in understory communities in response to climate change may provide a more accurate assessment of the elevational shift of the BDE over time and can help determine that extent to which communities will shift as intact units. Herbs have a wide variety of dispersal mechanisms, and generally have faster generation times than trees. This allows some understory plants to be able to shift more quickly with changes in climate and migrate upslope (Lenoir et al. 2008, IPCC 2014). In contrast, tree migration is limited by long generation times, slow maturity and can also be restricted by dispersal. As a result, the speed at which herbs are able to move upslope may be more indicative of the maximum rate of forest response to climate change. Herbaceous communities do have limits to their migration however, including soil and light conditions, interspecific competition and dispersal.

Like other understory plants, tree seedlings offer a way to approximate the amount of disequilibrium present between the distribution of overstory trees and the current range of suitable climatic conditions (Lenoir et al. 2009, Zhu et al. 2012). Adult trees germinated and became established at a location and in a set of climatic conditions that was suitable at some point in the past. As a result, these ranges do not represent the current geographic extent of suitable climatic conditions for a given species. Seedlings offer a more up-to-date picture of a species' potential range, but cannot be relied upon as a direct proxy for the potential range of adults because limits on their range beyond climate still exist. For instance, seedling range may be impacted by dispersal limitations or established seedlings may experience natural competitive exclusion during later stages in life. At high elevations, range expansion and migration may be limited by abiotic factors like temperature, soil conditions or light. Competitive interactions are more likely to control the lower elevational limits of species' ranges where individuals are in contact with species that typically have higher maximum growth rates (Loehle 1998, 2003).

1.2 Factors that Control the Rate of Ecotone Shift

There are many factors that can contribute to the presence and shift of an ecotone over time. These factors can be climatic, environmental or biological. Most often, many factors influence ecotone location simultaneously, making their identification difficult. However, by understanding what limits species migration into new habitats, and as a result, what limits ecotone shift, we may be able to predict how future changes are likely to impact species and ecotones.

Anthropogenic climate change is perhaps the most important cause of recent ecotone shift globally. Warming temperatures have resulted in the upward or poleward migration of many ecotones and changes in precipitation patterns have further shifted species' ranges. However, climatic changes do not influence forest species in isolation. Instead, species experience a constantly changing environment where factors such as disturbance, pollution, disease, invasive species, interspecific competition, and human activities (e.g. logging) are all interacting. These factors can interact synergistically with climate to positively or negatively affect the ability of species to cope with climatic change. While each of these factors can contribute significantly to the long-term survival of a species, I will first focus on the interactions between natural climatic disturbances and anthropogenic climate change.

Climatic Disturbance

Though climatic events may be considered part of the climate, for my purposes I am treating them differently and calling them disturbances because of their stochastic nature. However, climatic change influences the frequency of climatic disturbances, which may also be interpreted as extreme weather events. In function, climatic disturbances also differ from gradual warming in their scope. Warming influences whole regions while a climatic disturbances could potentially affect only a single tree. Climatic disturbances and extreme weather events are some of the most influential factors affecting forests and their rate of change. In many northeastern forests, they also represent the dominant disturbance regime. Extreme weather in the form of hurricanes, small-scale wind events (e.g. microbursts), short-term droughts, heavy rains, late spring freezes and early winter thaws are likely to become more frequent or intense in the future as a result of global climate change (Strimbeck et al. 1995, IPCC 2007b, 2013). While direct mortality, particularly as a result of wind events, can be common in some forests, other climatic disturbances cause indirect mortality by predisposing trees to other stressors. For instance, a prolonged summer drought may increase the susceptibility of an individual to insect defoliation, fungal infection or may cause early leaf fall, reducing annual carbon stores. In this case it is difficult to identify a single cause of death, but drought certainly contributed to it.

In addition to the type of the disturbance, the spatial scale of the disturbance is also important and can alter a species' ability to migrate. Events that tend to create single-tree sized gaps will favor the advancement of shade tolerant species, which can capture a site from a state of advanced regeneration in the understory. Stand replacing disturbances like hurricanes and events that cause large gaps such as fir waves may favor the establishment of shade intolerant species. Though the recurrence time of any natural, sporadic event is difficult, if not impossible, to precisely estimate for a given forest stand, we know that over long periods and over large areas, the frequency of extreme weather events is likely to increase. The rate and nature of the future changes in climatic disturbance will help to determine the ecological trajectory of northeastern forests and will help determine which species will survive in a rapidly warming world.

Climatic disturbance is not the only type of disturbance that indirectly affects mortality by predisposing trees to secondary stressors. Acid deposition is another example of a contributory factor that can sometimes lead to decline or death of a tree, but rarely causes death directly. The effects of acid deposition may be more important to species' migration rates, however, because of their distribution.

Acid Deposition

Acid deposition has been influencing Northeastern forests since at least the 1950's and continues to impact forest health. Acidic deposition causes reductions in soil base cations by slowly reducing buffering capacity and acidifying the soil. Prolonged exposure to acidic deposition will, in many cases, eventually begin to affect biological systems. The severity of the impacts of acid deposition are dependent on a number of factors including 1) initial soil base cation concentrations / bedrock composition, 2) proximity to a pollution source and 3) elevation (Miller 2005b).

Acidification, and therefore negative biological impacts, are more severe in areas with low initial buffering capacity, near industrial centers and at high elevations (Johnson 1992). High elevation forests are at elevated risk for two reasons. First, high elevations have increased exposure to acidic deposition through cloud mist, which can increase overall precipitation by up to 50% in some areas in the Green Mountains (Vogelmann et al. 1968). In addition to acidifying the soil, acidic clouds can damage foliage directly and reduce its cold tolerance (Schaberg et al. 2000, Borer et al. 2005). The second predisposing factor for high elevation forests is that they are typically found on thin, well-drained, acidic soils, which easily lose base cations (Miller 2005b).

While much is known about the recent impacts of acid deposition and soil acidification and its role in red spruce (*Picea rubens*) and sugar maple (*Acer saccharum*) decline, far less is known about how long forests have been declining. Additionally, reductions in sulfur emissions mandated by the Clean Air Act (1970) and its amendments (1990) have resulted in increases in the pH of rainwater throughout the Northeast (Likens et al. 1996, Driscoll 2001). This has translated into improvements in the chemistry of streams and acidified lakes in the areas hardest hit by acid deposition (Skjelkvale et al. 2005), however, it is not clear whether those improvements have led to any natural recovery of affected forest ecosystems.

Despite its negative impact on ecosystems, acid deposition presents an interesting example of an anthropogenic disturbance that may, under certain circumstances, help some tree species migrate with rapid climate change. As with any increase in disturbance, an increase in tree mortality due to acidification will result in a rise in the number of sites available for colonization. With acid deposition, a disproportionate number of these canopy gaps will be created in forests above the BDE because red spruce grows at high elevations and is one of the species most susceptible to acid-mediated decline. With continued climate change, warming temperatures at high elevations will allow species previously restricted to lower elevations to compete for these sites. Since warm-adapted species generally have higher maximum growth rates, a disproportionate number of gaps above the BDE, which were occupied by boreal trees in the past, are likely to be captured by northern hardwoods

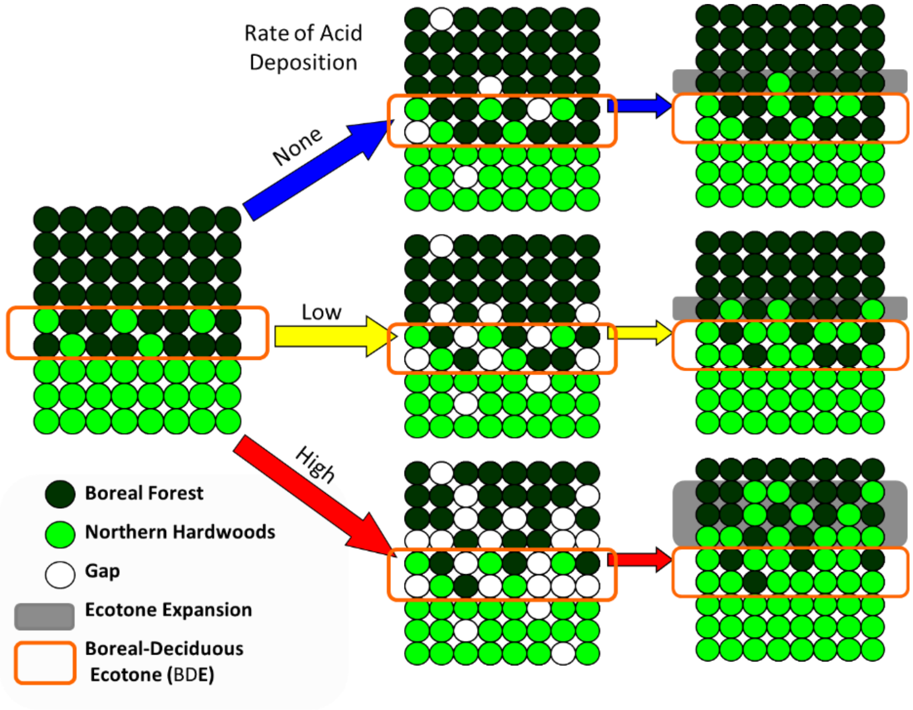

Figure 1.1: A mechanism for ecotone rise and expansion with different rates acidic deposition.

(Figure 1.1). The existence of this mechanism in the Green Mountains has been supported by the observed rapid, upslope expansion of the BDE (Beckage et al. 2008). Additionally, the more affected a site is by acid deposition, the greater the BDE expansion is expected to be. Therefore, the greater the impacts of acidic deposition, the greater the rate of potential upslope northern hardwood advance. This is good news for sugar maple, yellow birch and other low elevation species that will require rapid upslope migration to keep pace with climate change, which will, in turn, increase the odds of their long-term survival.

Non-native Species

Acid deposition and climatic disturbance are not the only factors that act synergistically with climate to influence forests: disease, invasive species and human activities can also affect forest health and species' potential for long-term survival. Non-native threats such as emerald ash borer (*Agrilus planipennis*), hemlock wooly adelgid (*Adelges tsugae*) and Asian longhorn beetle (*Anplophora blabripennis*) are poised to impact forests in the Green Mountains in much the same way that Dutch elm disease (*Ophiostroma ulmi*), beech-bark disease (*Nectria coccinea* var. *faginata*) and chestnut blight (*Cryphonectria parasitica*) did in the 20th century (Barnes 2009). They have the potential to drastically alter species compositions and influence the future trajectories of forest succession. Aiding the spread of these pests are climatic changes, which extend their potential range by causing winter temperatures to less frequently dip below the insects' cold tolerances (Barnes 2009). Another example of an introduced species that may influence future species compositions are earthworms (*Lumbricus sp.*). Earthworms have gradually invaded northeastern forests from the south where they were introduced by early European settlers. Subsequent introductions have occurred through the spread of recreational fishing (Hale et al. 2006). Invaded forests experience changes in the soil environment and altered understory communities with reduced herbaceous species richness (Hale et al. 2006, Holdsworth et al. 2007). Additionally, earthworm invasion has been shown to increase the drought sensitivity of sugar maple (Larson et al. 2009). With increases in drought frequency expected with future climate change, the impact of earthworms on northern hardwood forests may only worsen.

Other Anthropogenic Effects

Many human activities such as logging, development and recreation have also affected forests and their ability to migrate with changes in climatic conditions. Fragmentation by development or large-scale logging can impose barriers to dispersal and limit habitat availability that will slow migration rates. Poor logging practices, like high grading, may also limit the genetic variability of a species and can reduce the overall fitness of a population, making it less able to adapt to future environmental conditions. Recreation and development can have many impacts on forests such as pollution, increases in invasive species introductions (i.e. earthworms) (Bohlen et al. 2004), and degradation of habitat. All of these factors can influence current populations and influence future migration rates.

Intrinsic Limits on Migration

In addition to the external factors controlling species migration, there are intrinsic controls that limit the ability of species to expand their ranges and ultimately migrate with climate change. Life history characteristics such as dispersal distance, fecundity, shade tolerance and climatic tolerances will all influence the ability of species to migrate with climate change. Dispersal as it relates to migration potential has been well studied for current species to determine whether they will be able to shift their ranges with optimal climates as temperatures continue to warm (Brooker et al. 2007, Zhu et al. 2012). However, in studying post-glacial migration, gaps in our understanding of extreme long-distance dispersal have been rectified which seem to suggest that trees may fare better than predicted in response to future rapid climate change (Clark 1998). In addition, trade-offs between dispersal distance, fecundity, seedling survival and shade tolerance (Hughes and Fahey 1988) will influence their competitive ability and will determine the success of species in the future. While most of these demographic characteristics are well described for tree species, they are unknown for many herbaceous understory species. This creates very large uncertainties around the rates of migration for these species (Lenoir et al. 2008, IPCC 2014).

1.3 Individual or Shared Responses to Climatic or Environmental Change

In response to all of the forces interacting to affect migration rates, species able to migrate will do so either as individuals or with their established communities. While it is unlikely that a community will experience purely individual or community shift, the extent to which each scenario is represented is unclear. We have evidence from the pollen record that since the last glacial maximum, species compositions existed that no longer exist today (Overpeck et al. 1992, Umbanhower et al. 2006). Since these communities existed in the recent past, we must assume that to some extent, they will also be present in the future. What is unclear however is the rate and extent to which current community compositions will change. If species migrate more or less as intact communities, we know roughly how those communities will function. However, if species shift their ranges independently, we are likely to observe novel communities in the future. These communities will have new competitive hierarchies that will respond differently than current communities to environmental and climatic changes. The degree to which species will migrate as a community is determined, at least in part, by the strength of the abiotic stress in an environment. In stressful environments, species tend to migrate as a unit (Freestone 2006). Species within a community are also more likely to migrate in unison if facilitative relationships exist between species (Bruno et al. 2003). If a community experiences relatively little abiotic stress and species compositions are determined by competitive interactions, species are more likely to react to environmental change individualistically, creating more novel communities in the future.

1.4 Species Migration and Climate Change

The ability of species to migrate and keep pace with the climatic and environmental changes ahead hinges on a number of factors including the rate of warming and climatic change, the disturbance frequency, and factors that limit the ability of plants to disperse or establish in new suitable habitats. The slower global temperatures rise, the better chance forests have at remaining within their optimal climatic envelopes. However, this rate is determined by anthropogenic carbon emissions, which have shown no sign of slowing (IPCC 2013). Contrary to intuition, it is likely that increases in disturbance in the form of extreme weather events, disease outbreaks or acid deposition-mediated decline, will aid in the migration of species. Increases in gap frequency caused by disturbances will correspondingly increase the proportion of a forest available for colonization. In this manner, disturbances that are likely to become more common in the future with climate change will promote migration. This increase in migration rate will translate into range shifts only if dispersal is wide enough to access suitable habitats. If this is not possible, assisted migration may be the only viable option able to maintain biodiversity in the future.

1.5 Objectives

In this dissertation, I aim to comprehensively address how recent, rapid climate change and other anthropogenic disturbances (e.g. acid deposition, invasive species) have interacted to affect the forest communities living in and near the Boreal-Deciduous Ecotone (BDE) of the Green Mountains in Vermont. In the process, I will examine how communities shift over time, the factors that control the rate of forest shift and the impacts of multiple anthropogenic disturbances on forest populations. The information presented here may be used to build or improve existing climate-vegetation models that help us predict how ecosystems will look and behave in the future given continued climatic change. These models can then be used to help guide conservation and legislative efforts that will, in part, determine the future trajectory of global change. The better we understand the responses of species and communities to past climatic change, the more informed we will be as to how these species may respond in the future as climate change continues.

In Chapter 2, I examine how communities change over time by quantifying changes in the distributions of understory species and communities between 1965 and 2006 in the Green Mountains. By resurveying historic vegetation plots, I have been able to examine the degree to which species have shifted as intact groups or as individuals, in response to multiple anthropogenic disturbances. It is important to identify the circumstances that lead to novel community formations because these novel species assemblages may behave unpredictably to environmental change. I have also compared the changes in these understory herbaceous communities to those of the canopy and the woody sub-canopy in order to identify the degree to which each group has been able to migrate or shift with climate.

In Chapter 3, I experimentally identify the factors that influence growth and survival of tree seedlings in the Green Mountains in order to identify the causes of current range boundaries. Using reciprocal transplantation of seedlings across an elevation range, I have examined the relative importance of soil nutrition, light, elevation and temperature on the survival of four species of seedlings common within the BDE. The resulting seedling distributions were compared to natural seedling distributions in order to identify the extent to which dispersal or germination limitations may be influencing current species' ranges. The information gleaned from this study can improve our understanding of the obstacles faced by species attempting to migrate with climate change. The results could also be used to develop strategies that could aid in natural or assisted migration of trees in the future.

In Chapter 4, I examine tree rings in order to identify the role that acid deposition has had, and is still having, on northern hardwood and ecotonal forests in Vermont. Given that tree species need space to colonize in order to migrate, gap frequency rates are an important metric in determining potential migration. Using dendrochronological and dendrochemical methods, I have investigated the degree to which acid deposition has affected the health and growth of sugar maple (*Acer saccharum*) in the past. Additionally I have examined whether continued, but reduced levels of acid deposition are causing further damage or whether forests are beginning to recover.

Through this dissertation, I hope to have presented a clear story about how montane forests have responded to past climatic and environmental change and how they may respond to future changes. Having examined the forests of the Green Mountains in so many ways, from the soil, to the understory herbs and seedlings, to the sub-canopy and canopy communities, I have been able to gain perspective on the connections between groups that what we often consider or study separately.

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CHAPTER 2: SPECIES SHIFTS IN RESPONSE TO CLIMATE CHANGE: INDIVIDUAL OR SHARED RESPONSES?

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Formatted for publication in:

The Journal of the Torrey Botanical Society

2.1 Abstract

PUCKO, C. (Department of Plant Biology, University of Vermont, Burlington, VT 05405), B. BECKAGE (Department of Plant Biology, University of Vermont, Burlington, VT 05405), T. PERKINS (Proctor Maple Research Center, University of Vermont, Underhill, VT 05490), W. KEETON (Rubenstein School of Natural Resources, University of Vermont, Burlington, VT 05405). Species shifts in response to climate change: Individual or shared responses? J. Torrey Bot. Soc. XXX: 000 000. 20XX. -- Individual species are expected to shift their distributions in response to global climate change. Species within existing communities may respond to climate change individualistically, resulting in the formation of novel communities, or may instead shift as intact communities. We examined whether montane plant communities in the northeastern United States have shifted their elevational range as intact assemblages or individualistically in response to recent regional climatic and environmental change. We used non-metric multidimensional scaling (NMDS) to examine changes in plant community composition and species distributions using vegetation surveys repeated five times between 1964 and 2006 across an elevational gradient (549 – 1158 m) on Camels Hump Mountain, Vermont, USA, in conjunction with an analysis of local climate change. We found evidence that species' elevational distributions and community compositions have shifted in response to a 0.49°C per decade warming. These species' responses were complex and largely individualistic at some elevations, while at other elevations species in a given community tended to respond similarly. The magnitude of community compositional change was largely dependent on location with respect to the ecotone between northern hardwood and boreal forests. While climate change likely contributed to the large shifts in species within NMDS space, these shifts may also be a response to invasive earthworms at low elevations and to prolonged exposure to acid deposition at high elevations. Though we found evidence of shared species responses within communities, future species responses may become increasingly divergent as the magnitude of climate change increases causing species-specific environmental thresholds to be reached and as the synergistic effects of multiple anthropogenic perturbations rise.

Keywords: Climate Change; Acid Deposition; Community Shift; Non-metric Multidimensional Scaling (NMDS); Elevation Shift

2.2 Introduction

Understanding how species will respond to ongoing climate change is increasingly important as the rate of anthropogenic climate change increases (Walther 2003, IPCC 2007, Walther 2010). The effects of recent warming have already been observed in an array of terrestrial, aquatic and marine habitats (Scavia et al., 2002, Naidoo 2004, Winder and Schindler 2004) and are evidenced by the shifting ranges of many species either poleward or upward in elevation (Root et al. 2003, Krajick 2004, Beckage et al. 2008b, Kelly and Goulden 2008). While the literature on species' responses to recent climate change is extensive (cf. Parmesan and Yohe, 2003), less attention has been given to the examination of community responses. Investigations of community responses to climate change have recently become more common (Genner et al. 2004, Suttle et al. 2007, Grime et al. 2008, Willis et al. 2008, Kelly and Goulden 2008), but studies of community response that also comprehensively examine species' responses to climate change have remained much more limited (Walther 2003).

We examine species assemblages across an elevational gradient in order to distinguish between two historically competing hypotheses of community assembly (Clements 1916, Gleason 1939, Callaway and Walker 1997, Brooker et al. 2008). The 'individualistic response hypothesis' (IRH) asserts that co-occurring species will respond independently to changes in the environment (Gleason 1939, Jackson and Overpeck 2000, Williams and Jackson 2007), forming novel species assemblages with climate change (Walther 2003, le Roux and McGeoch 2008). There is substantial evidence in support of this hypothesis, provided, for example, by tree pollen extracted from lake sediment cores from around the world (Overpeck et al. 1992, Umbanhower et al. 2006); however, similar data for understory forest herbs are extremely limited (Cain et al. 1998). The 'shared response hypothesis (SRH) predicts that co-occurring species will respond similarly to changes in their environment due to common climatic tolerances (Walther et al. 2002) or interspecific facilitative relationships that promote co-occurrence (Bruno et al. 2003, Freestone 2006). This hypothesis suggests that communities will shift as intact assemblages, preserving species' associations, in response to climate change.

Recent evaluations of this dichotomy acknowledge that neither hypothesis satisfies the complexities observed in natural communities (Bruno et al. 2003, Lortie et al. 2004). Instead, it is preferable to view the responses of co-occurring species to climatic or environmental change in terms of a continuum (Brooker et al. 2008). Though not a novel viewpoint (Goodall 1963, Callaway and Walker 1997), Lortie et al. (2004) called this concept the integrated community (IC), and theorized that the level of shared response was based on the relative influence of species interactions, abiotic factors, and stochastic processes. This view of species assemblages postulates that harsh environments lead to increased levels of facilitation among species (Callaway and Walker 1997, Brooker and Callaghan 1998), which can result in intact community shifts while simultaneously allowing for species to exhibit divergent responses to more subtle environmental change (Lortie et al. 2004, Brooker et al. 2008).

In this study, we examined plant communities in order to determine the degree to which species have shifted independently in response to recent climate change. We examined changes in community composition across an elevational gradient in the northeastern United States using permanent vegetation plots that spanned four decades. Our vegetation plots were established on Camels Hump in the Green Mountains, Vermont, in 1965 (Siccama 1968) and were resurveyed in 1979, 1983, 1986 and 2006. Montane environments provide ideal locations to study climate-related species shifts because their steep slopes result in spatially compressed climate gradients (Kupfer and Cairns 1996, Kelly and Goulden 2008) where even relatively small changes in climate can result in observable shifts in species' elevational distributions (Beckage et al. 2008b, Lenoir et al. 2008). We focused on understory communities because of their higher species richness relative to the overstory in our study system. This allowed us to investigate the effects of climate change in terms of both individual species' shifts as well as changes to community composition, and thus, to examine the relative support for the individualistic versus shared response hypotheses. In addition, understory species may be capable of responding more quickly to changes in climate, sometimes exhibiting more rapid altitudinal shifts than long-lived canopy species due to shorter generation times (Lenoir et al. 2008). We concurrently examined the response of canopy tree species to determine whether overstory shifts might be driving any observed understory changes.

The specific objectives of our study were i) to determine if montane understory communities shifted their elevational range in response to recent climatic and environmental change, and ii) to determine to what degree observed responses were consistent with either the individual or shared response hypothesis. If species have shared responses to environmental change, we would expect current communities to be analogous to those observed in 1965 with correspondingly few communities defined by novel species assemblages. However, if species are responding individualistically, we expect to see divergence in both the magnitude and direction of species' shifts within a community, resulting in new species assemblages.

2.3 Methods

Study Site. We conducted our study on Camels Hump (44° 19' N, 72° 53' W), which, at 1244 m a.s.l., is the third highest peak in Vermont, U.S.A. The geology of Camels Hump is representative of the Green Mountains, a northern extension of the Appalachians, and is dominated by schist (graphitic, quartz-albite-muscovite) and gneiss (Siccama 1974) bedrock. Soils are predominantly spodosols, consisting of acidic stony loams (NRCS 2006, NRCS 2008). The climate in this region is characterized by large daily and annual temperature ranges, with an average January temperature of -7.8°C and an average July temperature of 21.4°C. Precipitation is evenly distributed throughout the year, averaging 91.6 cm annually (Burlington International Airport Station, NOAA 2002). However, at high elevations, cloud water deposition can increase precipitation by a conservative estimate of 50 to 65% (Vogelmann et al. 1968, Lovett et al. 1982).

Two general forest types, stratified by elevation, occupy the majority of the area on Camels Hump and other montane regions of New England. Northern hardwood forest is found at elevations below approximately 750 m and is dominated by sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.) and yellow birch (*Betula alleghaniensis* Britt.). Boreal forest occurs at higher elevations, above approximately 900 m, and is dominated by red spruce (*Picea rubens* Sarg.), balsam fir (*Abies balsamea* (L.) P. Mill.) and mountain paper birch (*Betula papyrifera* var. *cordifolia* (Regel) Fern.) (Siccama

1974, Cogbill and White 1991). This boreal forest extends upward until it reaches the small alpine summit of Camels Hump at approximately 1200 m. Between the northern hardwood and boreal forests, from approximately 700 to 900 m, lies a spatially compact transition zone referred to as the boreal to deciduous ecotone (BDE) (Siccama 1974, Beckage et al. 2008b).

The vegetation survey plots used in this study were located in the Camels Hump Forest Ecology Research Area, which has a well-documented land use and disturbance history (Siccama 1968, Whitney 1988). In order to minimize the influence of successional changes in our sites, plots were established in locations free from major disturbance or recent human activity (Foster et al. 1998, Hall et al. 2002). While the majority of the upper slopes of Camels Hump have not been logged, there has been some limited removal of trees at lower elevations. However, with the exception of the removal of individual yellow birch and red spruce at elevations extending up to 700 m in the mid 1930's and 1950's (Whitney 1988), no other potentially disruptive logging activity has been located in the research area (Siccama 1968, Whitney 1988). In 1964, during the initial canopy survey, the forest composition was classified as late successional (Siccama 1968), containing the same overstory species as today. Hence succession has probably not contributed to any stand-scale changes in species composition in the subsequent forty years. However, the forest is likely to have developed structurally (Franklin et al. 2002) and ongoing gap phase processes may influence species composition at small scales within our study sites (e.g., Perkins et al. 1992, Battles and Fahey 2000, Beckage et al. 2008a). These internal dynamics alone should not result in distributional changes of species but could, however, influence the rate at which species are able to respond to shifting climate (e.g., Beckage et al. 2008b).

Field Methods. Vegetation was sampled using a nested plot design established in 1964 (Siccama 1968) to capture both over- and understory vegetation characteristics. Overstory plots were distributed up the western slope of Camels Hump in 1964 at intervals of 61 vertical meters (200 feet) between 549 and 1158 m for a total of 11 sample elevations, e.g., 549, 610, 671, 732, 792, 853, 914, 975, 1036, 1097, and 1158 m. At each elevation, 5 to 10 overstory plots (3 m x 30 m) were placed perpendicular to the contour and separated by approximately 6 m. Rebar marks the top and bottom of each plot's centerline. The six lower elevation sites had 10 such plots, while the upper five elevations had only five plots in order to better maintain a westerly aspect. In 1964 and 2004, the species and diameter at breast height (dbh) for each tree with a basal diameter ≥ 2 cm within each overstory plot was recorded. Nested in each of these plots were six 1 × 1 meter square understory quadrats that are distributed evenly on alternate sides of the center line for a total of 510 understory quadrats. To sample understory vegetation within each quadrat we performed a stem count and visually estimated percent cover (Dethier et al. 1993) of each vascular species present including club mosses (*Huperzia* spp. Bernh.), in accordance with the original understory survey conducted in 1965 (Siccama 1968). All taxonomy and nomenclature were updated and are consistent with Magee and Ahles (1999). Woody shrub species incapable of reaching the canopy, with a dbh less than 2 cm, were included as part of the understory (i.e. *Viburnum lantanoides* Michx, *Cornus alternifolia* L.). We excluded canopy tree species from the understory analyses. As in the initial survey, percent cover of mosses was recorded while lichens, liverworts and fungi were excluded.

Community Composition. A species assemblage was defined as the suite of species found within a plot. Overstory assemblages were defined by the basal area of canopy species present rather than stem counts. This was done in order to more accurately represent the community structure of canopy stems and to avoid overrepresentation of smaller, sub-canopy individuals (Hedman et al. 2000). Understory assemblages were defined by the average percent cover of species found within plots (Collins et al. 2006). Average percent cover represented the mean cover of species present within the six-1 m^2 understory quadrats nested within each overstory plot.

Each plant in an understory quadrat was sampled once in each survey year. Though most individuals were identified and recorded at the species level, some were aggregated by genus or family for one of three reasons: As a result of surveying each plot only once per growing season, some plants sampled could not be identified to species since flowers or other diagnostic field characteristics were not always present at the time of data collection (e.g. *Trillium* spp. and *Viola* spp.) (Smith et al. 2008). Some species were aggregated at the genus or family level to maintain consistency across sampling years (*Rubus* spp. and *Galium* spp.) (Siccama 1968). Other species were aggregated to accommodate changes in taxonomy (e.g. *Streptopus* spp.). In addition, mosses were aggregated into either the genus *Sphagnum* or with all other genera of mosses combined into a single group.

Our analyses of understory communities only considered species that were present in at least three of the five sampled years (Table 2.1). This was done to preclude any disproportionate influence that rare species might have on community characterization (Hedman et al. 2000) and also to decrease the impact of survey timing by reducing the number of spring ephemerals included in the analyses. Tree species found in our plots were analyzed separately from the understory due to differences in physiognomy and life history characteristics.

Climate. We examined trends in regional climate over the period of our vegetation censuses. Regional climate change was examined through the use of annual climate variables, derived from data collected at the Burlington International Airport, Burlington, Vermont, located less than 30 km from our study site. These data are archived and maintained by the US Historical Climatology Network (Williams et al. 2006). Seasonal temperatures and precipitation were also calculated for winter (December, January and February) and summer (June, July and August) months in order to highlight seasonal differences in long-term trends. Additional climatic and biologically significant variables such as the number of frost-free days (FFD) and growing degree-days (GDD) were also derived. FFD was defined as the number of days annually in which the minimum temperature was above 0°C, while GDD was defined as the cumulative number of degree-days above a base of 10°C. Linear regressions were then performed using R statistical software (R Development Core Team 2006) to estimate the long-term trends between 1965 and 2006.

Vegetation Analysis. We analyzed individual species and community responses to observed climate change through the use of non-metric multidimensional scaling (NMDS). NMDS was used because of its ability to highlight patterns within multidimensional data without making distributional assumptions, and is widely used in community change analyses (Hedman et al. 2000, McCune and Grace 2002, Smith et al. 2008, Greenstein and Pandolfi

2008). The objective of the non-parametric NMDS is to reduce the dimensionality of multivariate data and group more similar observations closer together by preserving rank-order distances between observations. NMDS therefore allows for the visualization of the ranked dissimilarities between multivariate data points in a reduced number of dimensions (Kruskal and Wish 1978). NMDS was selected over other ordination techniques (DCA, PCA, PCoA, CA) because of its ability to accurately identify gradients beneath overlapping and non-normal data distributions. This type of data is common in studies of plant community composition and has led to the wide acceptance and use of NMDS as a tool in community change analyses (Wentworth and Ulrey 2000). In addition, NMDS is able to dimensionally reduce data containing outliers, which occur frequently and are important in identifying range shifts, but can be problematic for other ordination techniques that rely on distributional assumptions such as detrended correspondence analysis (DCA) (Ruokolainen and Salo 2006).

The NMDS ordinations of our species and assemblage data were based on Bray-Curtis dissimilarities of non-transformed percent cover (understory analyses) or basal area (overstory analyses) data (Bray and Curtis 1957). Dissimilarities of zero, resulting from the existence of identical compositional or distributional data, were maintained in the analyses by assigning them a small dissimilarity that would not affect the overall rank-order of points. We did not have to address zero dissimilarities resulting from joint absences, because there were no empty vegetation plots and only species that were observed in a given year were used in the computation of the Bray-Curtis dissimilarity matrices. For both community and species analyses, the data were summarized by plot. Community NMDS analyses therefore, resulted in either 5 or 10 individual data points per elevation per year. Species' NMDS analyses sought to characterize changes in distribution over time by using the percent cover data for each species from all 85 plots surveyed, in each of the five survey years. This resulted in a single data point representing each species in each year it was observed. Ordinations were based solely on metrics of species' abundance, i.e., percent cover for understory analyses and basal area for overstory analyses. Analyses did not include any elevational information; therefore, any grouping of communities or species through NMDS by elevation is strictly a product of similarities in the abundance of species. All NMDS analyses were performed in the R statistical software package using the metaMDS function (vegan library; Oksanen et al. 2009).

The efficacy of the dimension reduction is measured by the stress value. Stress is a measure of mismatch between the rank-ordered multivariate distance between points and their relative distances in two-dimensional ordination space, e.g., a measure of goodness of fit of the ordination. Lower stress values indicate smaller mismatch between calculated and ordination distances and thus a better ordination. Stresses reported from a majority of our NMDS analyses are <0.2, and are therefore reliable for interpretation based on the rule-of-thumb presented in Clarke (1993). One of the two-dimensional analyses resulted in a stress greater than 0.2, but was still below the 0.3 threshold value considered to represent a poor ordination (Clarke 1993, Zuur et al. 2007).

Each of the four NMDS analyses presented in this paper (understory communities, understory species, overstory communities and overstory species) represents a single two-dimensional ordination. The two-dimensional ordinations were used for their ease of interpretation though we also examined three-dimensional ordinations that resulted in very similar point configurations but lower stress values. The resemblance of two-dimensional and three-dimensional ordinations (which all had stress values below 0.2) supports the reliability of the two-dimensional analyses presented.

Elevation isolines and vectors were added to community change ordinations in order to more clearly illustrate how compositions have changed over time. The isolines in each panel were calculated using the 'ordisurf' function (vegan library; Oksanen et al. 2009) in R and were derived from the ordination position of each community recorded in the initial survey year (1964 or 1965) using generalized additive models (GAMs). The locations of communities in subsequent years with respect to the isolines indicate their relative similarity to these initial communities. Points representing communities that are located outside the bounds of the isolines indicate the presence of species assemblages not found on Camels Hump in 1965. Similar contours could not be added to NMDS plots representing species distributions because the data used in these analyses were vectors of species' abundance across elevations. Change vectors were added to community ordinations to represent shifts over time of study plots within NMDS space. The terminus of each vector represents the average position within NMDS space of communities in the most recent vegetation survey (2004 or 2006), while the start of each vector represents the average position of those same communities in the initial survey year (i.e., 1964 or 1965).

2.4 Results

Average annual temperatures in Burlington, VT increased by 0.49°C per decade between 1965 and 2006. During this time period, winter temperatures (DJF) warmed more rapidly than summer temperatures (JJA) at the rate of 0.78°C versus 0.32°C per decade

(Figure 2.1). The number of growing degree-days and frost-free days also increased with temperature at a rate of 55 GDD and 4.7 FFD per decade, indicating that climate has gradually warmed. Winter precipitation has decreased slightly since 1965, despite an overall increase in annual precipitation of over 2 cm per decade. Resulting changes to the snow pack could influence understory species compositions and alter seedling establishment rates (Frey 1983).

The results of the NMDS ordination of understory communities revealed that the largest observed changes to species assemblages occurred at elevations near the upper end of the ecotone (Figure 2.2 G, H; elevation panels 914 and 975 m) as determined by the length of the change vector in each panel. The least amount of understory community change occurred at the lowest elevations (Figure 2.2 A-C; elevation panels 549 to 671 m), while intermediate amounts of change were seen surrounding the upper ecotone (Figure 2.2 E, F, I, J; elevation panels 792, 853, 1036 and 1097). In addition to variations in the amount of compositional change that took place across elevations, the nature of the change also differed. In a majority of the elevations examined, current species assemblages were analogous to those found at lower elevations in the past, evidenced by change vectors terminating near lower elevation contours within NMDS space. However, in the upper ecotone, at elevations 914 m and 975 m, the vectors do not point to lower elevations within the bounds of the isolines, but instead point to NMDS space unoccupied by communities measured in 1965. This indicates that the current species assemblages at these elevations are unlike any observed in 1965 at any elevation.

Overstory communities showed relatively little change in community composition over our study period, particularly in comparison to the changes observed in the understory (Figure 2.3). These differences could be due to the long generation times of trees and the resulting demographic inertia. Balsam fir and paper birch for instance can live up to 200 years, while red spruce and sugar maple may live up to 400 years (Burns et al. 1990). The apparent decoupling of understory and overstory community dynamics suggests that climate and other abiotic factors can affect ground-level vegetation independently of the overstory.

While individual understory species' abundances and distributions changed in a variety of ways between 1965 and 2006, most species experienced declining populations (Table 2.2). Though it would be easy to attribute these changes to differences in cover estimation between researchers, most species exhibiting an overall decline in abundance did so gradually, showing declines between each of the five survey years (Appendix 2A Figure 2A.1). Despite general reductions in cover, *Aralia* spp., *Cardamine diphylla, Mitchella repens, Polystichum acrostichoides* and *Rubus* spp. increased in abundance at the upper limit of their range. Also, most species found exclusively in upper elevations, *Coptis trifolia, Cornus canadensis* and *Monotropa uniflora*, increased in abundance within the core of their range and declined at the tails. *Sphagnum* spp. was the only high elevation taxa with more widespread increases. Among the 48 species used in our analyses, only *Arisaema triphyllum* increased in abundance across its entire range.

Shifts in NMDS space of individual understory species are also broadly similar, particularly for species at similar elevations (Figure 2.4). Species at lower elevations had the largest shifts over the period of this study and these shifts were mostly in a similar direction within NMDS space. The higher elevation species generally had smaller shifts in NMDS space, with slightly less concordance in the direction and magnitude of these shifts across species. The distributions of a few species, however, had markedly different responses (i.e. *Arisaema triphyllum* and *Cardamine diphylla*). Changes in canopy species distributions do not exhibit any coherent pattern (Figure 2.5), again suggesting the decoupling of understory and overstory species.

2.5 Discussion

Community Shifts. We identified changes in understory communities that are consistent with observed regional climate warming and other anthropogenic disturbances over the period of 1965 to 2006. Communities near a climatic threshold along an elevational ecotone are expected to exhibit the most compositional shift in response to climate change, while communities that are further away from these thresholds may exhibit relatively little change (Figure 2.6) (Kupfer and Cairns 1996). We found greater compositional change in the uppermost elevations than might be expected with global warming alone (Figure 2.7A), but that is consistent with the combined effects of global warming and acid deposition (Figure 2.7B). The observed understory compositional change generally followed a unimodal distribution centered on the upper bound of the ecotone between forest types (Figure 2.7C). Previous studies on acid deposition in the northeast confirm that acidification has caused changes to forest ecosystems since the 1960's primarily by decreasing soil pH and leaching away essential nutrients such as calcium (Yanai et al. 1999, Oimet et al. 2006). These effects generally increase with elevation due to higher inputs through precipitation and exposure to acidic cloud moisture (NEG/ECP 2005, Vogelmann et al. 1968, DeHayes et al. 1999, Richardson et al. 2004). While canopy communities were exposed to the same environmental changes in climate and acid deposition as the understory, they did not display the same magnitude of compositional change, suggesting that understory species may be more responsive indicators of environmental change and may respond largely independently of the overstory.

The direction and magnitude of compositional change across elevations can help determine whether species are shifting as intact communities or as individuals. As expected given our conceptual model (e.g., Figures 2.6 and 2.7), understory communities in the lowest of our studied elevations changed relatively little over the study period. Understory communities in both the lower ecotone and in our highest elevation sites changed more substantially than at low elevations, as illustrated by the change vectors in Figure 2.2. The change vectors of these communities point more consistently toward lower elevation isolines, and stay within the bounds of the isolines, supporting the shared response hypothesis (SRH). In contrast, species assemblages currently found in the upper ecotone sites (i.e., 914 and 975 m) likely represent communities that have no prior analog in our 1965 vegetation surveys and seem to be the result of the gradual loss of *Dennstaedtia punctilobula* and *Ribes* spp. along with the addition of *Aralia* spp., *Trientalis borealis, Maianthemum canadense* and *Viburnum lantanoides* among others. The emergence of these novel communities in the upper ecotone indicates the independent shift of some species at these elevations, in contrast to the dominant trend across elevations of similar species responses to recent climatic and environmental change. This places these montane forests much closer to the SRH end of the shared/individualistic response continuum.

Species Shifts. Understory species shifts across all elevations were relatively similar within NMDS space (Figure 2.4). This corroborates evidence from the community analyses and provides further support for a largely shared response of species to climate change. The degree of coherence of species' shifts, however, appeared to vary with elevation. Lower elevation species had similar directional shifts but exhibited a wide range of magnitudes. Mid-elevation species had less directional coherence as they likely responded to both climate change and acid deposition. With the exception of *Monotropa uniflora,* most of the co-occurring species at high elevations had comparatively small shifts. *M. uniflora* is a non-photsynthetic plant which tends to be short lived, weather dependent, and easily missed in surveys done at different times during the growing season. This could lead to its unique response within NMDS space (Figure 2.4). In general, the resulting shift of many understory species in NMDS space is the result of complex responses that included, for example, changes in frequency internal to their elevational range, as well as shifts both upward and downward in elevation, suggesting the importance of other biotic or abiotic controls (Table 2.2).

We also see evidence suggesting that both climatic and non-climatic factors have affected species distributions. For instance, *Aralia* spp., *Cardamine diphylla*, *Mitchella repens, Polystichum acrostichoides* and *Rubus* spp. increased in abundance at the upper limit of their ranges, while some boreal species such as *Coptis trifolia* and *Cornus canadensis*, declined at their lower elevational limits which is consistent with expectations under increasing temperatures (Table 2.2). Two understory species that have likely responded to non-climatic controls are *Arisaema triphyllum* (Jack-in-the-Pulpit) and

Cardamine diphylla (Toothwort). Both of these species exhibit unusual patterns of change in NMDS space (Figure 2.4). Studies in northern forests have shown that both *A. triphyllum* and *C. diphylla* are abundant in sites with high densities of non-native earthworms (Corio et al. 2009). *A. triphyllum* has been shown to increase in abundance in response to earthworm invasions, although similar studies have not been done for *C. diphylla* (Bohlen et al. 2004, Hale et al. 2006). The responses of these two species in our study is consistent with our observations of non-native earthworms at low to medium densities (~50 - 100 worms/m^3) in sites up to at least 700 m in elevation. Earthworm invasion has been shown to cause changes in forest herb communities by facilitating the mixing of soil layers, altering nutrient cycling rates and disrupting belowground microbial communities (Bohlen et al. 2004, Hale et al. 2006).

While support for both the shared and the individual response hypotheses are found in the literature (Bruno et al. 2003; Williams and Jackson 2007), the degree of coherence likely depends on both the environmental driver (e.g., climate change, acid deposition, biological invasion, or a combination of these) and the magnitude of the change in the driver. We might not, for example, expect a coherent response across species within a community to a perturbation such as acid deposition in the absence of a strong alkalinity gradient, whereas we might *a priori* expect a more coherent response to climate change in the presence of a strong temperature gradient (i.e., elevation). We also suggest that the degree of coherence in species shifts in response to climate, for example, should vary with the magnitude of climate change: The responses of most species to climate change are likely to be nonlinear (reflecting climatic thresholds) over broad temperature and precipitation ranges, but their shifts might appear linear in response to small climatic perturbations. This could result in a high coherence across species in response to moderate changes in climate, but an increasing divergence of species across larger changes in climate, particularly as multiple climatic components (i.e. temperature, precipitation, frost free period) may change independently in a complex manner (e.g., precipitation may increase or decrease with temperature and plant available water further depends on the rate of these changes). As the magnitude of climate change increases, we might expect that species would diverge in their responses to climate change, reflecting species-specific threshold responses to different components of climate change with the potential for novel ecological community formation. The question of individualistic versus shared responses of species within communities might thus depend on the magnitude of climate change, accommodating evidence of novel communities associated with large climate shifts (e.g., Williams and Jackson 2007) while being consistent with shifts of intact communities with more modest climate change. The divergence of species' responses to climate change are also likely to be increased by the concurrent occurrence of other anthropogenic perturbations such as acid deposition and biological invasions, as these disturbances are likely to introduce additional species-specific thresholds.

We expect the rate of species shifts to remain constant or accelerate over the next century. The changes we observed in the overstory and understory vegetation resulted from an increase in annual mean temperature of less than 2°C, while regional climate models predict that the northeastern US can expect an additional 2.9 to 5.3°C increase in average annual temperature by 2100 with associated increases of 6.4 to 11.4 % in precipitation (Hayhoe et al. 2007, Tang and Beckage 2010). This amount of climate change is likely to have a large impact on future species distributions, resulting in increasingly divergent responses among co-occurring species with the potential for the formation of novel communities. Responses of vegetation to recent climate change may therefore not be indicative of future responses as climate thresholds for individual species are reached. Interactions between climatic changes and other anthropogenic stressors, such as airborne pollution, land use changes, and the spread of exotic organisms, are likely to exacerbate rates of change and the potential for localized extirpations, rendering future projections of vegetation change uncertain (Aber 2001), and increasing the potential for ecological surprises or state shifts (e.g., Paine et al. 1998, Platt et al. 2002, Beckage and Ellingwood 2008).

2.6 Conclusion

We examined understory species shifts across an elevational gradient in response to 40 years of regional climatic and environmental change. The pattern of observed responses indicates that species are responding to multiple anthropogenic perturbations in a complex manner with relatively similar species responses at some elevations, while at others, species respond more individualistically. We suggest, however, that due to nonlinear responses to species-specific climatic thresholds, communities will become increasingly divergent as the magnitude of climate change increases. Anthropogenic acid deposition and invasive earthworms, in conjunction with climate change, may have contributed to individual species responses and community shifts at affected elevations. The increasing magnitude of climate change together with interactions with other anthropogenic perturbations such as acid deposition and the spread of invasive organisms may cause rapid changes in species distributions and the formation of novel plant assemblages as the responses of species within communities diverge.

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2.8 Tables and Figures

Tables

Table 2. 1: The species used in our over- and understory analyses. The community analyses were limited to understory species that were observed in at least 3 of the 5 survey years and the species analysis were further limited to species found in 1965 and 2006, the end points of our vegetation censuses. This resulted in more species used for the community analysis than the species analysis. The taxa not included in the species analyses are identified with an (*). All nomenclature is consistent with Magee and Ahles (1999).

Understory Species	**Overstory Species**
**Actaea pachypoda* Ell.	*Abies balsamea* (L.) P. Mill.
Aralia spp. L.	*Acer saccharum* Marsh.
Arisaema triphyllum L.	*Betula alleghaniensis* Britt.
Aster spp. L.	*Betula papyrifera* var. *cordifolia* (Regel) Fern.
**Athyrium* spp. Roth	*Fagus grandifolia* Ehrh.
**Botrychium virginianum* (L.) Sw.	*Fraxinus americana* L.
Cardamine diphylla (Michx.)	*Picea rubens* Sarg.
Caulophyllum thalictroides (L.) Michx.	
Clintonia borealis (Ait.) Raf.	
Coptis trifolia (L.) Salisb.	
Cornus alternifolia L.	
Cornus canadensis L.	
Cyperaceae	
Dennstaedtia punctilobula (Michx.) Moore	
Dryopteris spp. Adans.	
Galium spp. L.	
Huperzia spp. Bernh.	
Hydrophyllum virginianum L.	
Impatiens capensis Meerb.	
Laportea canadensis (L.) Wedd.	

Lonicera canadensis Bartr.

Maianthemum canadense Desf.

Maianthemum racemosa (L.) Link

**Medeola virginiana* L.

Mitchella repens L.

Monotropa uniflora L.

Moss (except *Sphagnum* spp.)

**Osmorhiza claytonii* (Michx.) C.B. Clarke

Oxalis spp. L.

Phegopteris connectilis (Michx.) Watt.

Poaceae

Polystichum acrostichoides (Michx.) Schott

Prenanthes altissima L.

Ribes spp. Wildl.

Rubus spp. L.

**Sambucus* spp. L.

**Solidago* spp. L.

**Sphagnum* spp. L.

Streptopus spp. Michx.

**Thalictrum pubescens* Pursh

**Thelypteris noveboracensis* (L.) Nieuwl.

Tiarella cordifolia L.

Trientalis borealis Raf.

Trillium spp. L.

Uvularia sessilifolia L.

Veratrum viride Ait.

Viburnum lantanoides Michx.

Table 2. 2: Table 2.2: Trends in percent cover between 1965 and 2006 are shown by elevation for each understory species used in the understory community analysis. "0" indicates no change and "NA" indicates that the species was not found at the given elevation.

Species	**Elevation (m)**										
	549	**610**	**671**	**732**	**792**	**853**	**914**	**975**	**1036**	**1097**	**1158**
Actaea pachypoda[1]	0	-	-	0	NA	NA	NA	NA	NA	NA	NA
Aralia spp.[2]	+	+	+	-	-	-	-	+	NA	NA	-
Arisaema triphyllum[3]	+	+	+	+	NA	+	NA	NA	NA	NA	NA
Aster spp.[4]	-	-	-	-	-	-	-	-	-	-	+
Athyrium spp.[5]	-	-	-	-	-	0	NA	NA	NA	NA	NA
Botrychium virginianum[6]	NA	-	0	-	NA	NA	NA	NA	NA	NA	NA
Cardamine diphylla[7]	-	NA	+	NA	NA	NA	NA	NA	NA	NA	NA
Caulophyllum thalictroides[8]	-	-	-	+	NA	0	NA	NA	NA	NA	NA
Clintonia borealis[9]	+	-	-	-	-	-	-	-	-	-	-
Coptis trifolia[10]	NA	NA	NA	NA	NA	-	+	+	+	-	-
Cornus alternifolia[11]	+	-	+	-	NA	NA	NA	NA	NA	NA	NA
Cornus canadensis[12]	NA	NA	NA	NA	NA	NA	-	-	+	-	-
Cyperaceae[13]	-	-	-	-	-	-	-	0	+	-	-
Dennstaedtia punctilobula[14]	-	+	-	-	+	-	-	-	0	NA	NA
Dryopteris spp.[15]	+	-	-	-	-	-	-	-	-	-	-
Galium spp.[16]	-	+	-	0	-	NA	NA	NA	NA	NA	NA
Huperzia spp.[17]	+	-	-	-	-	-	-	-	-	+	-
Hydrophyllum virginianum[18]	-	-	-	-	NA	NA	NA	NA	NA	NA	NA
Impatiens capensis[19]	-	-	-	-	-	NA	NA	NA	NA	NA	NA
Laportea canadensis[20]	-	-	-	-	NA	NA	NA	NA	NA	NA	NA
Lonicera canadensis[21]	0	0	0	0	-	NA	NA	NA	NA	NA	NA
Maianthemum canadense[22]	-	-	-	-	-	-	+	0	NA	-	+
Maianthemum racemosa[23]	-	-	-	-	0	NA	NA	NA	NA	NA	NA

Medeola virginiana [24]	-	NA	0	NA	NA	NA	NA	NA	0	NA	NA
Mitchella repens [25]	+	NA	+	-	NA	+	NA	NA	NA	NA	NA
Monotropa uniflora [26]	NA	NA	0	NA	0	-	+	+	0	0	NA
Moss [27]	+	+	-	-	-	-	-	+	+	-	-
Osmorhiza claytonia [28]	-	-	-	-	NA	NA	-	NA	NA	NA	NA
Oxalis spp. [29]	-	-	-	-	-	-	-	-	-	-	-
Poaceae [30]	-	-	-	-	-	-	NA	0	+	NA	NA
Polystichum acrostichoides [31]	-	-	-	+	NA	NA	NA	NA	NA	NA	NA
Prenanthes altissima [32]	-	-	-	+	-	NA	NA	NA	NA	NA	NA
Ribes spp. [33]	NA	-	-	-	+	-	-	-	-	-	-
Rubus spp. [34]	-	+	-	-	-	+	NA	NA	NA	NA	NA
Sambucus spp. [35]	-	-	-	-	-	NA	0	NA	NA	NA	NA
Solidago spp. [36]	0	-	-	-	-	-	NA	NA	NA	-	-
Sphagnum spp. [37]	NA	NA	NA	NA	NA	+	+	+	+	-	+
Streptopus spp. [38]	-	-	-	-	-	+	0	0	NA	NA	NA
Phegopteris connectilis [39]	+	0	-	0	+	-	-	-	-	-	NA
Thalictrum pubescens [40]	+	+	+	0	NA	NA	NA	NA	NA	NA	NA
Thelypteris noveboracensis[41]	-	0	-	-	-	0	0	NA	NA	NA	NA
Tiarella cordifolia [42]	-	-	-	-	-	NA	NA	NA	NA	NA	NA
Trientalis borealis [43]	+	NA	-	0	NA	NA	NA	+	0	-	-
Trillium spp. [44]	-	-	-	-	-	-	NA	NA	NA	NA	NA
Uvularia sessilifolia [45]	-	-	0	0	0	NA	NA	NA	NA	NA	NA
Veratrum viride [46]	NA	-	+	+	-	NA	NA	NA	NA	NA	NA
Viburnum lantanoides [47]	+	+	-	-	-	-	-	0	0	NA	NA
Viola spp. [48]	-	-	-	-	-	-	NA	NA	NA	NA	NA

Figures

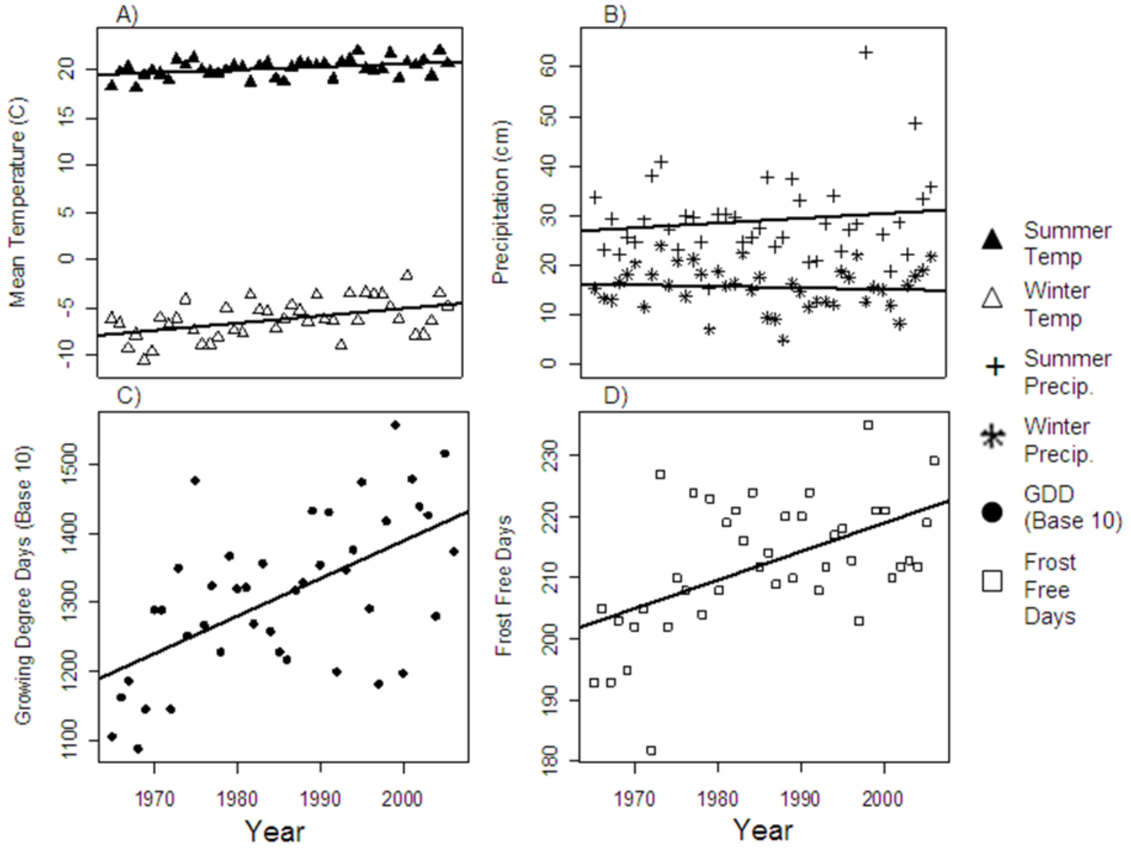

Figure 2.1: Trends in A) mean winter and summer temperatures, B) winter and summer precipitation, C) annual number of growing degree-days with a base of 10°C, and D) number of frost free days between 1965 and 2006, based on records from Burlington International Airport, Burlington, VT, USA

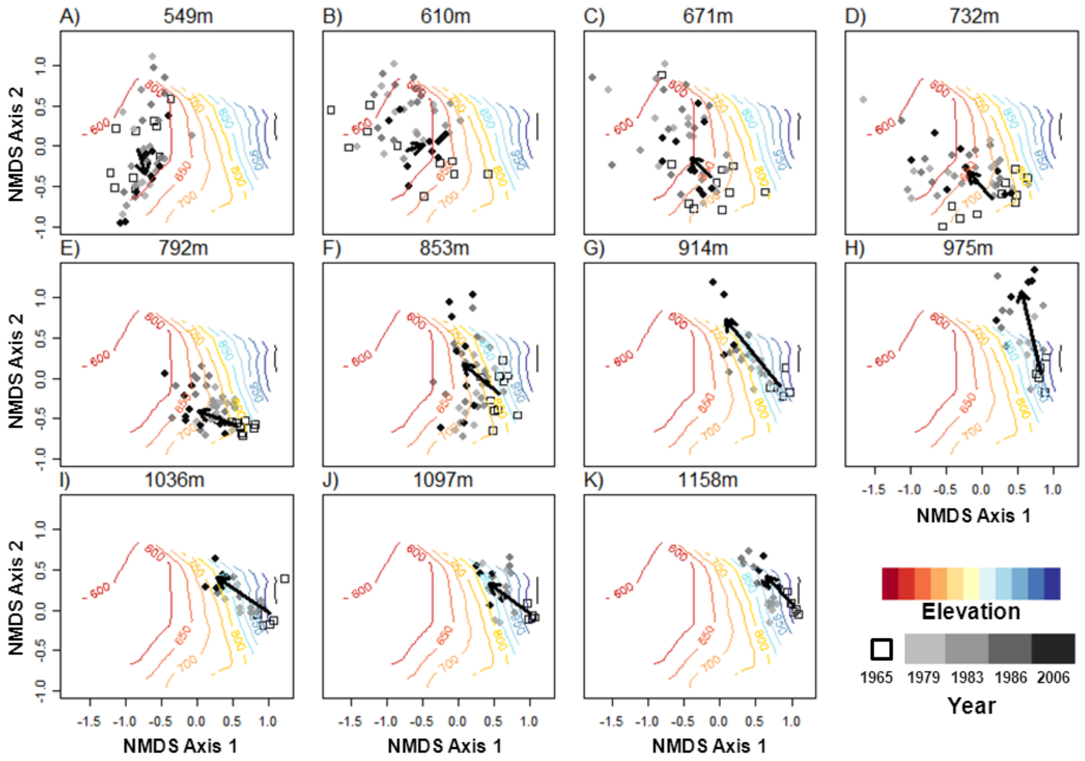

Figure 2.2: Changes in understory community composition within NMDS ordination space by elevation. Each point represents an understory community as defined by the average percent cover of each species present in a plot. All point locations are the result of a single ordination. Vectors represent the average magnitude and direction of community shift between 1965 and 2006 within the NMDS ordination space at each of the 11 sampled elevations. Panels A through D represent the northern hardwood forest elevations, panels I through K represent boreal forest elevations, and panels E through H represent ecotonal elevations between the two forest types. Isolines were calculated based on the elevational position of understory communities in 1965. Vectors that indicate a shift from high to low elevation, based on the isolines, represent communities that currently contain species assemblages previously found at lower elevations. For example, a data point representing a community sampled in 2006 at 792 meters (panel E) located close to the 650 meter isoline indicates that the species assemblage found at this location is most similar to assemblages found at 650 meters in 1965. Stress: 0.19

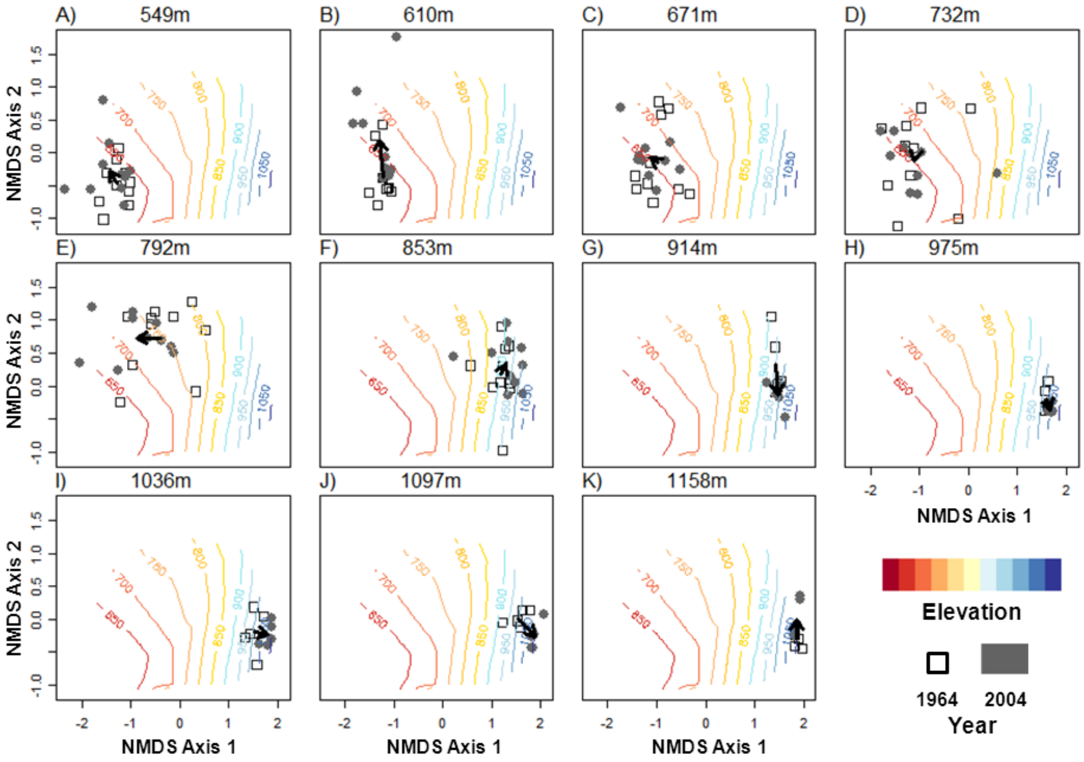

Figure 2.3: Change in overstory community composition within NMDS ordination space by elevation. As in Figure 2.2, all point locations are the result of a single ordination and vectors indicate the canopy compositional change within NMDS ordination space between 1964 and 2004 at each of the 11 sampled elevations. Isolines were again calculated based on the elevational position of communities in 1964. Stress: 0.12

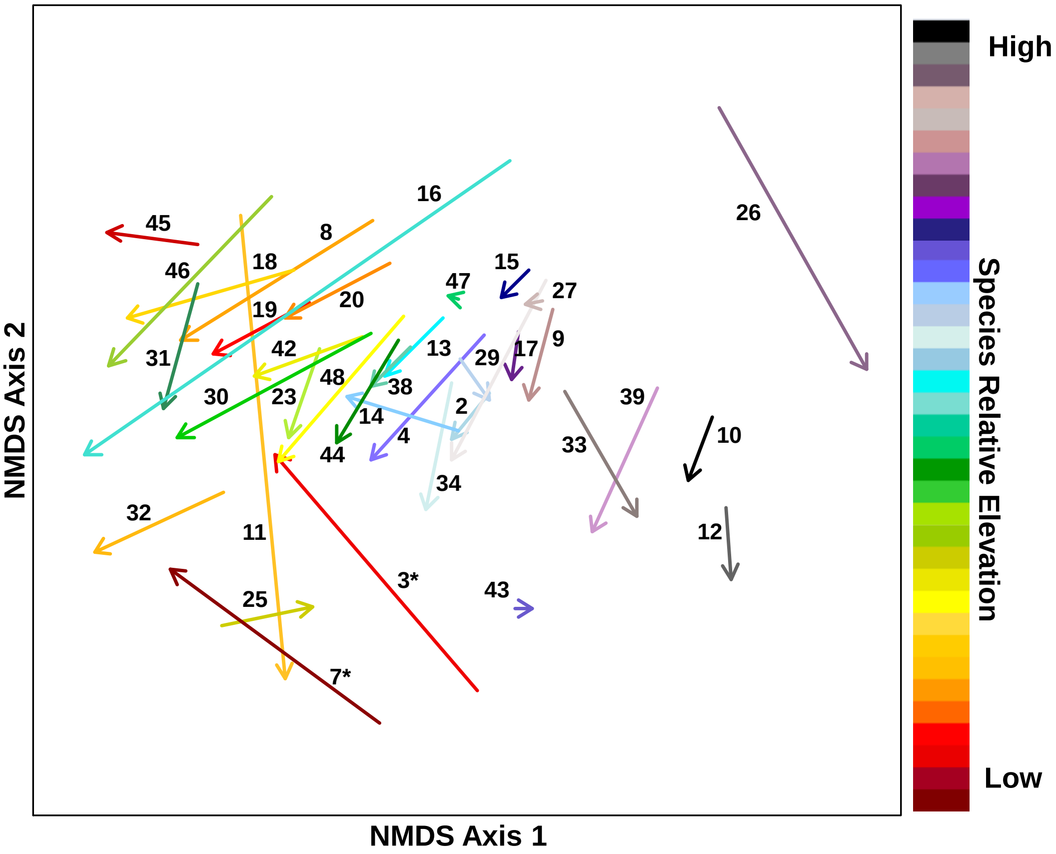

Figure 2.4: Changes in the elevational distribution of understory species within NMDS ordination space from 1965 to 2006. Each vector connects the location of species in their initial survey year to their location in the most recent survey, indicating overall change. The color of the points in this case does not correspond to a specific elevation, but instead conveys the rank-order of species from low (red) to high elevations (black) based on their average elevation. The numbers identifying each vector correspond to the superscripts assigned to each species in Table 2.2. The asterisks (*) in the figure denote the understory species *Arisaema triphyllum* and *Cardamine diphylla.* Stress: 0.25

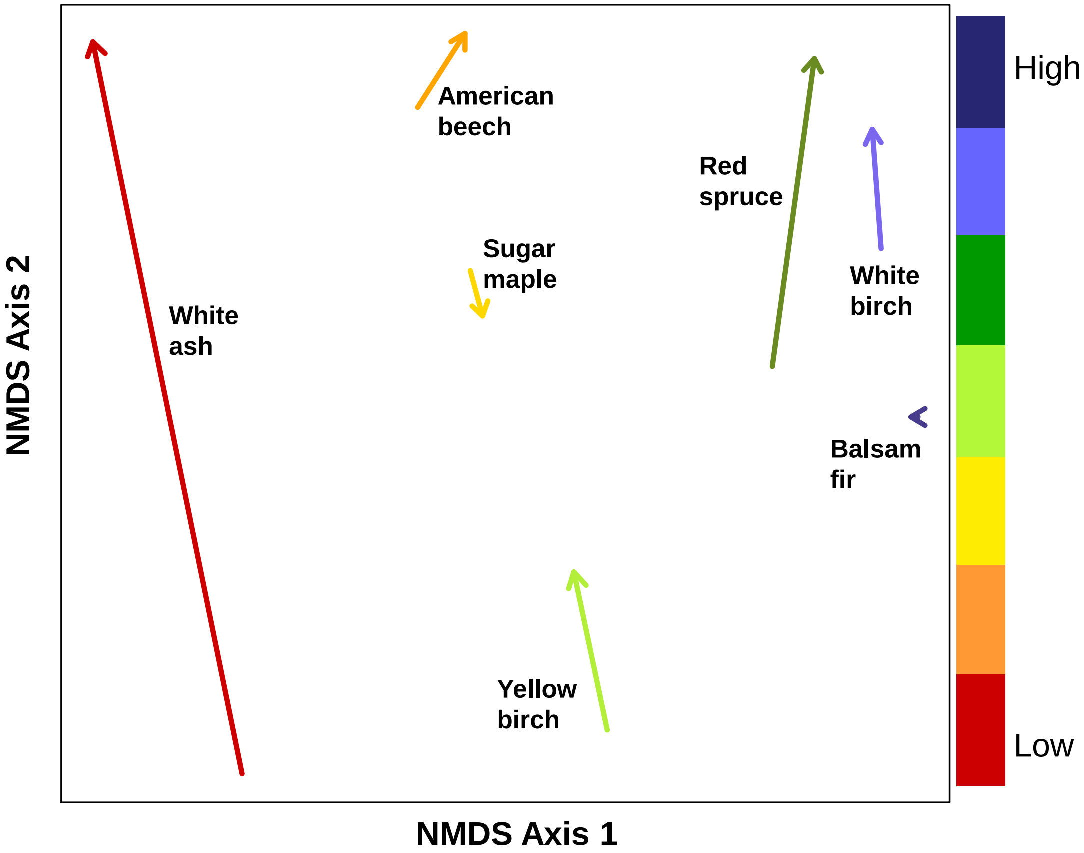

Figure 2.5: Changes in the elevational distribution of overstory species from 1964 to 2004. Vectors indicate change as in Figure 2.4 and colors represent elevation from low (red) to high (blue). Stress: 0.07

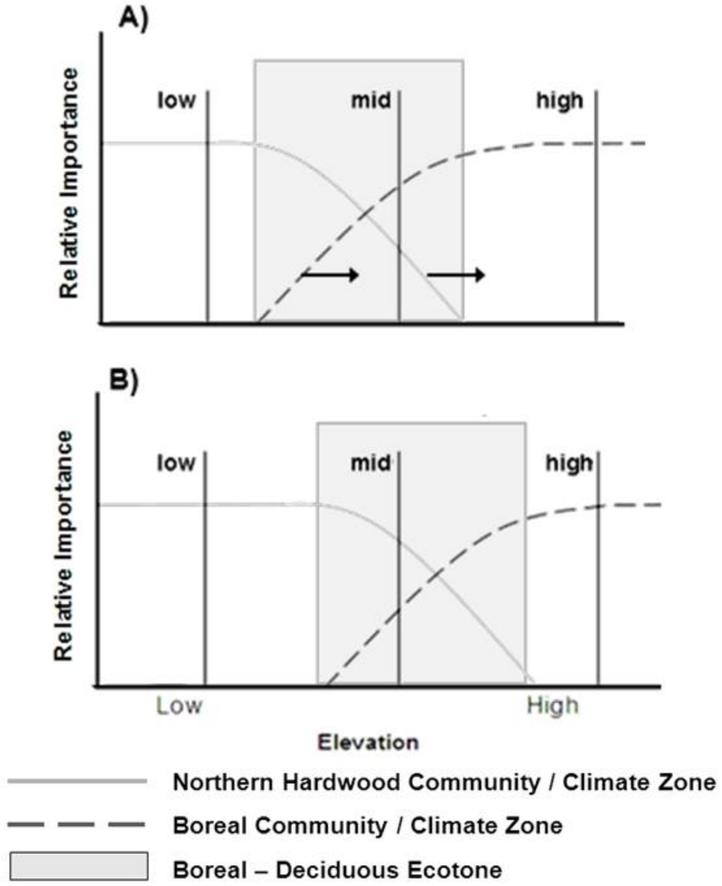

Figure 2.6: A conceptual representation of community change in response to warming temperatures between northern hardwood and boreal species at three elevations (low, mid and high). A) The relative importance of community types and climate zones before any warming has occurred. The height of the curves represents the relative importance or performance of each community type at a given elevation. B) The abundance of community types and the location of climate zones following warming at the same three elevations.

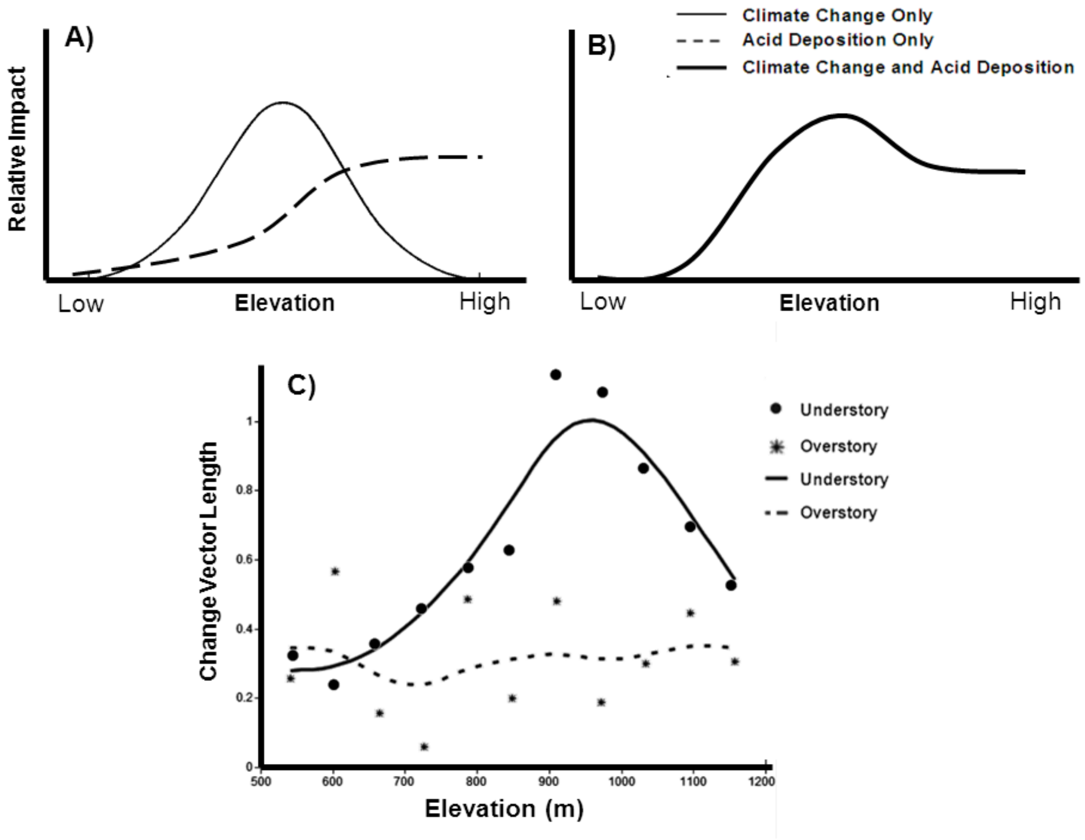

Figure 2.7: The expected impacts of climate change and acid deposition on community composition. A) The expected relative contributions of climate change and acid deposition on plant community compositional change across our elevational gradient. B) The combined impact of climate change and acid deposition on plant community compositional change across our elevational gradient. C) Arrow lengths for over- and understory communities indicating the average change in community composition at each sample elevation. Trends in arrow lengths across elevations were smoothed with a cubic spline. λ=0.05

2.9 Supplemental Material

Appendix 2A: Detailed Historic Species Abundance

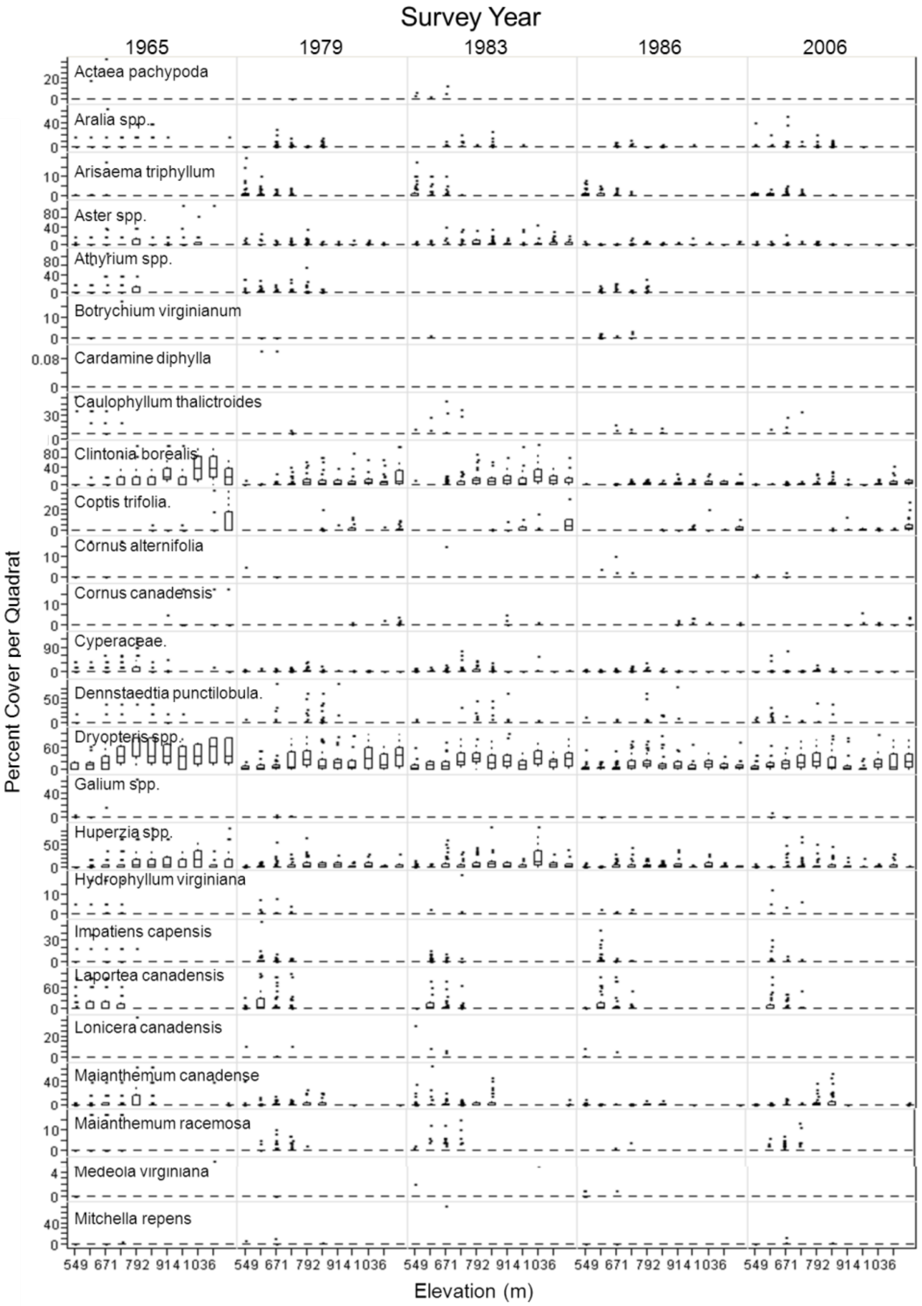

Figure 2A.1: The percent cover of each species in each of the five survey years across the entire elevational range. Notice the scaling of the y-axis varies across species.

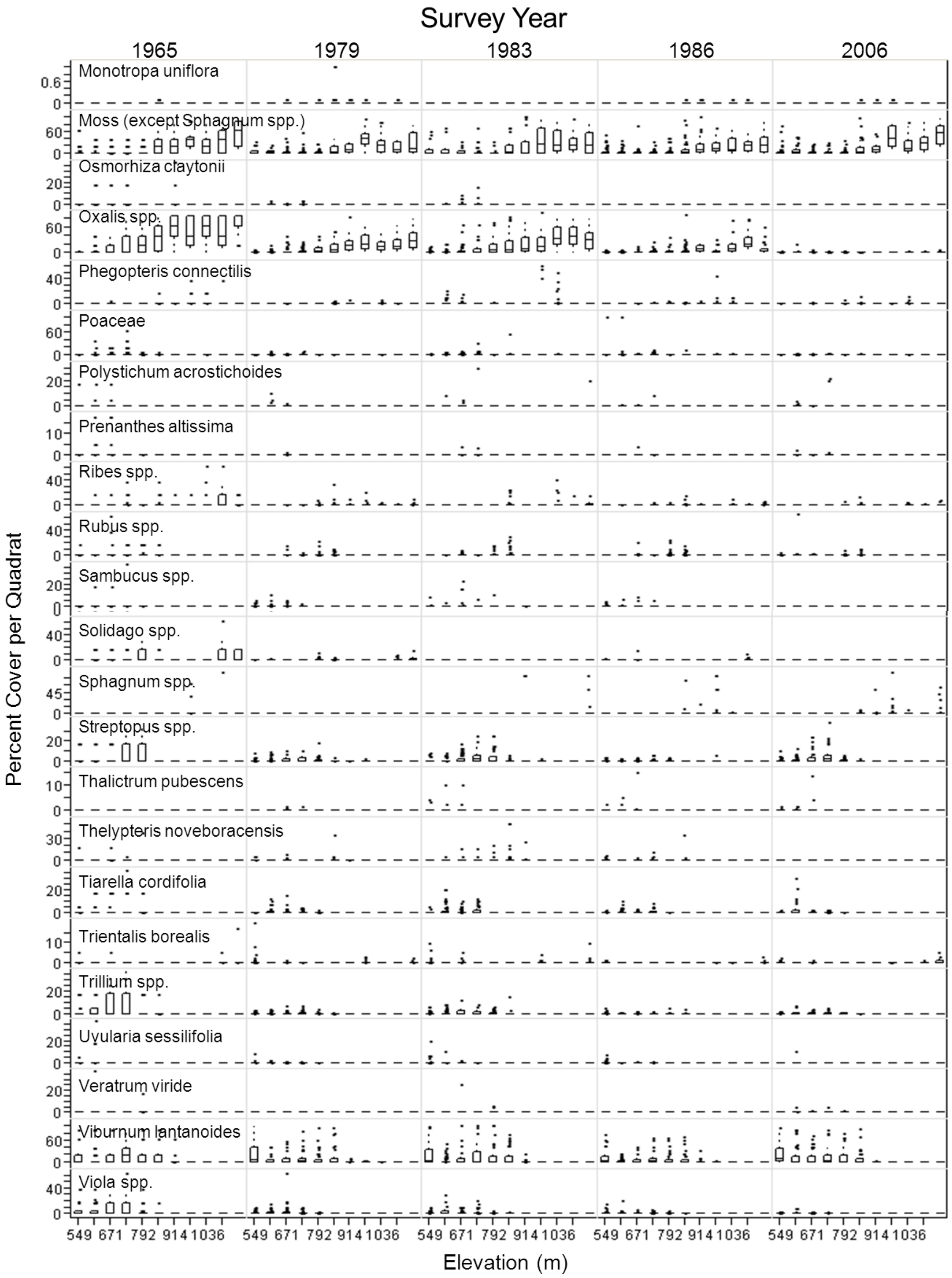

Figure 2A.1 cont.

Appendix 2B: Detailed NMDS Results

Table 2B.1: Arrow lengths as seen in the NMDS community analyses (Figures 2.2 and 2.3). These arrow lengths represent the magnitude of total compositional change in communities between 1965 and 2006 at each elevation.

Elevation (m)	Understory Arrow Length	Canopy Arrow Length
549	0.3295	0.2584
610	0.2374	0.5644
671	0.3565	0.1578
732	0.4598	0.0623
792	0.5734	0.4829
853	0.6204	0.202
914	1.1255	0.4785
975	1.0705	0.1904
1036	0.8517	0.2993
1097	0.7026	0.4437
1158	0.5243	0.3055

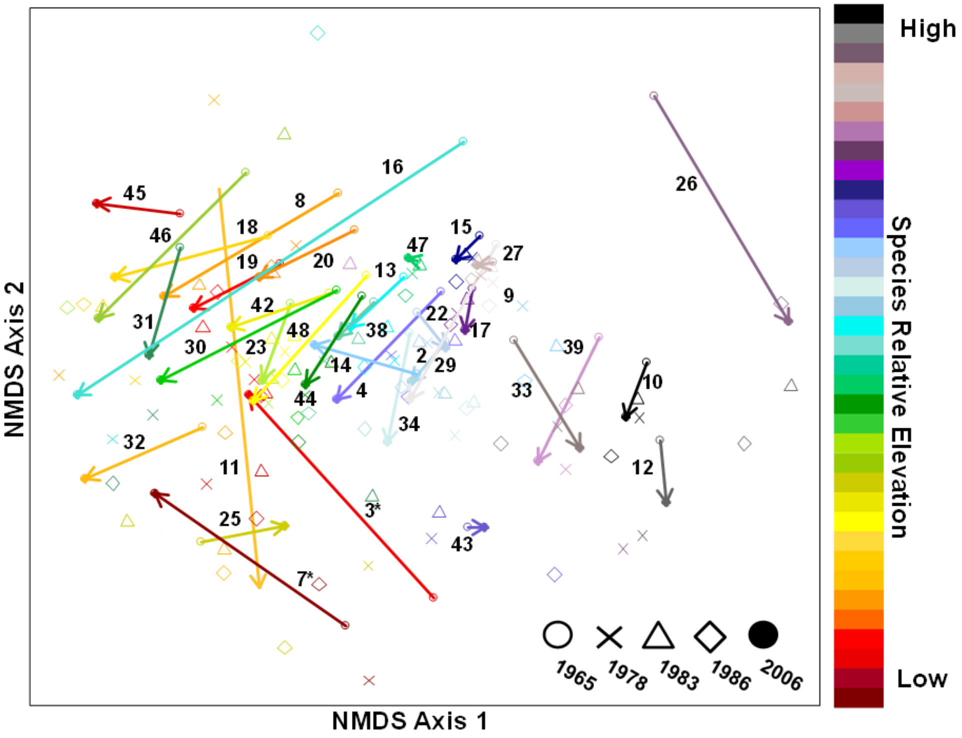

Figure 2B.1: Changes in the elevational distribution of understory species within NMDS ordination space from 1965 to 2006. Each vector connects the location of species in their initial survey year to their location in the most recent survey, indicating overall change. Other points represent species in 1978, 1983 and 1986. The color of the points and vectors in this case does not correspond to a specific elevation, but instead conveys the rank-order of species from low (red) to high elevations (black) based on their average elevation. The numbers identifying each vector correspond to the superscripts assigned to each species in Table 2.2. The asterisks in the figure denote the understory species *Arisaema triphyllum* and *Cardamine diphylla* that exhibit a shift that contrasts with other low elevation species and may be indicative of establishment of invasive earthworms.

CHAPTER 3: ARTIFICIAL WARMING ALTERS SEEDLING COMMUNITY COMPOSITIONS ALONG AN ELEVATION GRADIENT IN A TEMPERATE FOREST

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3.1 Abstract

Tree species are expected to shift their ranges in response to global climate change, but the rate at which range shifts occur is likely to be mediated by environmental or biological factors that inhibit or promote seedling establishment. We examined the potential for global warming to interact with overstory light conditions and soil nutrients to determine recruitment success across elevations in the boreal-deciduous ecotone (BDE). We specifically examined the potential for seedling establishment of two low-elevation northern hardwood species, sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*), and two high-elevation boreal species, red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*) across an elevational ecotone between these two forest types in the northeastern US. We monitored growth and survivorship responses of seedlings reciprocally planted across a range of elevations, light conditions, soil calcium concentrations and growing season temperatures. Our results indicate that sugar maple survivorship was 62% lower at 950 m.a.s.l. than at 500 m.a.s.l. ($p<0.0001$). Yellow birch survivorship, though consistently low, was not significantly affected by elevation. Experimental warming with open-top-chambers (OTCs) increased sugar maple survivorship above the ecotone at 950 m.a.s.l. by 22% ($p<0.0001$), 25% for spruce ($p=0.0180$) and 6% for fir ($p=0.0169$). Birch survivorship was not significantly affected by warming at any elevation suggesting that warming will increase maple survivorship in the boreal zone, but not birch. Birch survivorship was instead mediated almost exclusively by light ($p<0.0001$), however, warming did increase the relative growth rate (RGR) of birch by an average of 63%. Additionally, evidence suggests that dispersal or germination limitation contributes to the exclusion of maple and birch from high elevations in natural communities. As a result, we expect continued climate change will increase the relative abundance of maple in the boreal zone, effectively raising the BDE. However, because birch survivorship does not increase with warming, we believe it is more likely that birch migration will lag behind the rate of climate change, ultimately altering future high elevation forest composition in favor of sugar maple and red spruce.

Keywords: Acidic Deposition, Artificial Warming, Climate Change, Light, Montane Forests, Northern Hardwoods, Migration

3.2 Introduction

Continued anthropogenic climate change is expected to increase global mean temperatures by up to 4.8°C degrees by the end of this century (IPCC 2013). Species are expected to migrate poleward and upward in an attempt to maintain their current relationship with climate and stay within their climate envelope (Lenoir et al. 2008, Tang and Beckage 2010, Thomas 2010). Evidence of range shift in response to recent climate change has been observed globally in a wide range of habitats (Beckage et al. 2008, Greenstein and Pandolfi 2008, Kelly and Goulden 2008, Forbes et al. 2010). However, predicting the rate at which species' ranges will shift remains difficult due to the complexity of climate change (Williams et al. 2007), non-linear biological responses to warming (Brooker et al. 2007), interactions with non-climatic environmental limitations (i.e. topography, light, soil, land use) and other anthropogenic disturbances (i.e. acid deposition, invasive species, carbon and nitrogen fertilization) (Walther et al. 2002, Higgins et al. 2003a). This complexity and the number of interacting factors have limited the number of experimental studies focused on forest migration (Zhu et al. 2012).

Species responses to climate change are likely to be mediated by several different environmental conditions. Species ranges can respond to changes in precipitation (Lutz et al. 2010), disturbance regime (Stevens and Beckage 2009), biotic interactions (Brooker et al. 2007, Ibanez et al. 2009), land-use (Hofgaard 1997), or pollution accumulation (Johnson and Taylor 1989, Rusek 1993). The accumulation of acidic deposition over the past century, for example, has reduced soil calcium concentrations in the northeastern US (Likens et al. 1996, Hawley et al. 2006) and elsewhere (Thimonier et al. 2000) causing canopy decline in sugar maple (*Acer saccharum*) (Schaberg et al. 2006) and red spruce (*Picea rubens*) (Schaberg and

DeHayes 2000). The interactions between these environmental changes and anthropogenic warming can affect the rate of species migration and determine whether a species is able to keep pace with current climate change and stay within their optimal climate zone (Walther 2003, Brooker et al. 2007).

In this study, we examined the factors that limit establishment and growth of temperate tree seedlings in the northeastern United States across an elevational gradient. These factors ultimately control the distribution of tree species and limit upslope advance of the lower elevation northern hardwood forest community into the upper elevation boreal forest. Previous studies in this region across the Boreal-Deciduous Ecotone (BDE) have shown that since the mid-1960's, forest trees and understory herbs have shifted upslope, corresponding to increases in temperature and precipitation (Beckage et al. 2008, Pucko et al. 2011).

Our objectives were to determine i) whether climate currently limits northern hardwood seedling survival and/or growth at elevations above the BDE, ii) whether the increases in temperatures expected with continued climate change will increase the survivorship and/or growth of northern hardwood seedlings at elevations above the BDE and finally, iii) whether other environmental or biological factors influence seedling establishment along this elevational gradient. Northern hardwood and boreal seedlings were monitored across elevations to determine whether current species compositions are the result of environmental conditions, dispersal, germination or competition. To determine the ecotone controls, we examined the growth and survivorship of seedlings planted across the BDE at four elevations from 500 to 950 m.a.s.l.. We planted seedlings at each elevation beneath single-tree sized gaps and under closed canopies with calcium addition and warming treatments factorially applied to seedling plots. We monitored subsequent seedling survival and growth in response to elevation, light, soil calcium and temperature. We chose to study seedlings and their distributions as opposed to mature trees so that we can determine the relationship between species establishment and current climate instead of past climate (Lenoir et al. 2009).

3.3 Methods

Site Description

This study was conducted on Mount Mansfield (44°31'33.95"N / 72°48'55.00"W), which is the highest peak in Vermont at 1337 m.a.s.l.. Mount Mansfield is part of the Green Mountains, a northern extension of the greater Appalachian Mountain chain, and is dominated by glacial topography with (chlorite, mica and garnet-bearing) schist bedrock (Christman 1959, Munroe 2006). Soils are predominantly entisols and spodosols, consisting of acidic, stony, and sandy loams (NRCS 2010). Mount Mansfield's climate is similar to that of other northeastern montane regions and is characterized by large diurnal and annual temperature fluctuations (Siccama 1974). The base of Mount Mansfield (338 m.a.s.l.) experiences average January and July temperatures of -8.7 °C and 19.6 °C respectively, while the average summit (i.e., 1204 m.a.s.l) temperatures are significantly lower at -12.5 °C in January and 14.8 °C in July. Precipitation on Mount Mansfield and throughout much of the Northeast is evenly distributed throughout the year, averaging 109.8 cm annually at the base and 200.2 cm annually at the summit (NOAA/NESDIS/NCDC 2005). In addition to precipitation, cloud water deposition can augment moisture availability at high elevations by 50 to 65% (Vogelmann et al. 1968, Lovett et al. 1982).

Northern hardwood and boreal forests are the two dominant forest types, stratified by elevation, that occupy the majority of our study area on Mount Mansfield and the surrounding mountains (Siccama 1974, Cogbill and White 1991, Beckage et al. 2008). Northern hardwood forest is dominant below 700 m.a.s.l. and is characterized by presence of sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*) and yellow birch (*Betula alleghaniensis*). Boreal forest is dominant above approximately 900 m, and is primarily a coniferous forest with red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*), though mountain paper birch (*Betula papyrifera* var. *cordifolia*) and mountain ash (*Sorbus americana*) are also common (Siccama 1974, Cogbill and White 1991). This boreal forest extends upward until it reaches a krummholz zone and the alpine summit at approximately 1200 m.a.s.l.. Between the northern hardwood and boreal forests, from approximately 700 to 900 m.a.s.l., lies the spatially compact transition zone referred to here as the boreal - deciduous ecotone (BDE) (Siccama 1974, Beckage et al. 2008, Pucko et al. 2011).

Seedling Preparation

For this study, we collected and transplanted seedlings of four of the most dominant tree species in the northern montane forests, sugar maple, yellow birch, red spruce and balsam fir. Beech was not chosen because a majority of beech reproduction takes place vegetatively through root sprouting (Held 1983). Sugar maple, yellow birch and balsam fir seedlings were collected as germinants (with cotyledons) soon after emergence on Mount

Mansfield or on Camels Hump (44° 19’ N, 72° 53’ W), approximately 25 km away. The collection of these seedlings took place between mid-May and the first week of June in 2007 and 2008. Seedlings collected in the field were temporarily re-planted in potting soil with no added fertilizers and were kept outdoors under 50% shade cloth to minimize mortality due to transplant shock (Table 3C.1). Due to an inadequate supply of red spruce seedlings in the field, we started red spruce seedlings from seed collected in Maine (Angelgrove Seed Co., Harbour Grace, Newfoundland, CANADA). Seeds were started in early May in greenhouse conditions, but were moved outside with the other tree seedlings as soon as possible in an effort to standardize pre-planting conditions. Seedlings were potted for 2-5 weeks before being transplanted into the field.

Treatments

We examined the influence of elevation, light availability, temperature and calcium availability on seedling establishment. These treatments were applied in June of 2007 or 2008 and maintained through October of 2009 when seedlings were removed from the field. We describe each treatment in detail below.

We planted seedlings at four elevations spanning the BDE. The highest and lowest elevations, 500 and 950 m.a.s.l., represented non-ecotonal forest in the northern hardwood and boreal forests, respectively. The two remaining elevations were located near or within the BDE at 650 (lower ecotone) and 800 m.a.s.l. (upper ecotone). In 2007, we planted seedlings only at the highest and lowest elevations, while seedlings were planted at all four elevations in 2008.

Each year we selected three planting sites per elevation, each containing a single pair of plots. At each site, one plot was located under a single-tree sized gap (GAP) while the other was located beneath an intact canopy (SHADE). Plots in each site were placed less than 20 m apart to reduce uncontrolled spatial variability, e.g., underlying bedrock composition. We used naturally occurring canopy gaps but, in some cases, removal of saplings or large branches was necessary in order to create a gap large enough for our treatment applications. The differences in the light conditions between GAP and SHADE plots differed by elevation, gap size (Table 3D.1), tree height and aspect. Unfortunately, the complexity and dynamic nature of the light environment in forests proved difficult to describe and our efforts to quantify the light environment in each plot were inconsistent and ultimately unreliable.

Within each plot, we applied experimental calcium and temperature treatments to 0.5 x 0.5 m quadrats as described below. Plots that originated in 2007 each contained 16 quadrats; those we planted in 2008 each contained eight. In each quadrat, we planted a single sugar maple, yellow birch, red spruce and balsam fir seedling. Factorial treatment combinations of temperature and calcium treatments were randomly assigned to quadrats, allowing us to examine their individual and combined impacts on seedling growth and survivorship with respect to light and elevation.

Using open-top-chambers (OTCs), we examined the influence of anthropogenic warming on seedling performances. Temperatures were modified in quadrats with passively warmed OTCs. Our hexagonal OTCs were made of translucent 1.5 mil polyethylene plastic sheeting and galvanized steel wire (Figure 3.1) modeled after OTCs used by the International

Tundra Experiment (ITEX) for monitoring changes in arctic vegetation(Hollister and Webber 2000). Sheeting reduced light quantity by approximately 18% under each OTC, but did not affect the spectral characteristics of the sunlight (Appendix 3A, Figure 3A.1). All OTCs sat approximately 3-4 cm above the ground so as to not affect water flow or access of insects and small mammals to the seedlings.

We implemented two types of OTCs: full OTCs and half OTCs. Half OTCs were initially designed as controls to test the effects of the presence of an OTC structure without inducing any warming since the presence of an OTC could, for instance, influence seedling herbivory by deer or small rodents. However, since warming did occur under the half OTCs, we instead consider them a separate, intermediate warming treatment. Therefore, in 2008, 50% of quadrats were outfitted with full OTCs, while half OTCs were placed over an additional 25% of quadrats with the last 25% of quadrats remaining open. In 2007, half of all quadrats were open with the other half outfitted with full OTCs. We placed OTCs over quadrats immediately after planting was completed on June 28, 2007, June 26, 2008 and as soon as sites were accessible by car on May 29, 2009. We removed all OTCs in late October of each year to prevent physical damage from the weight of the snowpack. As a result, experimental warming occurred only during the growing seasons and was not present over winters.

The amount of warming that the OTCs provided each quadrat differed with OTC type, elevation and light condition (e.g. GAP versus SHADE). Half OTCs altered the ambient growing season temperature by between -0.1 and 0.6 °C. Full OTCs increased internal temperatures by between 0.2 and 1.0°C (Table 3.1). OTCs placed under closed canopies produced greater overall warming, despite receiving less direct sunlight and having lower daily maximum temperatures than quadrats containing OTCs in gaps. These larger temperature increases reported in SHADE plots are the result of OTCs in these sites providing greater nighttime insulation, resulting in smaller diurnal temperature ranges (Table 3.2). This insulating effect is not as pronounced in GAP plots because higher wind speeds (Chen et al. 1999) facilitate the mixing of air inside and outside of the OTCs. See Appendix 3A for additional information on the effects of OTCs.

We applied calcium fertilizers to half of the quadrats to determine the impact of soil calcium depletion, potentially caused by prolonged exposure to acid deposition. Commercial gypsum ($CaSO_4 \cdot 2H_2O$) (Espoma brand) fertilizer was applied to seedlings in 2007, while calcium fertilizer was applied to quadrats in the form of commercially available lime ($CaCO_3$) (LimeRite brand) at a rate of 30.5 g Ca m^{-2} in 2008. This was within the range of calcium applied to soils in similar studies in the Northeast aimed at identifying the impacts of soil calcium depletion in forests (25 g Ca m^{-2} (Moore et al. 2000) to 85 g Ca m^{-2} (Juice et al. 2006b)). Additional calcium was not added to quadrats following initial application.

Planting Procedure

We planted seedlings into the field and applied experimental treatments in mid- to late-June, 2007 and 2008. In order to mimic recent gap formation, avoid disturbing the below ground environment, reduce above ground competition and limit the differences between gap and shade plots, we cut above ground herbaceous vegetation at ground level within each quadrat. This process of cutting herbaceous vegetation continued throughout the study. Additionally, we planted seedlings in a square pattern at least 20 cm apart (Figure

3.1c) to reduce the chance that seedlings would affect each other through above ground competition within the time span of this study. The location of each species within the OTCs was selected randomly. Two weeks following the initial planting, we replaced dead seedlings and assumed their mortality was a result of transplant shock (Table 3C.1). Mortality of those seedlings was not included in any of our analyses.

Climate Data

We estimated temperatures and growing degree days (GGDs) for each site and under each type of OTC for the length of a growing season by comparing temperatures recorded in our plots using mobile dataloggers in 2009 with temperatures recorded at three nearby permanent weather stations. We used MicroLog PRO 700 and 750 dataloggers with a ±0.2°C accuracy to record temperatures every half hour at each site and under each of the different warming treatments. Dataloggers were moved from site to site, spending a minimum of two weeks at each location. The weather stations were located at three sites on Mount Mansfield; the first was located at the western base of Mount Mansfield at 338 m.a.s.l. in Underhill, VT at the Proctor Maple Research Center. The second and third weather stations were located at 884 m.a.s.l., one on the east slope and one on the west. These three weather stations recorded temperatures every 30 minutes.

We constructed full growing season temperature records for each OTC treatment in each plot by first pairing the temperatures recorded on the dataloggers with temperatures recorded at each of the three climate stations, then calculating the average difference between the logger temperatures and the temperatures at each weather station. We used these differences to extrapolate temperatures over the entire growing season, defined as

April 1 to October 31, for each of the weather station records. This yielded three complete growing season temperature estimates for each quadrat. We calculated a single growing season record by averaging these three records over each half hour period. Growing season growing degree-days (GDDs) with a base of 5°C (Eq. 3.1) were computed from this temperature record (Table 3.1) with $\hat{T}$ representing mean daily temperature (McMaster and Wilhelm 1997).

(Equation 3.1) $$GDD_{Growing\ Season} = \sum \left\{ if \begin{array}{ccc} \hat{T} & \geq 5 & \hat{T} - 5 \\ \hat{T} & < 5 & 0 \end{array} \right\}$$

The values reported in Table 3.1 estimate, as closely as possible, the actual GDDs and temperatures experienced by each seedling. The ambient temperature was used to determine GDDs and average growing season temperature for days before and after the application of OTCs. The cooling effect of the half OTC in GAP plots at 500 m.a.s.l. is within the error range for our data loggers and is, therefore likely to be instrumentation error (Table 3.1).

Camels Hump Forest Data Collection

We used elevational tree distribution data collected in 2004 and 2006 on nearby Camels Hump to compare with the results of our seedling experiments. Camels Hump was used to examine natural species distributions as opposed to Mount Mansfield because of its well-documented land-use history and more limited logging (Whitney 1988). Canopy composition and understory seedling abundance were surveyed in permanent vegetation plots at eleven elevations on Camels Hump in 2004 and 2006, respectively. In total, 85- 3 x 30 m overstory plots and 510- 1x1 m understory plots were surveyed between 549 and 1150 m.a.s.l.. For full site and data collection details, see Siccama (1974), Beckage et al. (2008) and Pucko et al. (2011).

Planted Seedling Data Collection

To measure seedling success, we monitored the survivorship and height growth of 1536 seedlings over the course of two growing seasons. Mortality and height measurements were recorded approximately once per month starting in May or June of each growing season and ending in late October. Height was measured from ground level to the tip of the apical bud. From these height measurements, we calculated relative growth rates (RGR_h) (Eq. 3.2) (Beckage and Clark 2003) where t equals time in days:

$$\text{(Equation 3.2)} \qquad RGR_h = \frac{\log\left(\frac{Height_t}{Height_o}\right)}{t}$$

Height was used to calculate growth rates as opposed to other measures of size or mass because of the biological significance of height in young seedlings. The seedling ultimately successful at a given location is likely to be the one that can overtop its neighbors and capture enough sunlight to maintain a positive carbon balance (Canham and Marks 1985). We found no significant within-species difference in initial seedling height for any of our treatments or treatment combinations ($p>0.05$).

Graphical and Statistical Analyses

Seedling growth and survivorship curves were plotted in R (R Core Team 2013) as Gaussian and beta distributions, respectively. RGR_h was plotted as a normal distribution where μ and σ were derived from generalized linear models using the *glm* function in R. The beta distribution we used to plot survivorship is defined as: $\beta(a, b) \sim \Gamma(a)\, \Gamma(b) / \Gamma(a+b)$, where *a*= 1+ # surviving individuals and *b*= 1+ # of dead individuals. We compared the effects of treatments on survivorship by comparing these beta distributions. Treatments were determined to be significant if the two distributions overlapped by less than 5%.

Model selection was used to identify the most important factors controlling survivorship and was calculated in two ways. First, we used the Akaike's Information Criterion corrected for small sample sizes (AICc), to identify the model of fixed effects most predictive of seedling growth and survivorship (Burnham and Anderson 1998). AICc values were calculated in R using the *glm* and *aicc* (qpcR library) (Ritz and Spiess 2008) functions. Models compared with AICc included all single factor models, all additive single factor models, a selection of biologically significant two-way interaction models and additive models containing those significant two-way interactions for a total of 34 models (Appendix 3B). We excluded interactions that were not *a priori* expected to influence each other, for instance light and calcium (LxC). In AICc analyses, all experimental variables were treated as factors.

We also employed Bayesian models to examine parameter estimates and identify significant variables in mixed models using the OpenBugs software program (version 3.2.1 rev.781) (OpenBugs Project Management Group, 2011). Bayesian methods were used so that we could better estimate the impact of both fixed and random effects. We used a Markov Chain Monte Carlo (MCMC) sampler to obtain parameter estimates by modeling survivorship as a Bernoulli process with a logit link. Survivorship probability θ was defined as: $\log\frac{\theta}{(1-\theta)} = X\beta + Z\omega$ where X and Z are the fixed and random effects design matrices, respectively. The fixed effects coefficient vector, β, contained the parameter estimates for elevation, light, calcium and temperature. The random effect vector, ω, contained parameter estimates for planting year, season and site. We used diffuse priors for all variables to allow the posterior parameter estimates to be primarily driven by the data. We report 1-tailed Bayesian p-values calculated as:

$$p = 2 * \left[\begin{matrix} \#of\ negative\ parameter\ estimates \\ or \\ \#of\ positive\ parameter\ estimates \end{matrix} \right] \div total\ \#\ of\ model\ estimates$$

Parameters were considered ‘significant’ if the Bayesian 1-tailed p-value was <0.05.

3.4 Results

Seedling survivorship without supplemental warming was greater at low elevations than at high elevations for all species (Figure 3.2). After two growing seasons, all four seedling species, regardless of planting year, survived better at 500 m.a.s.l. than at 950 m.a.s.l.. Sugar maple experienced the largest decline in survivorship with elevation, decreasing by an average of 62% between 500 and 950 m.a.s.l. ($p<0.0001$). Yellow birch, red spruce and balsam fir survivorship declined by an average of 22% ($p=0.003$), 25% ($p=0.002$) and 27% ($p=0.001$), respectively, between 500 and 950 m.a.s.l.. Even the conifers preferred 500 m.a.s.l. to 950 m.a.s.l., though maximum survivorship for both red spruce and balsam fir occurred at 800 m.a.s.l., averaging 42% and 83% survival, respectively (Figure 3.2). AICc model selection supported these findings and included elevation in the best models for both sugar maple and red spruce survivorship (Table 3.3). Bayesian model selection indicated that survivorship at 950 m.a.s.l. was significantly lower than survivorship at 500 m.a.s.l. for maple ($p=0.0002$), spruce ($p=0.0316$) and fir ($p=0.048$) (Table 3.4). However, elevation was not found to be an important factor influencing birch survivorship in either AICc or Bayesian model selection.

High light conditions present in GAP plots significantly increased the survivorship of yellow birch (p<0.0001), red spruce (p<0.0001) and balsam fir (p<0.0001), while conversely, sugar maple survivorship responded positively to the shaded conditions found under a closed canopy (p=0.0048) (Table 3.4). Light was chosen as a model component for birch, spruce and fir (Table 3.3). In ambient temperatures, yellow birch survivorship increased from 4% in SHADE plots to 29% in GAP plots (Figure 3.3). Additionally, none of the individual birches that survived in SHADE plots without warming was located above 500 m.a.s.l. (Figure 3.3). Without OTCs, maple survivorship increased slightly in SHADE plots at 500 and 650 m.a.s.l by 13% and 20%, respectively. However, it was at 950 m.a.s.l. that SHADE maple survivorship increased most dramatically. Without supplemental warming at this elevation, no sugar maple seedlings planted in 2008 were able to survive in GAP plots, but in SHADE plots, we observed 13% survivorship (p=0.038) (Figure 3.3). Spruce generally responded positively, but not significantly, to light and increased survivorship by an average of 8% in GAP plots (p=0.499). Fir seedlings grown in ambient temperatures also responded positively to high light conditions, averaging an increase in survivorship of 25% between GAP and SHADE plots (p=0.005). However, this trend was not consistent across all elevations (Figure 3.3).

On average, the warming in our half and full OTC treatments increased species' 2-year survivorship (Figure 3.4). With warming, sugar maple's average survivorship increased 16%, from 40 to 56% (p=0.002). OTCs also significantly increased red spruce seedling survival by 14% ($p=0.005$). Yellow birch and balsam fir did not experience a significant increase in survivorship with warming (Figure 3.4), nor was warming identified by AICc model selection as an important determinant of survivorship for those species (Table 3.3).

The impact of warming on survivorship was not consistent across all plots and instead varied with elevation, light and OTC type (Figures 3.4 and 3.5). OTC presence significantly increased overall seedling survivorship in GAP ($p<0.0001$) and SHADE plots ($p=0.047$). At 35%, survivorship under OTCs in GAP plots was higher than the 31% survivorship observed in SHADE plots with OTCs. However, OTCs in SHADE plots increased survivorship 7% more than OTCs in GAP plots (Figure 3.5). This corresponds to the greater warming produced by OTCs in SHADE plots than in GAP plots (Table 3.1).

Additionally, OTCs had a greater positive influence on survivorship at high elevation sites than at low elevation sites (Figure 3.4), which also correlates with the amount of warming OTCs produced across the elevation gradient (Table 3.1). At 950 m.a.s.l. survivorship under OTCs increased by an average of 22.4% for maple ($p<0.0001$), 25% for spruce ($p=0.0180$) and 5.8% for fir ($p=0.0169$) (Figure 3.4). Warming did not significantly increase birch survivorship at 950 m.a.s.l. despite having 12.5% seedling survival in SHADE quadrats with warming as opposed to 0% in un-warmed quadrats ($p= 0.451$) (Figure 3.5). Bayesian model selection confirmed the importance of warming at high elevations and identified significant increases in seedling survivorship at 950 m.a.s.l. with full OTCs for maple ($p=0.0012$), spruce ($p=0.0412$) and fir ($p=0.0198$) (Table 3.4). At 800, 650 and 500 m.a.s.l., warming did not significantly improve the overall survivorship of seedlings; however, seedlings in select combinations of experimental and environmental factors did experience significant increases in survivorship with OTCs. Maple ($p=0.0362$) and spruce ($p = 0.0164$) seedlings, for example, had significantly higher survivorship under full OTCs than in ambient temperatures in GAP plots at 650 m.a.s.l. (Figure 3.5).

In addition to increasing or decreasing the survivorship of individual species, warming altered the relative abundance of species, most often to the benefit of maple and spruce. In un-warmed, SHADE plots at 800 m.a.s.l., for example, fir was the most abundant seedling species (Figure 3.5). However, with the addition of full OTCs, maple survivorship increased from 50% to 75%, making it the most abundant species in SHADE plots (Figure 3.5). In gaps at 650 m.a.s.l., un-warmed quadrats were dominated by fir, which suffered no mortality over the duration of the study, while maple and spruce survived at a rate of 50% and 17%, respectively. Full OTCs altered conditions in favor of maple and spruce and increased their survivorship to 100% and 83% percent, respectively, while fir survivorship fell to 75%.

In addition to increasing seedling survival, OTCs increased relative growth rates (RGR_h) of all species with birch receiving the greatest benefit. OTCs provided birch with an average increase in RGR_h of 63% while maple, spruce and fir derived little, if any, increase in RGR_h from OTCs. Birch RGR_h increased from an average of 6.8×10^{-4} cm day^{-1} in ambient temperatures to 1.1×10^{-3} cm day^{-1} under OTCs (Figure 3.6). At 950 m.a.s.l. OTCs more than doubled the RGR_h of birch increasing from 1.5×10^{-4} cm day^{-1} to 3.6×10^{-4} cm day^{-1} to become the fastest growing species at that elevation. Other than birch, no other species experienced such a large change in RGR_h from warming at any elevation. At 500 and 650 m.a.s.l. birch was the only species in which RGR_h increased with the presence of an OTC. At

800 m.a.s.l., spruce and fir both experienced higher growth rates under OTCs and at 950 m.a.s.l., birch and maple both benefitted from OTCs in terms of height.

Calcium fertilization had no significant impact on maple or birch survivorship (Figure 3.7), but was identified through model selection as an important predictor of spruce and fir survivorship. Its influence was most pronounced for fir, which experienced reduced survivorship across all elevations with the addition of Ca fertilizers. AICc proved calcium to be a significant inhibitor of fir survival at 950 m.a.s.l. (Table 3.3, Figure 3.7). Model selection also identified calcium as the single most important factor determining spruce seedling establishment when grown without supplemental warming (Table 3.5). For these spruce seedlings, the addition of calcium fertilizers enhanced survival probability. For maple and birch seedlings, calcium fertilization generally, but not significantly, increased survivorship across all elevations (Figure 3.7).

We observed age-related differences in seedling mortality for all species defined by dramatically higher mortality rates during the first growing season (GS1) than for any subsequent season (Figure 3.8). This is consistent with the mortality patterns observed in other seedling studies (De Steven 1991, Houle 1994, Cleavitt et al. 2011, Cleavitt et al. 2014). In GS1 yellow birch and balsam fir planted in SHADE plots experienced the highest average daily mortality rates of 8.6 x 10^{-3} seedlings day^{-1} and 5.6 x 10^{-3} seedlings day^{-1}, respectively. Sugar maple mortality rate averaged 4.7 x 10^{-3} seedlings day^{-1} in GAP plots and 3.3 x 10^{-3} seedlings day^{-1} in SHADE plots. Red spruce mortality was on average slightly higher at 5.4 x 10^{-3} seedlings day^{-1} in SHADE plots and 4.7 x 10^{-3} seedlings day^{-1} in GAP plots (Figure 3.8).

Additionally, mortality rates for seedlings during GS1 were higher in 2007 than they were in 2008 for every species in both GAP and SHADE plots (Figure 3.8).

Seasonal mortality rates after GS1varied by species with hardwoods experiencing most of their subsequent mortality during the growing seasons while conifers experienced mortality that was more constant across all seasons (Figure 3.8). Sugar maple seedlings overwintered well with deaths occurring only rarely, despite a significant mortality rate in the second winter for seedlings planted in gaps in 2007. Yellow birch winter mortality was also low, though seedlings planted in SHADE plots in 2008 did have a significant mortality rate during their first winter, as did seedlings planted in shade in 2008 during their second winter (Figure 3.8). Most red spruce seedling cohorts experienced significant mortality during their first winter and second growing seasons. The 2007 cohort of balsam fir seedlings experienced significant rates of mortality during both winter seasons (Figure 3.8). However, balsam fir seedlings planted in 2008 had no single season with significant mortality rates beyond GS1. Regardless of species, overall mortality declined with age.

Due to low subsequent mortality, the final elevational distribution of seedlings was largely determined at the conclusion of GS1 (Figure 3.9). For un-warmed seedlings at 950 m.a.s.l., final survivorship was often identical to survivorship at the conclusion of GS1. As elevation decreased however, the amount of mortality occurring after the conclusion of GS1 increased (Figure 3.9). The lower two elevations experienced 42.2% of their mortality after GS1 while at 800 and 950 m.a.s.l., only 13.5% of seedling mortality occurred after GS1. Few examples of statistically different survivorship between the end of GS1 and final survivorship were found in our data but included maple and fir seedlings planted in 2007, which experienced significant changes in survivorship between the end of GS1 and the end of the 2009 growing season at 500 m.a.s.l. ($p<0.0001$ and $p=0.002$, respectively). Survivorship of fir planted at 950 m.a.s.l. was also significantly different over the same periods. Spruce survivorship only changed significantly after the first growing season at 650 m.a.s.l. ($p=0.010$) (Figure 3.9). While there were, in general, only small differences overall between survivorship at the end of GS1 and the conclusion of the study, there were vast differences between survivorship of the 2007 and 2008 cohorts.

Planting year influenced seedlings resulting in higher survivorship for those planted in 2008 than for those planted in 2007. Bayesian models indicate seedling survivorship of the 2008 seedling cohort was significantly higher than survivorship of the 2007 seedling cohort for maple ($p<0.0001$), spruce ($p=0.0014$) and fir ($p=0.0004$) (Table 3.4). Birch, in contrast, was the only species not affected by planting year alone. When we split the data by light condition, all groups of seedlings planted in 2007 exhibited higher daily mortality rates than those planted in 2008, regardless of light condition (Figure 3.8). Like overall mortality, these differences observed between seedling cohorts seem to be driven primarily by differences in mortality during their first growing season.

We examined the interactions between planting year and season and found that survivorship at the end of the 2007 growing season for first-year seedlings was over 20% less than survivorship at the end of the 2008 growing season for first-year seedlings ($p<0.0001$). These differences in survivorship between seedlings whose first growing season was 2007 versus 2008 produced lasting impacts that helped to determine final survivorship rates for each cohort. For sugar maple, the differences between the 2007 and 2008 growing seasons on first-year seedlings were most evident at high elevations. At 950 m.a.s.l. in plots without OTCs, for example, only 4.2 % of the seedlings planted in 2007 survived to the end of their first growing season, while 33.3 % of the seedlings planted in 2008 survived the same amount of time (Figure 3.9) (p=0.008). Even at low elevations, some species exhibited significant differences in the survivorship of different cohorts. For example, sugar maple survivorship at 500 m.a.s.l. was significantly lower after GS2 for seedlings planted in 2007 than seedlings planted in 2008 (p=0.001), despite not being significantly different after just one growing season (p=0.818). Balsam fir also showed a predilection toward the 2008 growing season at both high and low elevations. Overall, balsam firs planted in 2008 survived their first growing season 25% better than those planted in 2007 did, though this difference was not found to be significant. At 500 m.a.s.l. however, final survivorship was significantly higher for fir seedlings planted in 2008 than it was in 2007 (p=0.0003). Red spruce did not exhibit a significant preference for planting year. However, the 2008 cohort of spruce survived at a rate 5.26% higher than those planted in 2007 did. Birch at 500 m.a.s.l. represented the only group whose survivorship at the end of GS1 was higher for the 2007 cohort than it was for the 2008 cohort at 35.4% and 16.7%, respectively.

In addition to examining planted seedlings, we evaluated potential dispersal limitations by comparing natural adult tree and seedling populations from nearby Camels Hump and found that the distributions of naturally occurring seedlings and adult trees between 550 and 1000 m on Camels Hump were often incongruous. Sugar maple and fir seedlings were found well outside their adult ranges, while birch and spruce seedling distributions were more elevationally restricted than adult trees within our elevational range of 550 to 1000 m.a.s.l. (Figure 3.10). The distribution of maple seedlings extended over 50 m above the observed elevational limit of adult maples to approximately 853 m.a.s.l.. In contrast, the highest birch seedlings were observed at elevations no higher than 800 m.a.s.l., which was below the highest adult birch tree at 853 m.a.s.l.. Fir seedlings were twice identified at 549 m.a.s.l., far below the lowest observed adult fir at 853 m.a.s.l.. In contrast, the lowest naturally distributed spruce seedlings were found at 792 m and therefore, did not extend as far into the northern hardwood forest as the adult spruce. Adults were observed at elevations as low as 671 m (Figure 3.10).

We also evaluated dispersal limitation by comparing planted seedlings with naturally established ones. In general, northern hardwood seedlings planted as part of our study survived at elevations higher than naturally established seedlings. Maple seedlings were found no higher than 853 m.a.s.l. on Camels Hump where dispersal happened naturally, but were able to establish 100 m higher at 950 m.a.s.l. when planted (Figure 3.10). Similarly, planted birch seedlings were able to survive well above their natural elevational limit at 950 m.a.s.l. and 792 m.a.s.l., respectively. Conifers, in contrast to northern hardwood seedlings, survived at lower elevations when planted than they did naturally in most cases. Balsam fir seedlings, in both planted and natural conditions, showed establishment across a remarkable elevational range by surviving approximately 300 m below the lower limit of adult trees at 500 and 549 m.a.s.l., respectively (Figures 3.2 and 3.10). Spruce seedlings planted as part of our study survived at 500 m.a.s.l., almost 300 m lower than the lowest wild seedlings and 150 m lower than the lower elevational boundary of adult spruce (Figure 3.10).

3.5 Discussion

In this study, our results indicate that current sugar maple seedling distribution is limited at high elevations by temperature, while yellow birch survivorship was instead limited by light. Based on model selections (Table 3.3), the model that best predicted sugar maple survival included only elevation. Despite the 62% decline in sugar maple survivorship between 500 and 950 m.a.s.l. (Figure 3.2) (Table 3.4) however, warming offset some of these losses and increased survivorship above the BDE from 6.7 to 30 % ($p<0.0001$) (Figure 3.4). Therefore, due to the increase in maple survivorship that accompanied warming, it is likely that the elevational effect we observed is really a temperature effect and that maple is currently excluded from high elevations primarily by temperature.

Yellow birch survivorship was less affected by elevation than maple and declined by only 22% ($p=0.003$) between 500 and 950 m.a.s.l. (Figure 3.2). However, differences in birch survivorship at 950m.a.s.l. and lower elevations were insignificant. In 2008, despite the harsh conditions that exist for seedlings in high elevation gaps, birch survivorship even increased slightly with elevation from 8.3% to 16% between 500 and 950 m.a.s.l. (Figure 3.2). Instead, yellow birch survivorship appeared to be almost exclusively controlled by light (Table 3.3). Even warming did not produce significant increases in seedling survivorship at any elevation, reducing the likelihood that temperatures were the cause of general declines in survivorship of birch with elevation. (Figure 3.2). Instead, it is more likely that the light environment and gap structure of high elevation gaps is responsible for the decline. Gaps at high elevations tend to be smaller and more climatically extreme than gaps found in the northern hardwood forests. Shorter trees at high elevations mean that gaps tend to be exposed to direct sunlight for more of the day and because the canopy is primarily coniferous, the shade tends to be darker as well. The thin, rocky soils found above the BDE also heat up and dry out quickly compared to those found at lower elevations.

In addition to having direct effects on seedlings' growth or survivorship, warming influenced the factors that limit growth for all species except birch. Differences in the models selected by AICc for maple, spruce and fir seedlings planted with and without warming indicate that these species experience a shift in the factors that limit growth depending on temperature (Table 3.5). Sugar maple, for example, becomes less dependent on light environment for establishment with increasing temperatures. Warming also reduced the impact of calcium availability on red spruce survivorship and reduced the predictive value of elevation for balsam fir seedling survival (Table 3.5).

Warming with OTCs had very different effects on the RGR_hs of northern hardwoods than they had on survivorship. The effects of OTCs on the RGR_hs of yellow birch were also much different from their effect on the RGR_hs of sugar maple. These differences expose the different life history strategies employed by maple and birch. OTCs did not significantly increase the survivorship of birch, but did drastically increase their RGR_h (Figure 3.6). Conversely, warming increased sugar maple survivorship, particularly at high elevations, but did not result in an increase in RGR_h (Figure 3.6). This suggests that the less shade-tolerant yellow birch tended to divert excess resources into height growth instead of building up sugar reserves or extending root networks. Sugar maple, in contrast, appears to have deferred using the extra resources by allocating them for purposes other than height growth. At this time however, we cannot be sure where or how the sugar maple seedlings were storing these resources. The dichotomy between these two strategies was most pronounced at 950 m.a.s.l. At this elevation, the RGR_h of yellow birch seedlings doubled when grown under an OTC, while sugar maple RGR_h increased only slightly from 2.5×10^{-4} cm day^{-1} to 2.7×10^{-4} cm day^{-1}. Survivorship of yellow birch at 950 m.a.s.l. was not significantly different with or without warming, while sugar maple survivorship increased by 22.4 % under OTCs ($p<0.0001$). However, OTCs only act to amplify the life history characteristics already inherent in our northern hardwoods. In ambient temperatures, the RGR_h of yellow birch was usually the highest among our study species within a given set of conditions (mean $RGR_h = 6.84 \times 10^{-4}$ cm day^{-1}), while sugar maple RGR_h was often the lowest (mean $RGR_h = 2.62 \times 10^{-4}$ cm day^{-1}) (Figure 3.6).

While the small increases in RGR_h suggest that sugar maples did not prioritize height growth early in their lives, our experimental design may cause us to underestimate their allocation of resources toward height growth. Sugar maples are unique in that 90% of seedling growth in their first growing season takes place within three weeks of germination (Jacobs 1965). In our study, much of this time would have passed before OTCs were placed over plots, eliminating the effect of OTCs on early growth. The initial growth periods of other co-occurring species can be over three times longer (Godney et al. 1990) and are therefore, more likely to be affected by OTCs and captured in our growth measurements. This may contribute to the small increases in RGR_h for maple with warming compared to other species.

The dissimilarity of the effects of warming on survivorship and RGR_h emphasizes the importance of investigating both measures of success to determine the long-term establishment or migration potential of yellow birch and sugar maple. Yellow birch relies on high seedling growth rates (Figure 3.6) to compensate for low seedling survival (Figure 3.2) as opposed to sugar maple, which has very slow growth rates (Figure 3.6), but compensates with higher seedling survival rates (Figure 3.2). The warming produced by OTCs caused increases in the RGR_h of birch and the survivorship in maple but did not correspondingly increase the survivorship of birch or the RGR_h of maple. However, in each case, warming increased seedlings' likelihood of success above the BDE. Therefore, taking into account both growth and survival, it is reasonable to assume that in the Northeast, rising temperatures as a result of climate change will increase adult populations of sugar maple and yellow birch within the boreal forest, effectively shifting the BDE further upslope (Beckage et al. 2008, Tang and Beckage 2010). Despite the importance of warming, it was not the only factor we found that influenced seedling establishment. Environmental and biological factors such as light, extreme weather, herbivory and dispersal capability also influenced seedlings and could facilitate or limit the upslope migration potential of northern hardwoods.

Despite having no warming effect, half OTCs increased yellow birch survivorship at 500 m.a.s.l. (Table 3.1 and Figure 3.4). We believe that the presence of OTCs at low elevations provided a secondary benefit to seedlings, particularly yellow birch, by reducing browsing by white-tailed deer (*Odocoileus virginianus*) (Mattfield 1984) or snowshoe hares (*Lepus americanus*) (Saunders 1988). There was evidence of browse on yellow birch seedlings and saplings, particularly on larger individuals (> 30 cm), within our low elevation study sites (*personal observation*). This supports previous studies that have found that both deer and hares utilize both sugar maple and yellow birch year round as a preferred food source. In areas of high deer activity, yellow birch and sugar maple are impacted primarily by browsing. This significantly reduces the ability of sugar maple and yellow birch to reach the sapling stage (> 3 feet), however, in exclusion studies, no differences in seedling densities were identified between open and fenced sites (Leopold 1950, Webb et al. 1956, Tierson et al. 1966). As a result, we suggest that in this study, only the yellow birch grew fast enough to be influenced by deer browse activity. Had sugar maples grown taller, they too may have experienced the detrimental effects of deer browse. It is unlikely that the OTCs would have provided the same benefit at high elevations since deer move to sites with dense conifer cover only in the winter when the seedlings would have been inaccessible below the snow pack (Mattfield 1984, Horsely et al. 2003). Small seedlings would have been inaccessible to snowshoe hares below the snow pack as well.

Light environment plays a key role in determining future establishment potential for northern hardwood seedlings at high elevations since yellow birch prefers to grow in gaps ($p<0.0001$) and sugar maple seedlings under intact canopies survive at higher rates ($p=0.0048$) (Table 3.4). Yellow birch seedlings were generally unable to survive in the shade; out of the 224 total birch seedlings planted under a closed canopy, only 8 survived the duration of the study regardless of warming treatment (Figure 3.3). Light was also identified as the only environmental factor affecting yellow birch survival by both AICc (Table 3.3) and Bayesian parameter estimation ($p<0.0001$) (Table 3.4). Maple, conversely, was the only species that benefitted from shaded conditions, particularly at 950 m.a.s.l. where, under ambient temperatures, 13% of seedlings survived at least two growing seasons in the shade compared to 0% survival in gaps (Figures 3.3 and 3.5). This suggests that at their elevational limits, sugar maple seedlings prefer non-gap conditions where diurnal soil and air temperature fluctuations are lower and where there tends to be higher relative humidity (Collins et al. 1985, Chen et al. 1999) (Table 3.1 and Appendix 3A).

If the area occupied by gaps and closed canopy forest were equal, a preference toward one light condition over another would be irrelevant in terms of a species' ability to establish. However, because on average, without human interference, only 4 to 10% of mature eastern hardwood forests (Barden 1989, Lorimer 1989, McCarthy 2001) and 6 to 33% of high elevation boreal forest (McCarthy 2001) is occupied by gaps at any given time, gap or shade dependence can affect seedling establishment potential. For yellow birch, which requires high light levels, low natural gap formation rates can drastically reduce the area available for establishment. Therefore, as temperatures continue to rise and climatic conditions at high elevations improve for birch seedlings; their gap dependence will limit their ability to take advantage of improved conditions. Retaining birch in high elevation forests will likely depend on disturbances that create large gaps such as those created by large scale events such as hurricanes or fires. Fir waves, which are common in these mountain forests, are unlikely to provide suitable birch habitat because they are quickly occupied by advanced fir regeneration in the understory (Perkins et al. 1992). Single-tree gaps alone are also unlikely to provide the light conditions necessary to maintain birch populations at their current levels of relative importance (Runkle 1985). Conversely, maple seedlings will benefit from the low percentage of forest occupied by gaps since approximately 80% of the boreal forest will represent their preferred light environment (McCarthy 2001, Perkins et al. 1992). Ultimately, low gap formation rates reduce the ability of birch to establish at high elevations and migrate with climate change, while simultaneously increasing maple's ability to do so. However, gap formation rates are not necessarily constant over time.

Gap formation rates can be dictated by climate, extreme weather or biological phenomena and influence the ability of northern hardwood seedlings to establish above the BDE (Hughes and Fahey 1988). Climatically induced adult tree mortality is likely to rise as a result of predicted increases in extreme temperatures (Karl et al. 1995, Hayden and Hayden 2003), extreme precipitation events such as floods or droughts (Diffenbaugh et al. 2005, Hayhoe et al. 2007, Sheffield and Wood 2008), increased storm frequency (Hayden and Hayden 2003, IPCC 2007a, 2013), and more frequent freeze-thaw events (Schaberg and DeHayes 2000). The resulting increase in the proportion of northeastern forests that exist in a gap state will likely benefit yellow birch establishment. Biological events such as disease outbreaks that occur in natural cycles or because of introduced species also have the potential to drastically alter canopy structure and gap frequency (Castello et al. 1995). The continued expansions of beech-bark disease (Twery and Patterson 1984, Houston 1994, Morin et al. 2007) and red spruce decline (Siccama et al. 1982, Battles and Fahey 2000) have already had profound impacts on montane forests. Additionally, the impending arrival of the invasive emerald ash borer (*Agrilus planipennis*) (Kovacs et al. 2010, Pugh et al. 2011), Asian longhorn beetle (*Anoplophora glabripennis*) (Peterson 2004) and hemlock wooly adelgid (*Adelges tsugae*) (Paradis et al. 2008) into the Green Mountains, will increase the roles that diseases and insects play in future canopy gap formation rates (Dale et al. 2001).

We found no evidence that soil calcium depletion caused by acid deposition has directly affected northern hardwood seedling establishment (Figure 3.7). However, other studies focused on natural seedling populations have identified increases in growth that result from calcium fertilization. At the Hubbard Brook Experimental Forest (Grafton County, New Hampshire), for example, sugar maple germinants were found to weigh more in fertilized sites than in reference sites (Juice et al. 2006b). Though these results differ from our observations, it is possible that the differences observed in Hubbard Brook seedling weights were a result of higher quality seeds (i.e. parental health) rather than differences in their soil environment.

Whether soil calcium is affecting seedling growth and establishment or not, it is likely that the continued impact of acid deposition on the adult trees in the northeastern US could indirectly affect seedling recruitment by altering the understory light environment. Acid deposition has been shown to cause chronic depletion of calcium, which increases mortality in adult red spruce (Hawley et al. 2006, Lazarus et al. 2006), sugar maple (Duchesne et al. 2002, Schaberg et al. 2006) and is suspected to be a contributing factor in white birch decline (Halman et al. 2011). Continued declines in these species would result in increased gap frequency, particularly at high elevations because of their increased exposure to acidic cloud moisture (Miller et al. 1993, Miller 2005a). Like gaps formed by extreme climatic events, or disease, pollution induced gap formation could result in an increase in the rate that shade intolerant species like yellow birch are able to migrate. Recent studies however, have identified instances of recovery in natural sugar maple and red spruce populations (van Doorn et al. 2011). Should these positive trends continue, conditions will favor the migration of shade tolerant species like sugar maple.

In addition to temperature and light, we found that planting year significantly affected first-year seedling survival and resulted in differences in the final populations of maple ($p<0.0001$), spruce ($p=0.0014$) and fir ($p=0.0004$). These differences are likely the result of climatic differences between the 2007 and 2008 growing seasons. Birch survivorship was not significantly influenced by planting year because birch seedlings appear to be almost singularly dependent on light (Tables 3.3 and 3.4) and light environment was not expected to have changed significantly between 2007 and 2008. However, survivorship patterns indicate that the environmental conditions present during the 2007 growing season, while detrimental to most species, favored low elevation birch establishment. However, seedlings planted without added warming in 2008 had, on average, 20% higher survivorship by the end of their first growing season than those planted in 2007 ($p<0.0001$) (Figures 3.8 and 3.9). Since over 75% of total seedling mortality occurred during seedlings' first growing season (Figures 3.8 and 3.9), we suggest that the differences in survivorship between planting years arose during GS1. At high elevations, this temporal mortality pattern was even more pronounced. The percentage of mortality that occurred during GS1 at 950 m.a.s.l. was 91% (Figure 3.9). The percentage of mortality occurring during GS1 fell with elevation to 65% at 500 m.a.s.l. (Figure 3.9). For sugar maple, this means that establishment at high elevations may hinge on survival over a single, mild first growing season and it appears that 2008 was such a year. Maple first-year seedling survivorship at 950 m.a.s.l. was 30% higher in 2008 than it was in 2007 ($p=0.0008$) (Figure 3.9), emphasizing the importance of first growing season climate on migration potential.

Our examination of the 2007 and 2008 growing seasons revealed that the most likely climatic cause for the increased first-year seedling mortality during the 2007 growing season was drought. Seedlings have shallow root systems and at high elevations are often growing on well-drained, rocky soils. As a result, seedlings at high elevations are thought to be vulnerable to desiccation-induced mortality during even relatively short periods of hot, dry weather (Myster 1993, He et al. 2005). A comparison of the growing seasons revealed that the average growing season temperature was nearly the same for each year of our study and average daily precipitation was almost identical for 2007 and 2008 (Table 3.6). However, beginning in late July 2007 there was a two-week period with average daily temperatures at 800 m.a.s.l. above 20°C which as accompanied by very little precipitation. Neither the 2008, nor 2009 growing season had a comparable event with prolonged high temperatures and low precipitation (Table 3.6). While we cannot be certain this event was the one that caused higher 2007 mortality, a stretch of hot, dry days like this would likely be adequate to cause high mortality among first-year seedlings, particularly in high elevation gaps where intense sun and thin organic soils are common (Myster 1993).

In addition to climatic limitations, our results suggest that natural populations of both yellow birch and sugar maple are biologically limited by dispersal or germination at high elevations. The absence of naturally growing seedlings at elevations equal to or higher than the elevational limit of adult trees on Camels Hump suggests that the absence of seedlings is due to a factor that affects seedling establishment before emergence (Lenoir et al. 2009, Zhu et al. 2012). Seeds may fail to germinate or may die very soon after germination because of local climatic conditions or because of inappropriate seedbed conditions. Germination limitation is unlikely to be the cause of sugar maple exclusion at high elevations since it has an extremely high germination rate averaging 95% and does do best at low temperatures (Godney et al. 1990). Yellow birch however, does require specific seedbed conditions for germination and young seedlings and under a closed canopy will only establish on mossy or decaying wood. Yellow birch germination rates are also far lower than those for maple, topping out at around 20% (Erdmann 1990). This theory is supported when the survival of transplanted seedlings is above the elevational limit of natural seedlings.

We believe that the results in of this study indicate that dispersal or germination are limiting establishment for both yellow birch and sugar maple and that these conclusions are concurrent with previous studies (McEuen and Curran 2004). Adult yellow birch trees grew at elevations over 50 m higher than the highest naturally established seedlings (Figure 3.10). Dispersal limitation would only affect the presence of seedlings beyond the adult tree range. Additionally, planted birch seedlings were able to establish at 950 m.a.s.l., over 150 m.a.s.l. above the highest observed natural birch seedling and 100 m higher than the highest adult birch tree, suggesting that the absence of birch above their adult range is not the result of a limit on post-emergence survival. Combined, these data suggest that birch germination and initial growth limitations are suppressing range expansion. Naturally growing maple seedlings were found approximately 50 m higher than adult maples, suggesting that they may not be severely dispersal limited (Figure 3.10). However, planted maple seedlings were able to survive without additional warming at 950 m.a.s.l., 100 m higher than naturally germinated seedlings (Figure 3.2). This suggests that maple could be experiencing limitation after dispersal and most likely just after germination. Given the contrast between natural and planted seedling survival rates, it appears that the severity of pre-emergence limitation is greater for birch.

We found the absence of naturally occurring birch seedlings at high elevations to be somewhat unexpected given their seedlings' proven insensitivity to temperature (Figure 3.4, Table 3.5) and their large dispersal radius. Yellow birches produce small, winged seeds that travel effectively during primary dispersal. They are also adept at long-distance dispersal since they have the tendency to drop seeds late in the fall, which can then travel great distances as they are blown over the snowpack (Matlack 1989, Houle and Payette 1990, Houle 1998). As a result, dispersal limitation seems unlikely. However, germination limitations are possible since small-seeded species such as yellow birch are sensitive to seedbed conditions, which can affect their ability to anchor roots. In deciduous or mixed forests, a matted leaf layer can act as a barrier to establishment by preventing small, thin roots from reaching the soil (Marquis et al. 1964). As a result, birch would benefit from large wind events that cause tip-ups exposing mineral soil and providing nurse log habitat that birch seedlings are able to take advantage of (McGee and Birmingham 1997). An expansion of earthworm invasion could also increase the amount of exposed soil while reducing the litter layer (Bohlen et al. 2004). However, at this time is appears that limited suitable seedbed substrate could be determining wild birch distribution and may affect future migration potential.

The absence of natural northern hardwood seedling populations at high elevations could be caused, alternatively, by spatial or temporal limits to our sampling of natural seedling populations. For instance, the absence of wild birch seedlings above the BDE on Camels Hump (Figure 3.10) could result from sampling too few vegetation plots. Birch's very low intrinsic seedling survivorship rates (Figure 3.2) make this a plausible scenario since small populations are more likely to be missed in vegetation plot sampling (MacKenzie et al. 2005). The absence of naturally germinated high elevation northern hardwood seedlings could also be the result of infrequent, extreme climatic events such as severe droughts or early/late frosts that periodically decimate seedling populations (Hett and Loucks 1971, Bassow et al. 1994). If an event such as this took place the year before vegetation sampling, it is possible that seedling populations were underrepresented at high elevations.

While low temperatures reduced seedling establishment for most species at high elevations, our results do not suggest that conifers are excluded from low elevations by high temperatures. Planted spruce and fir seedlings were able to establish at ambient temperatures within the northern hardwood forest at rates of 37% and 40%, respectively (Figure 3.2). However, wild spruce seedlings were found on Camels Hump only at elevations above 792 m.a.s.l., over 100 m higher than adult red spruce (671 m.a.s.l.) (Figure 3.10). This suggests that spruce seedling establishment at low elevations is limited after dispersal, but before establishment, perhaps during germination because of temperature or seedbed condition. In contrast, we did observe a number of naturally occurring fir seedlings at very low elevations (550 m.a.s.l.) on Camels Hump (Figure 3.10), indicating that they are not dispersal limited. Instead, we suggest that fir at low elevations is limited by interspecific competition with northern hardwoods at early life stages (Loehle 2000). At the end of GS2, maple and birch seedlings planted at 500 m.a.s.l. without OTCs reached average heights of 11.2 and 26.7 cm, respectively. Spruce and fir in the same sites only reached average heights of 6.2 and 4.4 cm, respectively. These differences in height are important in determining which species will ultimately outcompete the others and capture a site. Relative seedling heights in our study do not follow the same pattern as relative RGR_hs (Figure 3.6) because of differences in our seedlings' initial heights. This is a result of differences in initial seedling heights, for which maple was significantly taller than all other species ($p=0.004$).

In addition to the factors affecting seedling establishment examined in this study, there are many other forces that impact the ability of trees to establish and eventually migrate. Among the factors we did not evaluate in this study, an important one affecting low elevation seedling establishment is likely American beech and the spread of beech bark disease (BBD) (*Cryptococcus fagisuga – Nectria coccinea* var. *faginata* Complex) (Houston 1994, Hane 2003). BBD kills virtually all large, adult beech trees and simultaneously simulates a root sprouting response in the beech trees (Evans et al. 2005, Morin et al. 2007, Wagner et al. 2010). Previous studies have shown that the shade beneath these thickets is dark enough to prevent the establishment of even shade tolerant species such as sugar maple (Hane 2003, Evans et al. 2005, Giencke et al. 2014), however, we did not find that this was the case in our sites. It is possible though, that shading out could become more detrimental to sugar maple seedlings as they get older. While this phenomenon is resulting in a regional increase in beech basal area and relative importance (Morin et al. 2007, Giencke et al. 2014), we suggest it is unlikely that beech will prove to be a long-term threat to sugar maple establishment at large scales. Because BBD can kill even pole-sized trees in affected stands (Giencke et al. 2014) and beech takes at least 40 year to mature (Erdmann 1990), few trees will grow to maturity and produce seed. In effect, this severely limits beech's ability to disperse and migrate with changing climate (Evans et al. 2005). As a result, beech may currently limit competing seedling establishment at low elevations, but is unlikely to significantly impact the ability of other northern hardwood species to expand upward in elevation, outside of beech's current range.

3.6 Conclusions

Our examination of northern hardwood seedling growth and survivorship in response to changes in elevation, light, calcium and temperature suggests that sugar maple seedling establishment is currently limited at high elevations primarily by temperature, while yellow birch seedlings are limited by light and seedbed during germination and the initial seedling growth phase. As a result, all things being equal, future warming will positively influence sugar maple survivorship at high elevations, but will not increase the ability of yellow birch to survive within the boreal zone. Future sugar maple establishment at high elevations will increase more than will yellow birch establishment, leading to an increase in sugar maple range within the boreal zone and ultimately, an elevational increase in the BDE itself.

Commensurate with an increase of northern hardwoods above the current BDE will be a decrease in the proportion of spruce and fir present within the current boreal forest zone. Our results indicate that exclusion of spruce and fir at high elevations is not likely to occur during the seedling stage. Instead, the absence of adult boreal trees below the BDE is most likely the result of increased competitive pressure from species adapted to warmer temperatures, which have higher maximum growth rates (Loehle 2000). Continued warming will further affect boreal species as the area of suitable habitat on mountaintops shrinks. This diminishing habitat has the potential to cause local extinctions of high elevation species (Dirnbock et al. 2011, IPCC 2014), forcing them northward if they are unable to find high elevation refugia.

The rate of northern hardwood migration upslope and boreal retreat will depend on climatic conditions and disturbance patterns. Sugar maple's responsiveness to temperature, particularly at high elevations makes it more susceptible to inter-annual climate variation than is yellow birch. Birch's shade intolerance, however, means that the birch migration rate will be dictated by the frequency of canopy gaps. Canopy gap formation rates can be influenced by disease, severe weather, precipitation patterns or by natural stand dynamics. Therefore, sugar maple recruitment rates at high elevations will increase with the frequency of favorable weather conditions, while birch recruitment is more indirectly dependent on climate since establishment potential is dictated by disturbance patterns.

Sugar maple and yellow birch each have characteristics that could make long-term persistence in New England possible and prevent them from lagging so far behind shifting climatic conditions that they become unable to disperse into suitable habitat. To the benefit of yellow birch, we have shown that birch seedling survivorship is remarkably unaffected by changes in temperature. As a result, yellow birch has a very broad temperature range in which it can establish. Within that range, warming increases the RGR_h of birch seedlings, which will increase its competitive ability. Preventing birch's rapid migration is its shade intolerance. Additionally, changes in moisture regime resulting in more frequent or prolonged droughts may adversely affect birch in the future (Erdmann 1990). Conversely, maple's ability to respond positively to warming in all light conditions with increased survivorship will allow them to take advantage of high elevation sites and expand their range quickly as climate changes. However, germination or dispersal limitations may exist that will limit the ability of maple to migrate with changes in climate (McEuen and Curran 2004, Massot et al. 2008). Ultimately, we believe that with a combination of local and long-distance dispersal it is possible that both sugar maple and yellow birch would be capable of overcoming dispersal limitation and migrate upslope fast enough to keep pace with climate change in the near future (Clark et al. 2001).

While northern hardwoods in montane regions may be able to migrate upslope with climate, the distances required for species to migrate and remain in climatic equilibrium elevationally pale in comparison to the distances required for species to migrate with climate latitudinally. In the Northeast, an increase of 1°C would require an upward shift of approximately 175 m (Richardson et al. 2004). That same 1°C increase on flat land would require species to migrate between 103 km and 145 km (Leffler 1981, Jump et al. 2009) to remain within their climatic envelope. In that case, it is unlikely that the northern hardwoods would be able to shift their ranges fast enough to keep pace with climate. A major limit to the ability of northern hardwoods to migrate across large distances is that trees have long generation times. Sugar maples take at least 22 years (Godney et al. 1990) to mature and produce seed and yellow birch rarely produce seed when younger than 40 years (Erdmann 1990). At that point, the lagging edge of suitable climate may already be out of dispersal range, preventing the necessary range expansion.

Our conclusions contribute to the larger body of research concerned with the migration of tree species in response to climate change and can be used to validate and train models to more accurately predict the extent to which climate change will affect future forest compositions. This study is particularly meaningful because of the number of environmental interactions that we examined and the scarcity of empirical studies that experimentally test factor interactions on tree migration potential. Additionally, the combination of naturally occurring and planted seedlings enhances the utility of our results and provides a unique opportunity to compare and examine realized versus potential seedling distributions.

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3.8 Tables and Figures

Tables

Table 3.1: Average growing season (April 1 to October 31) temperatures and growing degree-days (GDD) at each elevation, in each light condition and under each warming treatment. Changes from the average ambient temperature at each location are shown in parentheses. Calculation details can be found in the Methods section. Further information regarding temperatures under OTCs can be found in Appendix 3A.

Elevation (m)	Shade / Gap	OTC Level	Average Growing Season Temp	Average GDD per Growing Season
500	Shade	Open	11.8	1593
		Half	11.8 (+0.0)	1603
		Full	12.0 (+0.2)	1632
	Gap	Open	11.5	1551
		Half	11.4 (-0.1)	1518
		Full	11.8 (+0.3)	1587
650	Shade	Open	10.5	1369
		Half	10.5 (+0.0)	1374
		Full	11.0 (+0.5)	1467
	Gap	Open	10.9	1446
		Half	11.3 (+0.4)	1508
		Full	11.3 (+0.4)	1516
800	Shade	Open	9.5	1200
		Half	9.7 (+0.2)	1231
		Full	10.6 (+0.9)	1413
	Gap	Open	9.8	1257
		Half	10.2 (+0.5)	1332
		Full	10.6 (+0.8)	1400
950	Shade	Open	8.1	978
		Half	8.7 (+0.6)	1085
		Full	9.0 (+1.0)	1145
	Gap	Open	9.1	1143
		Half	9.3 (+0.2)	1175
		Full	9.6 (+0.5)	1226

Table 3. 2: The average temperature (°C) difference between quadrats with and without OTCs in gap and shade sites across all elevations during the day (10am to 4pm) and night (10 pm to 4 am) as measured in half-hour increments by the on-site dataloggers.

	Half OTC	Full OTC
Gap Day	1.77	2.08
Canopy Day	0.98	1.86
Gap Night	-0.16	0.54
Canopy Night	0.15	1.04

Table 3. 3: Models identified by AICc as best representing seedling survivorship for each species. Models shown here have a ΔAICc of < 3. See Appendix 3B for the full suite of models compared in this analysis. ΔAICc is indicated in parentheses. E=Elevation, O=Open Top Chamber, L=Light, C=Calcium

Species	**Metric**	**Model 1**	**Model 2** (Δ AICc)	**Model 3** (Δ AICc)	**Model 4** (Δ AICc)	**Model 5** (Δ AICc)
Maple	Survivor-ship	**Elevation**	**ExO** (0.16)	**(ExO)+(LxO)** (0.85)	**E+L** (1.15)	**E+O** (1.26)
Birch	Survivor-ship	**Light**	**O+L** (0.35)	**OxL** (0.53)	**L+C** (1.48)	
Spruce	Survivor-ship	**(ExL)+(OxL)**	**OxL** (0.70)	**O+L** (1.62)		
Fir	Survivor-ship	**L+C**	**ExL** (1.08)	**Light** (1.85)		

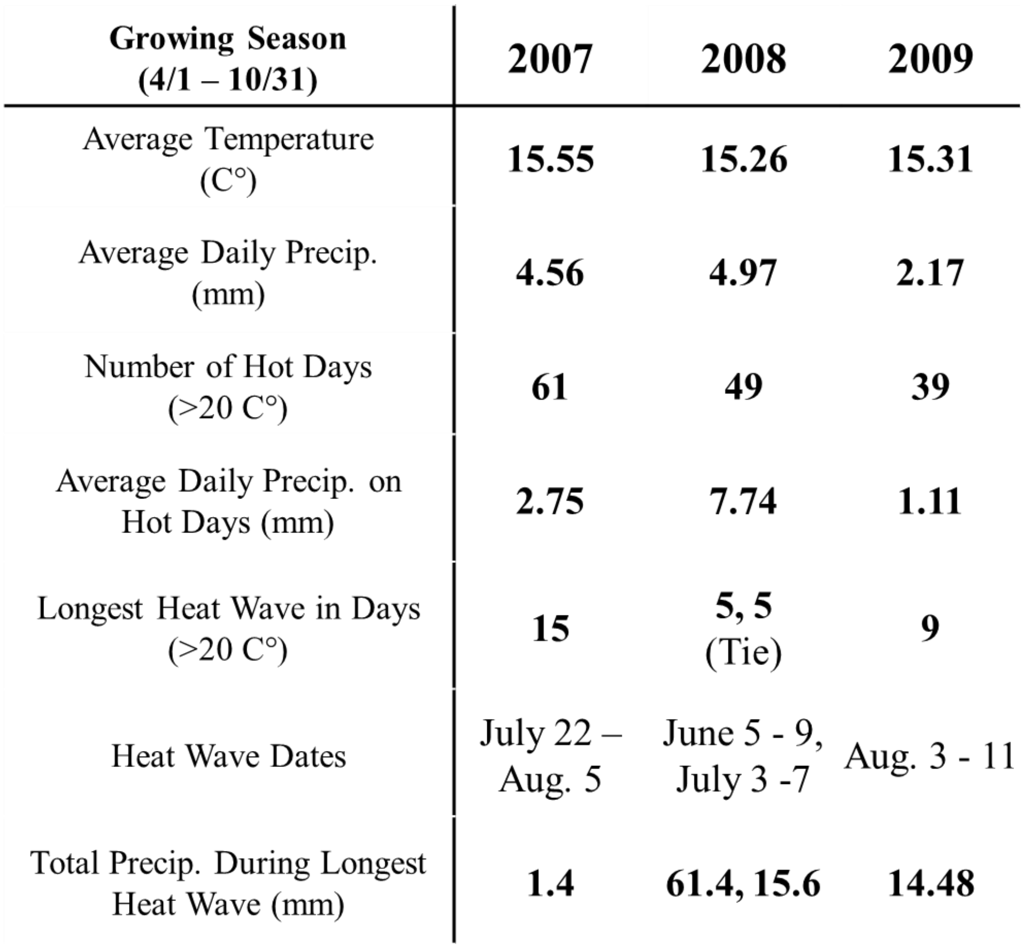
Table 3. 4: Variables found to be significant for each species as estimated by OpenBugs. Variables in these models are treated as factors with multiple levels. In addition to experimental treatments, planting year and season were included as interactions. In addition to the model variables and interactions shown, the model also tested the significance of 'Year x Light' and 'Year x Calcium'. Neither interaction was included here because no significant combinations were found. The Bayesian p-value is in parentheses following the sign of the coefficient for each significant variable.

	Maple	Birch	Spruce	Fir
Intercept		— (<0.0001)		
Elev 650				
Elev 800				
Elev 950	— (0.0002)		— (0.0316)	— (0.048)
Light	— (0.0048)	+ (<0.0001)	+ (<0.0001)	+ (<0.0001)
Calcium				
Half OTC	+ (0.0052)			
Full OTC				
Year	+ (<0.0001)		+ (0.0014)	+ (0.0004)
Elev 650 x Full OTC				
Elev 800 x Full OTC				
Elev 950 x Full OTC	+ (0.0012)		+ (0.0412)	+ (0.0198)
Elev 650 x Light				
Elev 800 x Light				
Elev 950 x Light				
Elev 650 x Calcium				
Elev 800 x Calcium				
Elev 950 x Calcium				
Elev 650 x Year				
Elev 800 x Year				
Elev 950 x Year				
GS 1	+ (<0.0001)			
Win 1	+ (<0.0001)	+(0.0006)		
GS 2		+ (0.0002)	+ (0.0004)	+ (<0.0001)
Win 2	+ (0.0086)			— (<0.0001)
GS 3		+ (0.001)	+ (0.0296)	+ (0.0054)

Table 3.5: Model selection using AICc assessing the factors influencing seedling survivorship in ambient temperatures and under elevated temperatures. Differences between the models selected for seedlings growing in ambient temperatures and those that are warmed indicate that warming affects survivorship and alters environmental relationships for seedlings. Models presented all have ΔAICc values less than 3.

Species	**Metric**	**Model 1**	**Model 2**	**Model 3**	**Model 4**
Maple	Ambient	**E + L**	**Elevation**	**E + Ca**	
	Warmed	**Elevation**	**E x Ca**	**E + Ca**	**E + L**
Birch	Ambient	**Light**	**L + Ca**		
	Warmed	**Light**	**L + Ca**	**E x L**	
Spruce	Ambient	**Calcium**	**Null**	**L + Ca**	**Light**
	Warmed	**Light**	**E x L**	**L + Ca**	
Fir	Ambient	**E x L**			
	Warmed	**L + Ca**	**Light**		

Table 3.6: Climatic conditions and weather phenomena during the three growing seasons over which our study took place (2007-2009). Temperatures and precipitation measurements were averaged over two weather stations on Mount Mansfield at 884 m.a.s.l.. Hot days are defined as days where the average temperature is greater than 20 ºC.



Growing Season (4/1 – 10/31)	**2007**	**2008**	**2009**
Average Temperature (C°)	**15.55**	**15.26**	**15.31**
Average Daily Precip. (mm)	**4.56**	**4.97**	**2.17**
Number of Hot Days (>20 C°)	**61**	**49**	**39**
Average Daily Precip. on Hot Days (mm)	**2.75**	**7.74**	**1.11**
Longest Heat Wave in Days (>20 C°)	**15**	**5, 5** (Tie)	**9**
Heat Wave Dates	July 22 – Aug. 5	June 5 - 9, July 3 -7	Aug. 3 - 11
Total Precip. During Longest Heat Wave (mm)	**1.4**	**61.4, 15.6**	**14.48**

Figures

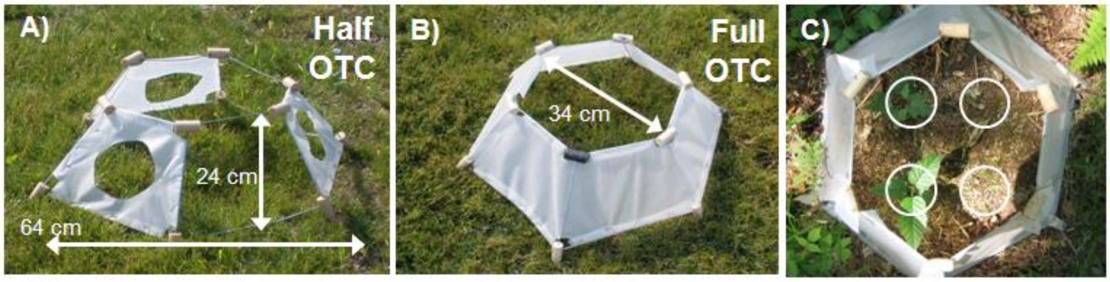


Figure 3.1: Photos of the A) Half Open Top Chamber (OTC) and B) Full OTC used to increase temperatures inside during the 2007, 2008 and 2009 growing seasons. C) An overhead photo of seedlings within each OTC. Species placement within each OTC was random.

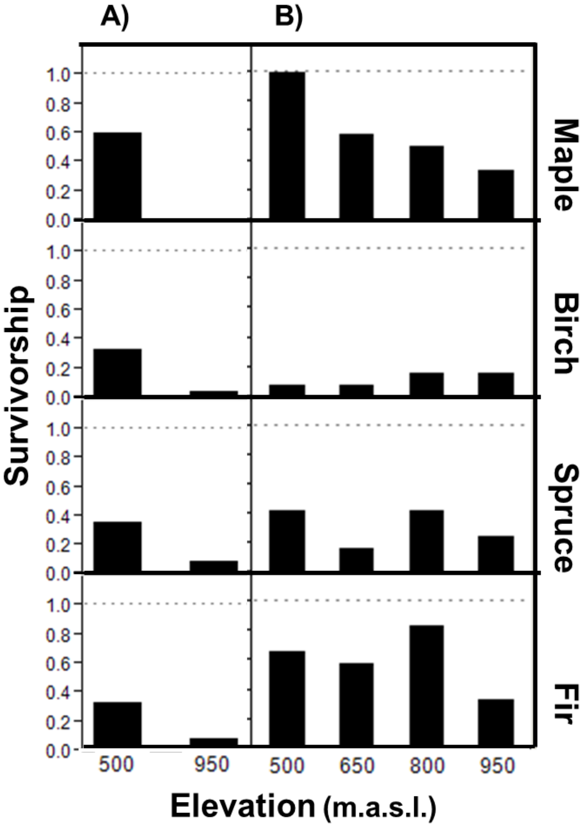


Figure 3.2: Survivorship for all seedlings grown without OTCs at the conclusion of the second growing season (GS2) averaged over seedlings in gaps and shade. Survivorship for seedlings planted in A) 2007 (n=48 at each elevation) and B) 2008 (n=12 at each elevation). Seedlings were planted at only the highest and lowest elevations in 2007 and at two intermediate elevations in 2008.

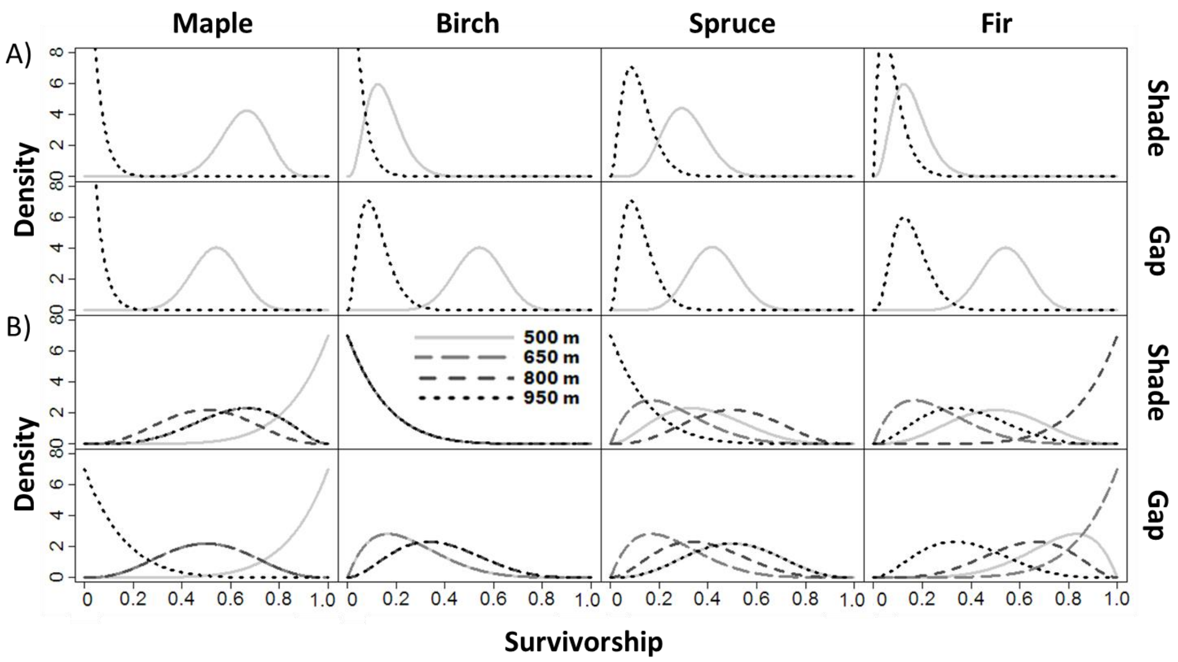


Figure 3.3: Probability estimates of seedling survivorship by species, elevation and light condition at the end of the second growing season (GS2) for seedlings growing without OTCs planted in A) 2007 and B) 2008. Survivorship generally decreased with increasing elevation and was higher in gaps. See Methods for details on how these estimates were calculated.

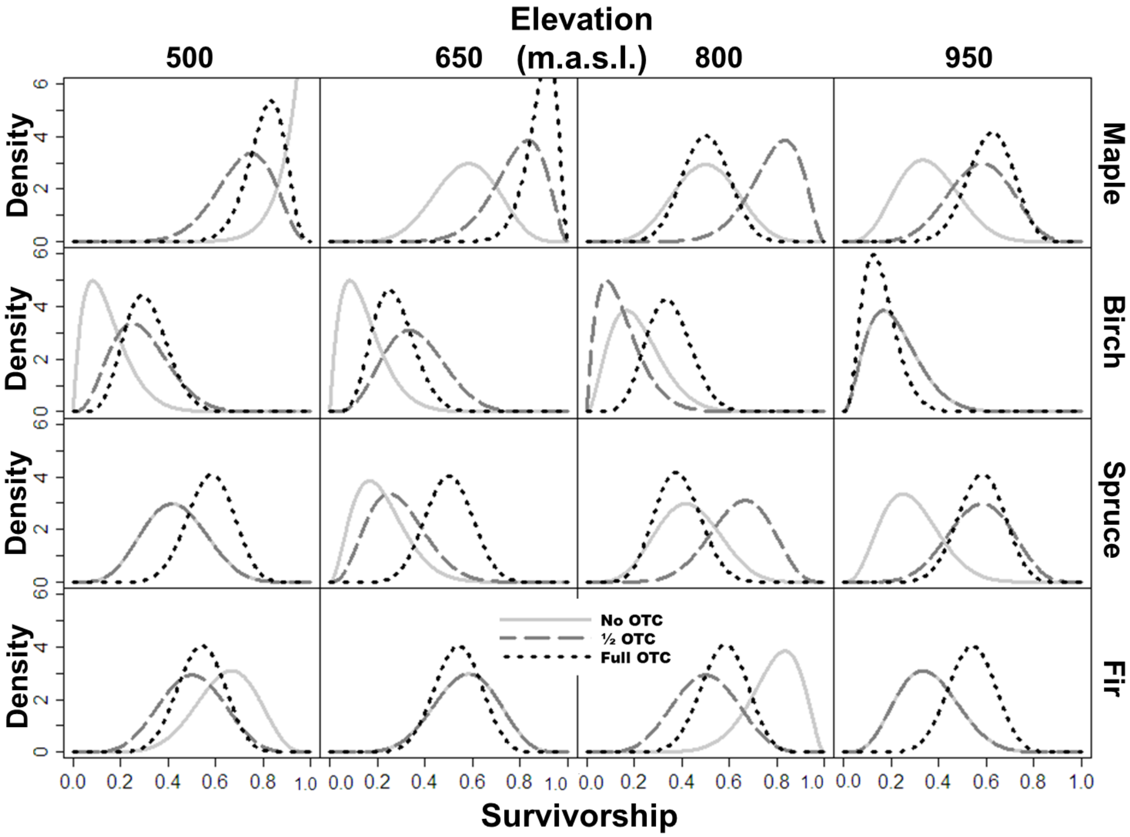


Figure 3.4: Probability estimates of survivorship for seedlings planted in 2008 across elevations and under different OTC treatments. Distributions for seedlings planted in ambient temperatures and under half OTCs were derived from data on 12 individuals at each elevation. Full OTC distributions were calculated with 24 individuals per elevation. See Methods for details on how these estimates were calculated.

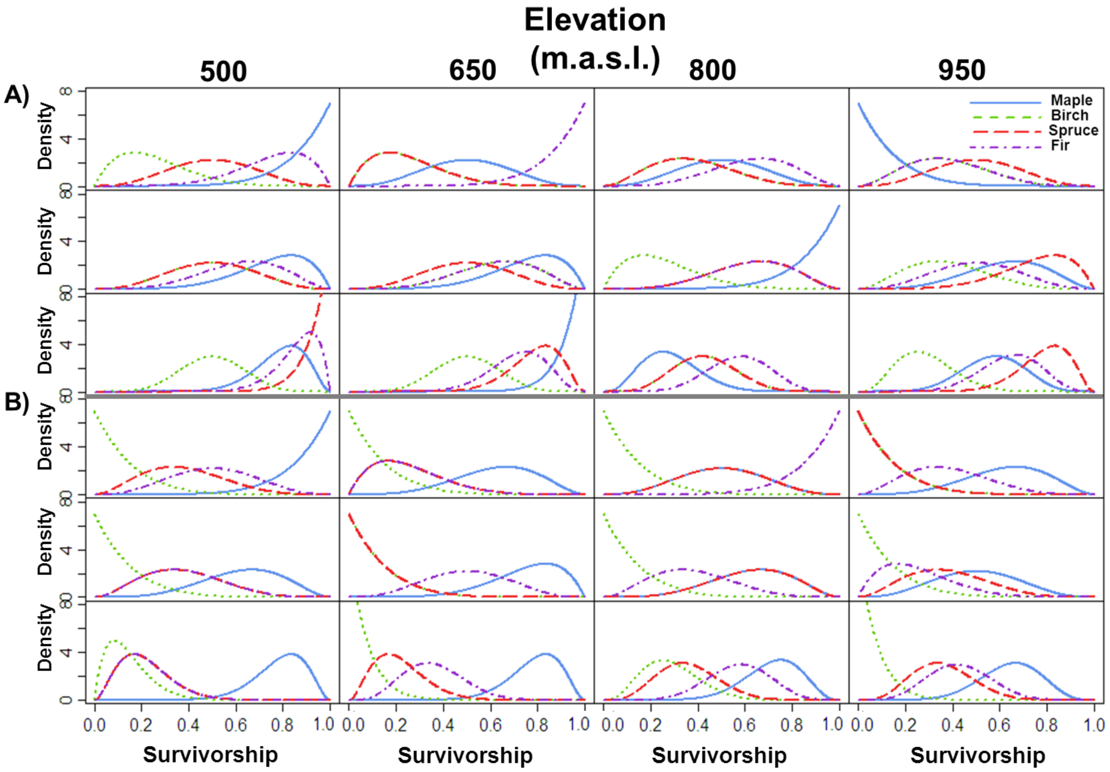


Figure 3.5: Survivorship probability estimates for seedlings planted in 2008 under A) gaps and B) shade with respect to elevation and OTC type. Survivorship is averaged over calcium treatment. Estimates for seedlings grown in half OTC's and in ambient temperatures were calculated with 6 individuals per elevation; survivorship estimates under full OTC's were calculated with 12 individuals per elevation. See methods for details on how these estimates were calculated.

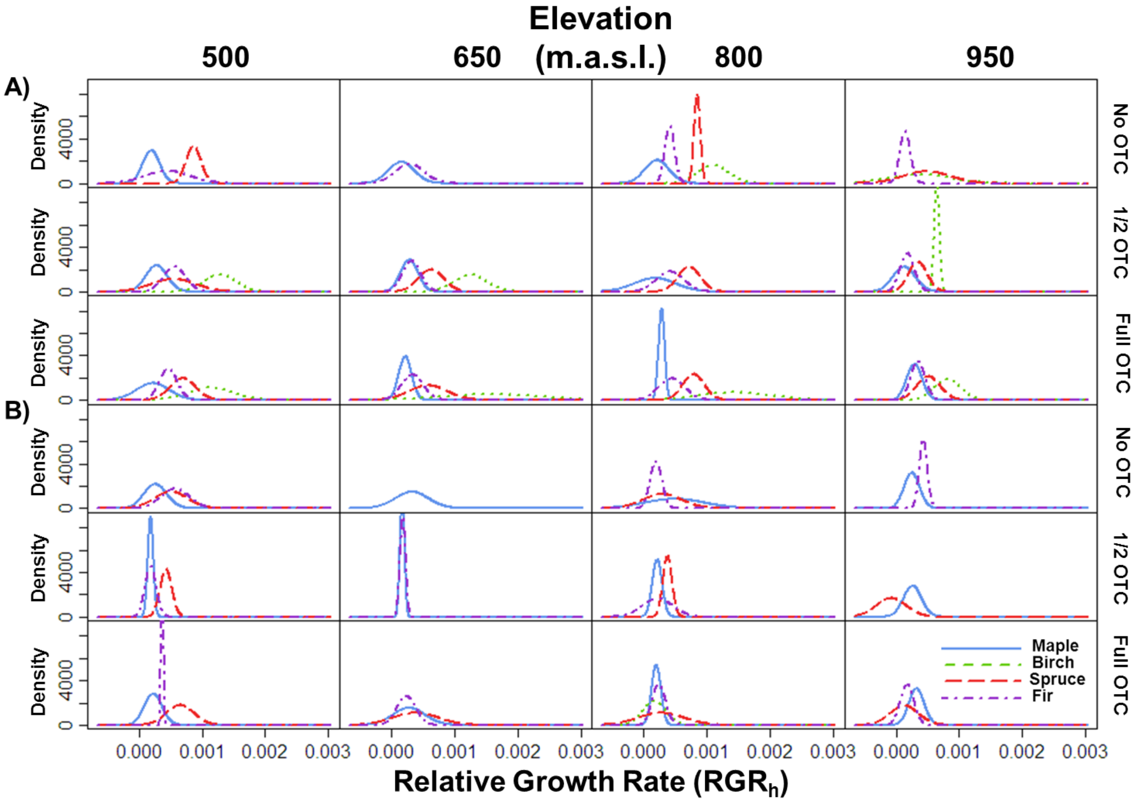


Figure 3.6: Estimates of RGR_h for seedlings planted in 2008 in A) gaps and in B) shade plots at the conclusion of our study (2 growing seasons) with respect to species, elevation and OTC treatment. Growth rates were only estimated when two or more individuals survived for a given species in a given treatment combination. Estimates for seedlings grown in half OTC's and no OTC's were calculated with a maxiumum of 6 individuals; Full OTC estimates were calculated with a maximum of 12 individuals. See methods for details on how these estimates were calculated.

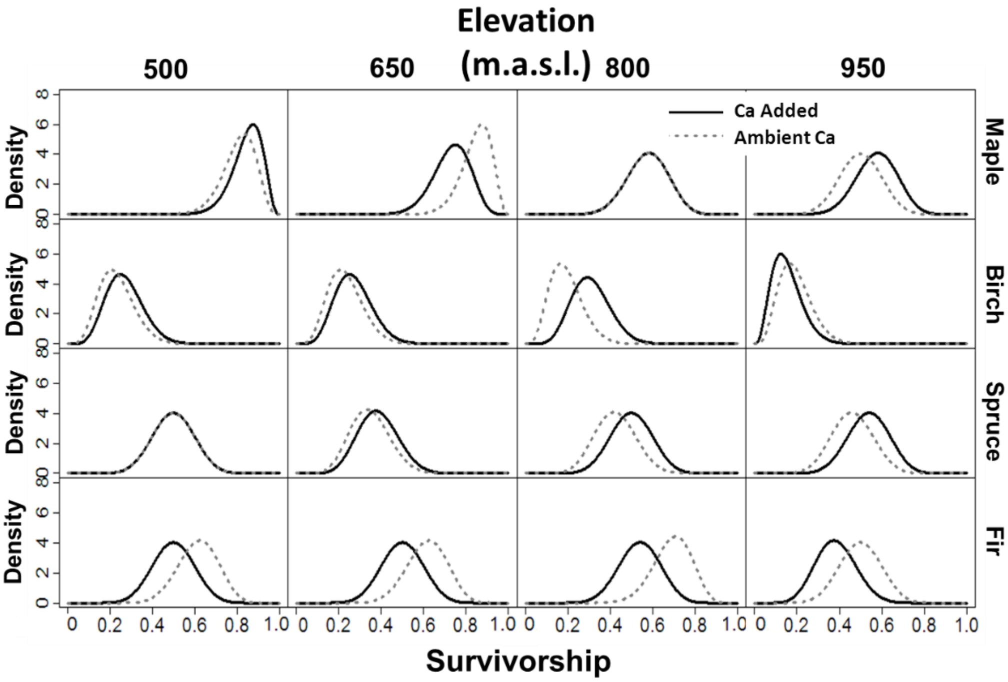


Figure 3.7: Probability estimates for survivorship of seedlings planted in 2008 with or without added calcium by elevation. Results are averaged across light conditions and OTC type. Therefore, these estimates were derived using data from 24 individuals per elevation. See Methods for further details on how these estimates were calculated.

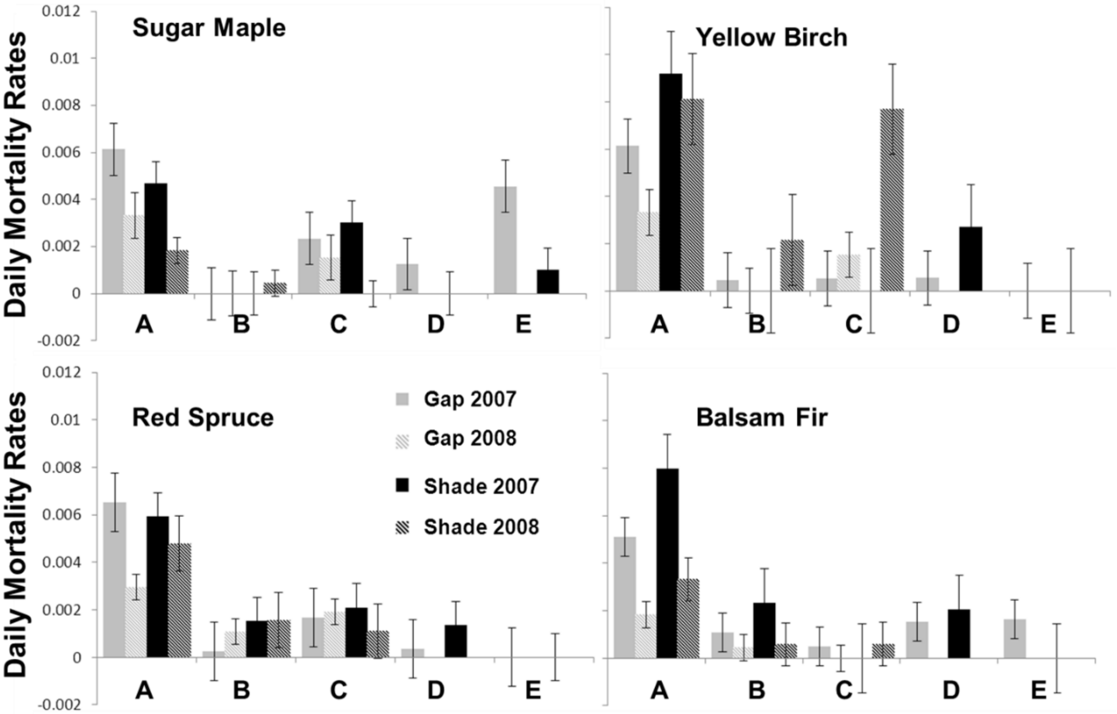


Figure 3.8: Daily seedling mortality rates for seedlings planted without OTCs in 2007 and 2008 in gaps and in shade. For all seedlings, mortality rates are presented for A) first growing season (GS1), B) first winter, and C) second growing season (GS2). Mortality rates are also reported for the D) second winter, and E) third growing season (GS3) for seedlings planted in 2007 only. Error bars represent the standard error of each estimate.

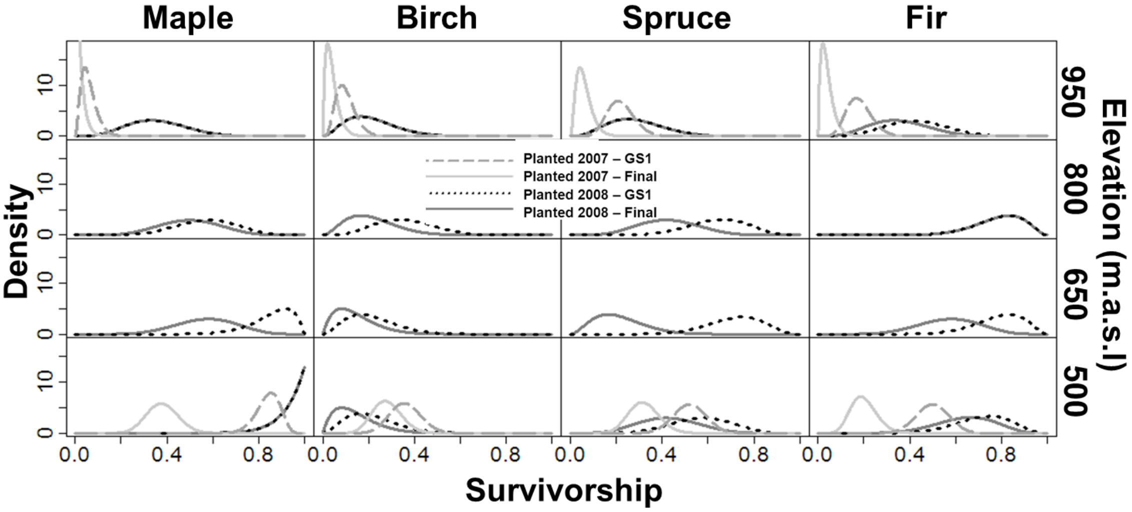


Figure 3.9: Survivorship probability estimates for seedlings planted in 2007 and 2008 without OTCs after their first growing season (GS1) and at the conclusion of the study by elevation. At high elevations, survivorship did not often change significantly after GS1, particularly for seedlings planted in 2008. See Methods for further details on how these estimates were calculated.

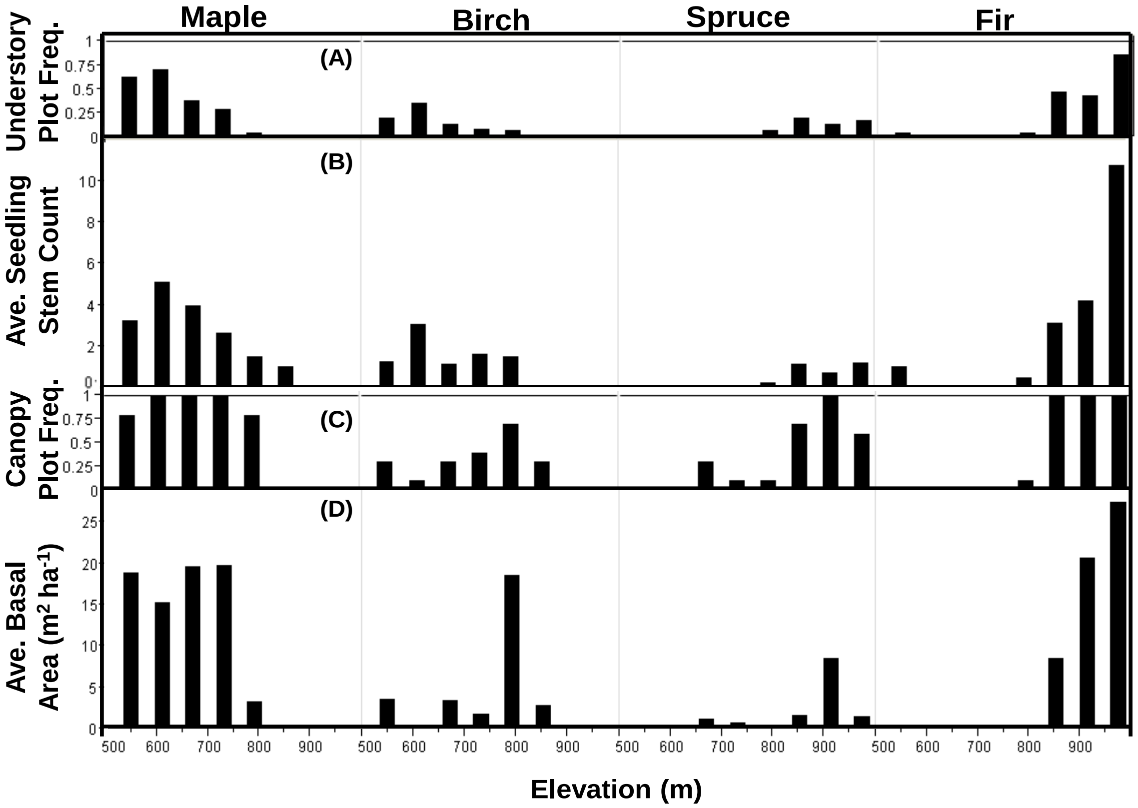


Figure 3.10: The distribution of mature trees and seedlings on Camels Hump in 2004 and 2006 respectively. A) The proportion of occupied understory plots by seedlings with a dbh< 2cm. B) The average seedling stem count in occupied understory plots. C) The proportion of canopy plots occupied by adult trees and saplings (≥ 2cm dbh). D) The mean basal area (BA) ha^{-1} of trees in occupied plots. Adult tree and seedling surveys represented here were taken at the following elevations: 549, 610, 671, 732, 792, 853, 914 and 975 (Beckage et al. 2008, Pucko et al. 2011).

3.9 Supplemental Material

Appendix 3A: Detailed information on the Open Top Chambers (OTCs).

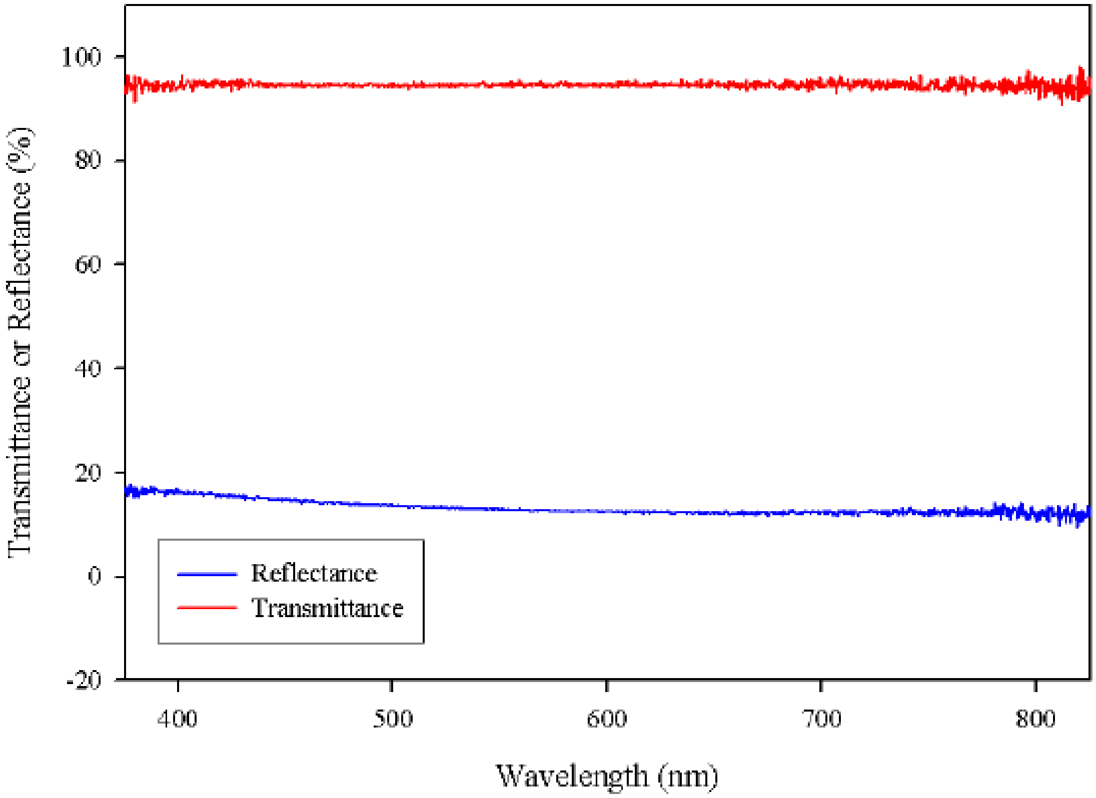


Figure 3A. 1: OTC Plastic Spectral Data. Transmittance and reflectance of light through the 1.5 mil polyethylene plastic sheeting used for OTC construction. Test was conducted across the entire visible spectrum.

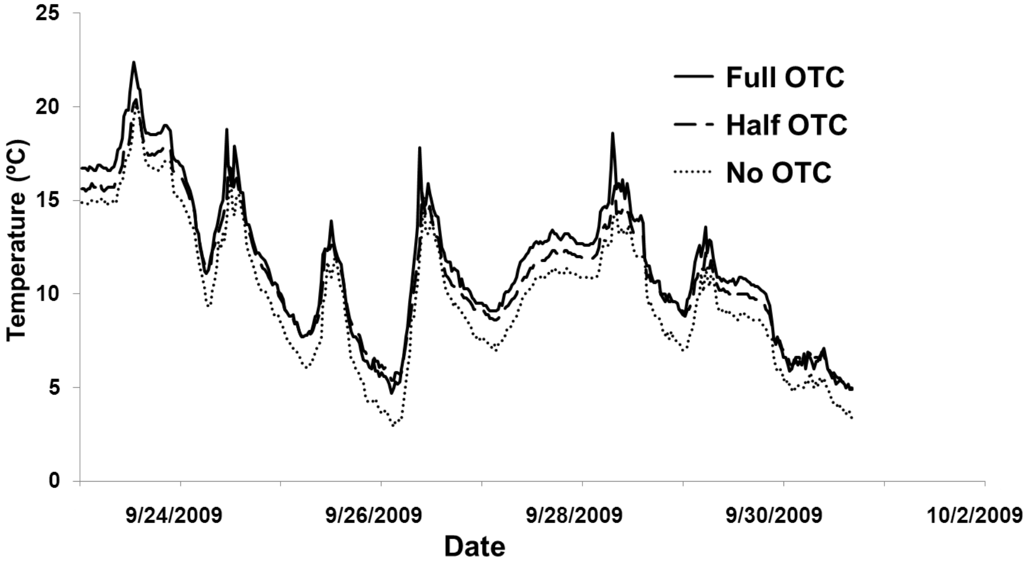


Figure 3A. 2: An example of temperatures measured simultaneously with MicroLog Pro700 mobile dataloggers over a one-week period (9/23/2009 to 10/1/2009) under the three temperature regimes tested in this study. Loggers were all located in a forest gap at 500 m.a.s.l. The solid line indicates temperatures under a full OTC; long dashed line represents temperatures under a half OTC and the dotted line tracks ambient temperature without any OTC.

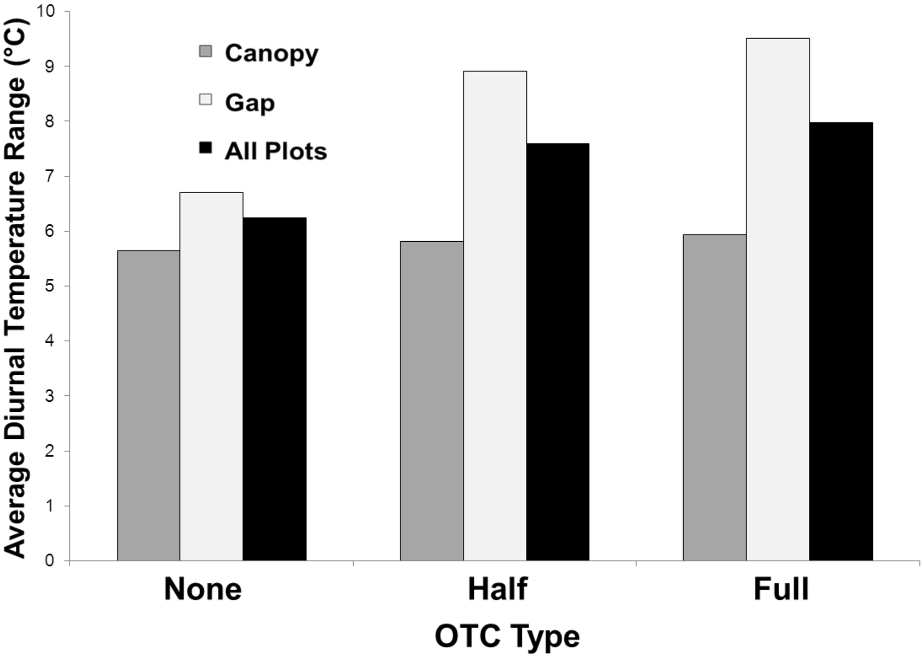


Figure 3A. 3: The average diurnal temperature range under no added warming, half OTCs and full OTCs in different plot locations.

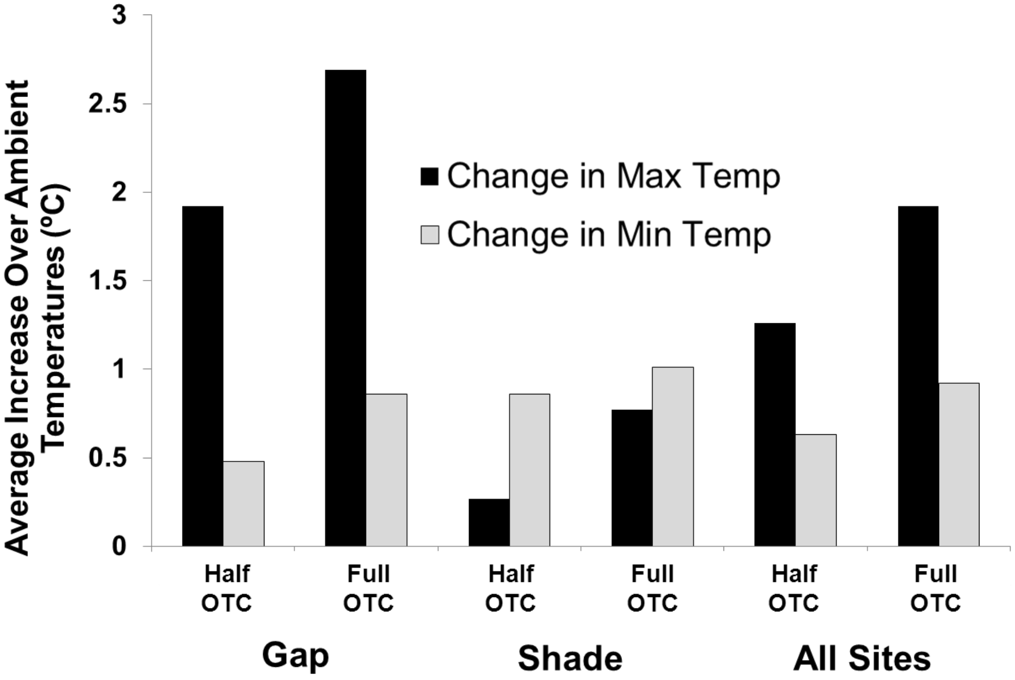


Figure 3A. 4: The average increases in temperature as a result of Half and Full OTCs by light environment between April and October.

Appendix 3B: AIC Model Selection

Table 3B. 1: A complete list of models tested in our AICc model selection analysis. All variables were treated as factors in the models. E = Elevation, O = OTC Level, L = Light Level (Gap vs. Canopy), C = Calcium

Model Type	Model
Null	Null
Single Factor Models	E O L C
Single Factor Additive Models	E + O E + L E + C O + L O + C L + C
Two-way Interactions	E x O E x L E x C O x L
Two Two-way Interaction Additive Models	(E x O) + (E x L) (E x O) + (E x C) (E x O) + (O x L) (E x L) + (E x C) (E x L) + (O x L) (E x C) + (O x L)
Multiple Two-way Interaction Additive Models	(E x O) + (E x L) + (O x L) (E x O) + (E x L) + (O x L) + (E x C)

Appendix 3C: Seedling Data

Table 3C. 1: Transplant shock mortality rates by species and elevation for seedlings planted in 2008. Mortality due to transplant was considered to be mortality which took place within 2 weeks of initial planting.

Elevation	Maple	Birch	Spruce	Fir
500	0 %	15 %	8 %	2 %
650	2 %	17 %	4 %	10 %
800	4 %	33 %	8 %	21 %
950	0 %	25 %	2 %	0 %

Appendix 3D: Site Characteristics

Table 3D. 1: Gap dimensions by site and elevation. Area calculations were made assuming gaps are ovate.

Site	**Measurement (m or m^2)**	**Elevation (m.a.s.l.)**			
		500	**650**	**800**	**950**
A	*Dimension 1*	8.5	5.0	7.2	4.5
	Dimension 2	11.9	5.8	5.5	6.2
	Area	***81.7***	***22.89***	***31.7***	***22.5***
B	*Dimension 1*	8.6	6.9	11.3	4.6
	Dimension 2	12.3	12.2	10.3	6.8
	Area	***85.7***	***71.6***	***91.6***	***25.5***
C	*Dimension 1*	5.7	5.8	7.7	4.6
	Dimension 2	10.2	5.1	5.1	5.1
	Area	***49.6***	***23.3***	***32.2***	***18.5***

CHAPTER 4: HISTORIC IMPACTS OF ACID DEPOSITION ON SUGAR MAPLE GROWTH: A DENDROCHRONOLOGICAL APPROACH

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Formatted for publication in:

The Journal of Biogeography

4.1 Abstract

Acid deposition has continuously affected forests in the northeastern US since at least the 1950's. While much is known about the effects of soil acidification on current forest health, historical impacts of acid deposition are more difficult to determine. In this study, we aim to identify the extent and duration of these historical impacts on sugar maple (*Acer saccharum* Marsh) in a single watershed in northeastern Vermont. Sleepers River Experimental Watershed (SREW) contains sites with a wide range of soil calcium concentrations that should respond differently to acidic deposition. We used dendrochronology and dendrochemistry in conjunction with foliar and soil chemical analyses to examine tree growth in one calcium rich site (RICH) and one calcium poor site (POOR) within SREW. Our results show that for much of the 20th century, tree growth in both sites was controlled by stand dynamics or climate. However, beginning in the late 1970's, tree growth in the POOR site declined while RICH site tree growth remained high. This divergence indicates that large-scale factors such as climate were no longer the dominant factor influencing POOR tree growth. At this time, the relationships that had existed between POOR tree growth and climate prior to 1950 shifted and tree growth became less correlated to climate. These changes and declining radial growth were likely the result of soil calcium limitation brought on by acid deposition-mediated soil acidification. Radial translocation of calcium ions within wood made dendrochemical conformation of this trend impossible. However, since 2000, elevated Ca concentrations in POOR tree rings suggest that soil calcium within this site may be increasing in response to effective reductions in acid deposition since the 1970's, representing evidence that natural recovery in some acidified sites has already begun.

Keywords: Acid Deposition, Sugar Maple (*Acer saccharum*), Tree Rings, LAI-CP-MS, Calcium, Acidification, Dendrochemistry

4.2 Introduction

Acid deposition has been recognized as an environmental hazard in the Northeastern United States since the 1950's (Likens and Butler 1981, Likens et al. 1996, Driscoll et al. 2001a, Driscoll et al. 2003) Since that time, scientists, governments and land managers have been working to understand how ecosystems have been affected, how to mitigate changes in species composition and restore losses of ecosystem function (Driscoll et al. 2001a). In the Northeastern US, acidification has been identified as a contributing factor in the loss of aquatic biodiversity (Baker and Schofield 1982, Husar et al. 1991, Driscoll et al. 2001a), altered soil nutrient cycling (Duchesne et al. 2002, Ouimet et al. 2008) and the decline of several important tree species. Among the northeastern tree species identified as having been affected by acid deposition are sugar maple (*Acer saccharum* Marsh) (Duchesne et al. 2002, Horsley et al. 2002, Schaberg et al. 2006), red spruce (*Picea rubens*) (Shortle and Smith 1988, Johnson 1992, Lawrence et al. 1997, DeHayes et al. 1999, Schaberg et al. 2000) and paper birch (*Betula papyrifera*) (Halman et al. 2011, Duarte et al. 2013). Declines in these species have produced changes in canopy compositions that may persist for decades to come (Schaberg et al. 2001, Kobe et al. 2002).

While much is known about how forests are currently affected by acid deposition, we know far less about when acid deposition began to affect forests (Duchesne et al. 2002, Long et al. 2009) and whether biological recovery has begun in the wake of acid deposition (Likens et al. 1996, Driscoll et al. 2001a). In this study, we aim to use tree rings from sugar maples (*Acer saccharum*) to identify the extent and duration of stress in trees that resulted from acidification and to determine whether there has been any recovery in natural forest stands previously affected by acid deposition.

Acid deposition can contribute either directly or indirectly to decline in trees. In extreme circumstances, acid deposition can cause damage to trees directly by killing leaf tissue that comes in contact with acidic rain drops or fog (Schaberg et al. 2000, Driscoll et al. 2001a, Driscoll et al. 2001b, Schaberg et al. 2001). Indirectly, acid deposition affects trees by causing acidification of the soil (Frenn et al. 2006). Over time, soil acidification has been shown to reduce the availability of beneficial base cations such as calcium (Ca) and magnesium (Mg), while simultaneously increasing the concentrations of antagonistic or potentially toxic cations such as aluminum (Al). It is this loss of beneficial cations that is thought to be the more widespread mechanism responsible for acid deposition-mediated forest decline (Lawrence et al. 1995, Frenn et al. 2006). Under neutral or near-neutral conditions, much of the soil Ca and Al is inaccessible, bound in biologically inactive compounds. However, as soil pH drops, cations are mobilized at which point they can either be taken up by plants or leached away. Al leaches less readily than Ca and subsequently leads to accumulations of Al in the soil, reaching potentially toxic levels (Shortle and Smith 1988, Schaberg et al. 2006).

Forested sites differ widely in their vulnerability to acid deposition-related decline depending on the amount of acid deposition they receive and their ability to neutralize acidic inputs. This ability of soils to neutralize acidic precipitation is referred to here as the soil acid neutralizing capacity (ANC), and it is determined primarily by the initial soil base cation concentration as well as soil depth, porosity, bedrock composition and weathering rate

(NEG/ECP 2003, Miller 2005a, Duarte et al. 2013). Soils with high ANC are able to accept larger inputs of acidic deposition without causing the pH to drop below the mobilization point for Ca and Al ions. Therefore, trees on sites with naturally high ANC are less likely to experience decline as a result of acid deposition. However, if cation depletion exceeds cation replacement through precipitation, hydrology or weathering, the ANC of a soil will gradually decrease. In most forests, once Ca levels in the soil are depleted, replacing them is a slow process that is controlled by soil weathering rates (St.Clair et al. 2008). Duarte et al. (2013) estimated that using a midpoint scenario for soil weathering rate, 56% of Vermont forests exist in a state of Ca deficit where more Ca is lost through leaching or land use than is replaced through bedrock weathering or deposition. In their high estimate, 99% of Vermont forests have exceeded their critical load of acid deposition and are susceptible to acid-mediated decline (Duarte et al. 2013).

When adequate levels of soil Ca are not available for sugar maples to take up, physiologic stress can result from either of two mechanisms. First, when Ca ions within tissues are limited, cell signaling is slowed or otherwise altered (Schaberg et al. 2001). This can result in an inability to respond to environmental stimuli and is particularly detrimental to sugar maples during the early spring and late fall when Ca ions help protect new growth and leaf tissues from frost damage. Alternatively, in the absence of adequate soil Ca concentrations, the Ca found in many structural cell wall compounds may be directly substituted with Al, resulting in altered functioning (Momoshima and Bondietti 1990, Schaberg et al. 2001). Affected trees often suffer reduced crown vigor, reduced cold tolerance and an increased susceptibility to secondary pathogens or drought (Juice et al. 2006). The duration of physiological stress that leads to decline symptoms is variable and difficult to identify since a tree could be experiencing stress long before it becomes evident externally.

While we continue to see the effects of acid deposition in forests, efforts to reduce the emissions that cause acid deposition have been successful (Driscoll et al. 2001a, Driscoll 2001b). The pH of precipitation in the Northeast has been increasing gradually since the 1970's with the passing of the 1970 Clean Air Act and its amendments in 1990 (Driscoll et al. 2001a, Driscoll et al. 2001b). This legislation acted to reduce acid deposition primarily by limiting sulfuric emissions (SO_2) from power plants. Efforts to reduce the other primary cause of acid deposition, nitrogenous (NO_x) emissions, have been less successful since a much larger proportion of these emissions come from cars rather than from more easily regulated point sources. Reductions in both SO_2 and NO_x emissions have not, thus far, led to significantly increased ANC in the lakes or streams of most affected areas (EPA 2005). However, some sites have experienced modest chemical recovery in streams or soils. Variable conditions throughout affected areas make it difficult to predict how long biological forest recovery from acid deposition will take or whether forests will be able to recover at all (Driscoll et al. 2001b). Experimental studies such as those at Hubbard Brook Experimental Forest, NH, which applied Ca fertilizers to sites 'naturally' depleted by acid deposition, have shown that growth of acid-sensitive species responds positively when Ca is replaced (Juice et al. 2006, Huggett et al. 2007). However, there have been very few recorded instances of natural biological recovery happening in unfertilized forests (Juknys et al. 2003).

In this study we aim to determine when northeastern forest decline due to acid deposition began and whether any recovery has taken place by examining sugar maple tree rings from within the Sleepers River Experimental Watershed (SREW) in Danville, VT. By using dendrochronological techniques coupled with chemical analyses of soil, foliage and wood samples, we aim to identify the extent and duration of acid deposition impacts, even in trees that appear healthy.

In addition to the effects of acid deposition, we expect trees to be responding simultaneously to internal stand dynamics, local climatic and hydrologic conditions and to climate change that has asserted influence on tree growth over the past century (Huang et al. 2010). While there are dendrochronological methods that can account for stand and local climatic conditions, dendrochronological studies on the impacts of acid deposition are challenging because of the difficulty in identifying low-frequency or gradual changes in tree ring data (Watmough 1997, Gavin et al. 2008). As a result, such studies are not frequently conducted (McLaughlin et al. 2002). Our study was designed, however, to identify and separate low frequency signals in the data by sampling trees from two sites within a small geographic area of the SREW. These sites experience nearly identical climatic conditions, but differ in their soil environment. Differences in the growth of trees in our two sites, as a result, are unlikely to be caused by climate or weather and instead must be the result of differences in soil environment or stand dynamics. The unique geology and hydrology within the SREW creates a mosaic of soil conditions resulting in significantly different Ca concentrations within a relatively small area, and therefore, vastly different acid neutralizing capacities (ANCs). By comparing the growth of sugar maples in high (RICH) and low (POOR) Ca sites, we aim to identify the degree to which maple growth has been affected by soil acidification, and thus, by acid deposition.

4.3 Methods

Site Description

Tree cores, soil and foliage samples analyzed in this study were all collected from within the Sleepers River Research Watershed (SREW) in Danville, VT (44° 29´30˝ N / 72° 10´06˝ W) (Figure 4.1) (Shanley 2000). The watershed occupies land from 201 m to 708 m a.s.l.. Below approximately 500 m, the land is dominated by agricultural fields above which, the land is forested (Shanley 2000). The forested portions of the watershed (Figure 4.1: W-9) are dominated by northern hardwoods including sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*) and white ash (*Fraxinus americana*). With increasing elevation, the proportion of conifers including red spruce (*Picea rubens*), white spruce (*Picea glauca*), balsam fir (*Abies balsamea*) and white cedar (*Thuja occidentalis*) also increases (McBride et al. 2008).

We specifically selected the SREW for this study because of its unique geology and hydrology that results in an extremely wide range of soil Ca levels within a geographically small area and across a small elevational range (~ 170 m). We selected two sites within SREW to represent a Ca rich site (RICH) and a Ca poor site (POOR). The POOR site was located along a ridgeline at the highest elevations of the watershed (677 m – 707 m) (Table 4.1). There, soil Ca levels were fairly low (Table 4.1) and comparable to other areas of the Northeast (Lawrence et al. 1997). Our RICH site was located on the slopes of the ridge where ground water runs close to the surface after flowing over a Ca-rich, metamorphosed (metapelite) limestone and calcareous schist bedrock (Lawrence et al. 1997). This results in areas with extremely rich soil. This area has been used in past regional studies to represent an extremely rich site (Hornbeck et al. 1997, Lawrence et al. 1997, Shanley 2000, Ross et al. 2009).

The SREW has been monitored continuously since 1958 by the United States Geological Survey (USGS) during which time detailed land use history records were assembled and continue to be updated. These records show that in 1929 large sections of the lower slopes, including some areas within our research site, were clear-cut (Shanley 2000). The ridgeline likely experienced some logging within currently forested sites through the 1920's as well. Pith dates from sugar maples cored in our RICH site suggest that clear-cutting of our study sites more likely occurred in the mid to late 1910's, however, at the highest elevations along the ridgeline, individual red spruce were found that were over 200 years old suggesting that logging in these areas was perhaps much more selective.

Soil and Foliage Collection

Soil was collected from the SREW early November in order to avoid sampling during the spring when decomposing leaves cause a pulse of Ca to be released into surface soils. In the fall, most of the Ca would be stored in plant tissues including leaves, which may have fallen but are unlikely to have begun decomposition. We used soil augers to collect the top 20 cm of soil excluding the O and OA layers. This soil was then air dried in paper bags, ground, sifted through a 2-mm sieve and analyzed for Ca and Al content using a 1M ammonium chloride (NH_4Cl) extraction. We used this extraction as opposed to a potassium chloride (KCl) extraction to avoid overestimating the biologically available soil Ca. Soil extracts were chemically analyzed using a Perkin-Elmer Optima D brand Inductively-coupled Plasma Atomic Emission Spectrophotometer (ICP-AES) at the University of

Vermont Agricultural Testing Lab. Ammonium chloride blanks and standard dilutions of Ca and Al were analyzed every five samples to ensure measurement calibration. Additionally, homogenized standard soil samples of known composition were analyzed every ten samples to ensure measurement accuracy. No significant drift was found within the data, requiring no post measurement corrections.

Maple foliage analyses were performed on samples we collected in late July when Ca concentrations were expected to be at their maximum. Sunlit foliage from the tree crowns was shot down from the canopy using stainless steel birdshot. Leaves were collected and dried for 48 hours at 60 °C then ground in a Wiley mill. Microwave digestion was then done using a concentrated nitric acid solution. Leaf extracts were analyzed to determine Al and Ca concentrations. Nitric acid blanks, sample duplicates and standard peach leaves with known concentrations of base cations (Ref 1537) (NIST 1993) were used as controls and were tested every ten samples using ICP-AES. Elements with a recovery rate of less than 90 % were corrected during data processing.

Dendrochemical Methods

The Ca, Al and carbon-13 (C-13) content of our tree rings were measured using a Laser-Ablation Inductively-Coupled-Plasma Mass Spectrometer Gas Chromatograph (LA-ICP-MS). We used an ESI 213 NWR 3.3.0.1 UV laser connected to an Elan 6100 ICP-MS at Hampshire College (Amherst, MA). This equipment gave us an advantage over traditional dendrochemical methods in which chemical extractions require many tree rings to be analyzed together in order to have enough sample material to test (Watmough and Hutchinson 1996). Using a LA-ICP-MS, it is possible to maintain annual, or even sub-annual resolution (Watmough et al. 1999, Durrant and Ward 2005). Because of budgetary constraints, we were only able to examine the wood chemistry from one previously cross-dated core from each site within the SREW. To examine both long- and short-term ring chemistry variation we employed a clustered sampling design. This meant we measured one ring every five years beginning with the outermost ring and every 15 years, five consecutive rings were sampled (Fig. 4.2). This resulted in the sampling of 38 rings from our POOR tree core sample and 27 rings from our RICH tree core sample. Cores were prepared for ablation by spraying them with a compressed air canister to remove dust and contaminants, then affixing them to glass slides before they were set inside a helium filled vacuum chamber. First, each ring was pre-ablated twice along the measurement path with the laser set to a low level (40%) and a wide aperture (80 microns) to a depth of 10 microns. This was done in order to remove as many surface contaminants as possible before actual data collection. Measurements were then recorded with the laser moving within the pre-ablated track but with a smaller diameter (50 microns). The laser was set to 45% and recorded at a rate of 10 microns per second. We chose to measure only two of the naturally occurring Ca isotopes, Ca-43 and Ca 44, instead of the most common Ca-40 isotope, in order to avoid overwhelming our spectral analyzer. Aluminum has only one naturally occurring isotope, Al-27, which we measured.

The data we collected using laser ablation required pre-processing to insure that only accurate measurements were included in our analysis of wood chemistry. Firstly, the data collected for each ring was plotted and visually truncated to exclude the measurements recorded by the mass spectrometer during the pre- and post-burn period (*i.e.* or before and after ablation took place). In addition, although the pre-ablation procedure did remove most surficial contaminants, occasionally sanding residue or dust trapped inside wood pores was errantly recorded. These errors were visually obvious when observing the data and typically presented as spikes in Al that were orders of magnitude higher than most of the other readings. In order to reduce the impact of these impurities on the overall data, we excluded recordings that fell outside of 95% confidence limits for each element in each ring. Within each ring between 75 and 911 measurements were taken, depending on width, of which 5% or between 4 and 46, were excluded.

Once we removed errors in the dataset, we accounted for differences in ring density that could skew results and prevent accurate year-to-year comparisons of Ca and Al, by dividing each measurement by its corresponding C-13 reading (Watmough et al. 1998, Watmough et al. 1999). This produced measurements of Ca and Al that are more comparable year to year. We also calculated Ca: Al ratios by dividing the total standardized Ca (both Ca-43 and Ca-44 isotopes) by the total standardized Al.

Tree Ring Data Collection

Within the SREW we removed tree cores from sugar maples at both the RICH and POOR sites using a standard 5 mm increment borer. In each site, we cored each living sugar maple tree with a diameter at breast height (DBH) >20 cm along two- 100 m transects. This was done to avoid biasing results by selecting healthy trees in the rich site or obviously declining trees in the poor site. As a result, we took cores from 36 trees in the POOR site and 32 trees in the RICH site. We took at least two cores from opposites sides of each tree, parallel to the slope, at breast height. Additional cores were taken if one of the first cores contained substantial rot. This resulted in the collection of 66 POOR tree cores and 64 RICH tree cores.

Tree Core Preparation

After extracting cores from trees, we prepared them for measurement and analysis. Tree cores were initially stored inside vented plastic straws and dried in an oven at 60 °C for at least 48 hours. We then glued each core to wooden core mounts and sanded them with progressively finer sandpaper. Because maple is a diffuse porous species, most cores required polishing with 800 grit sandpaper in order to visualize the rings (Stokes and Smiley 1968). We measured ring widths to the nearest 1000th of a millimeter using a sliding Velmex measuring stage (Velmex Inc., Bloomfield, NY) and recorded them using the MeasureJ2X software program (ProjectJ2X 2007).

Once we measured each ring, we cross-dated cores using both visual and automated methods. Cross-dating was initially done visually using skeleton plots and the list method, which can help to identify very large and very small rings and can aid in the placement of missing or false rings (Stokes and Smiley 1968). After completing preliminary visual cross-dating, we used the software program COFECHA (Grissino-Mayer 2001) to refine our identification of missing or false rings. Out of a possible 130 tree cores, 11 were removed because they were less than 35 years old, an additional 5 were not able to be cross-dated to a satisfactory level and were removed. The remaining 114 maple ring series were used in all subsequent analyses.

Climate Data Collection

We used both modeled and primary source measured climate data in this study. Because many climate data sources have gaps in their records or may not accurately represent the climate within the SREW, we chose to use PRISM climatic data as our main source. PRISM data (PRISM Climate Group 2010) include modeled estimates of monthly minimum and maximum temperatures as well as total monthly precipitation across the landscape on a 30 second grid scale. They were generated by combining multiple primary data sources and a digital elevation model (DEM) that can refine temperature and precipitation estimates based on elevation (Daly et al. 2000). These data are available for the entire conterminous United States starting in 1895 and are commonly used in in dendrochronological studies of recent climate. Seasonal NAO data were obtained from the National Center for Atmospheric Research (NCAR 1995). This station-based dataset extends back to 1865 and measures the pressure differential between Lisbon, Portugal and Reykjavik, Iceland (Cook et al. 1998, Visbeck et al. 2001, NOAA CPC 2012). The NAO is known to affect temperatures, precipitation patterns and storm tracks throughout the US and Europe.

Tree Core Statistical Analysis

Selecting the appropriate detrending procedures for our data was the first step in our tree ring analyses. To ensure that our results were robust and that trends that exist at different time scales were being identified.

Basal Area Increments (BAIs) were the primary measure we used to examine growth over time. BAI is a measure of the area of wood (mm^2) added by a tree each year at DBH. Unlike ring widths, which naturally decline with age, BAIs should remain constant throughout a tree’s lifetime (Biondi and Qeadan 2008a). This eliminates the necessity of detrending before chronologies are produced. However, some analyses required the use of detrended BAIs. When BAI series were detrended, it was done using the "mean" option within the *detrend* (dplR) function in R. This limits the impact of very large or very small trees on the master chronology. BAIs were generated in R using the *bai.out* function (dplR library) (Bunn 2008).

In addition to BAI, we also used a standardization method called Regional Curve Standardization (RCS) to account for the biological growth trend of trees and eliminate stand and other biological effects, (Esper et al. 2003, Biondi and Qeadan 2008b, Gavin et al. 2008, Briffa and Melvin 2011). RCS was selected because it can eliminate biological growth trends but retain gradual changes in growth patterns without assuming that the data follow a negative binomial growth curve. While trees that are not light limited ideally follow this growth pattern, most trees used in this study likely germinated and grew beneath a closed or nearly closed canopy. RCS does not assume a negative binomial growth pattern and instead generates a regional growth curve, which supplies the expected ring widths for trees of a given age. This curve is determined by averaging annual growth by cambial age rather than by calendar year. Deviations from this regional curve are recorded as a series of ring width indices (RWIs) for each core. Standardizing by cambial age rather than calendar year can reduce the impact of intra-stand variation, while preserving low-frequency variation (Esper et al. 2003, Bunn et al. 2004, Briffa and Melvin 2011). RCS detrending was done in the statistical program R (R Core Team 2013) using the *rcs* function (dplR library) (Bunn 2008).

In analyses in which we were more interested in short-term fluctuations in tree growth, we used a flexible smoothing spline to detrend ring widths. Splines remove low-frequency changes while enhancing short-term fluctuations in tree growth (Cook and Peter 1981). The spline applied to each tree ring series had a wavelength equal to half the length of that series (0.5 * nyrs) with a frequency response (Fig. 4.3) of 0.5. These calculations were done in R (R Core Team 2013) by modifying the *detrend* function (dplR library) (Bunn 2008).

The resulting RWIs or BAIs for each series were averaged to generate a master chronology. All master chronologies in our study were calculated using a Tukey's biweight robust mean (R *chron* procedure) that limited the influence of outliers. We did not attempt pre-whitening our using autoregressive models because of the potential for data loss, particularly, the removal of low frequency variation (Gavin et al. 2008). Chronologies were then truncated to avoid over-representation of individual trees by calculating the Expressed Population Signal (EPS) (Briffa and Jones 1990, Speer 2010). An EPS threshold of 0.85 was used to determine the start date for each chronology.

We examined the relationships between tree rings and climate over time in two ways. We first used the DendroClim2002 software program (Biondi and Waikul 2004) to map moving-window correlation values between tree rings and climate over time. DendroClim2002 uses bootstrapping to quantify relationships between monthly climate data and tree growth over time. Our analyses examined the relationships between annual mean-detrended BAIs and mean-detrended monthly climate variables (Maximum Temperatures, Minimum Temperatures and Precipitation) between December of each year (y) and June of the previous year (y-1). Correlations are reported in the final year of each 40-year moving window. For instance, a correlation reported in 1990 is the correlation calculated between a given climatic variable and BAI between 1950 and 1990. Our analysis of BAIs versus seasonal North Atlantic Oscillation (NAO) was done using an un-detrended BAI chronology so that we could retain all possible information from the tree ring series.

In our second correlation analysis, we modeled tree growth using a set of climatic variables selected to best describe tree growth between 1920 and 2009. Model selection was done in R using the *stepAIC* function (MASS library) (Venables and Ripley 2002). Significant selected variables ($\alpha = 0.1$) were used to model ring widths and create an "expected ring width chronology". This modeled chronology was compared to spline-detrended chronologies generated separately for RICH and POOR sites. We then calculated correlations between the expected and the observed chronologies for two time periods. The first time period was between 1920 and 1950. This interval represented the time before which we expected to see any impacts of acid deposition on tree growth. The second interval we examined was between 1980 and 2009. This period represents the most current condition of the sites. We tested the normality of each data set using the Shapiro-Wilke's Normality test (*shapiro.test*) in R. As a result of the non-normality of some data, we used non-parametric Spearman correlations to identify the strength of the relationship between RICH and POOR trees in two time intervals. These correlations were calculated in R using the *cor.test* function (*method = "spearman"*).

4.4 Results

Soil and Foliar Analyses

Our analysis of the edaphic conditions within the SREW found that some key soil variables were significantly different between our RICH and POOR sites. The Ca and Al concentrations found in soil samples taken from our POOR site (n=12) were significantly lower than the concentrations within the RICH site (n=8) (Table 4.1). The soil Ca:Al molar ratio was also significantly higher in our RICH site than our POOR site. In both sites, however, the Ca:Al molar ratio was >1, which is considered to be the threshold for causing stress in trees (Table 4.1) (Driscoll et al. 2001). Ca:Al ratios above 1 should be sufficient for healthy tree growth.

In addition to differences in soil chemistry in the RICH and POOR sites, we found significant chemical differences between the foliage of the sugar maple trees growing in the two locations. We found that the RICH site foliage contained significantly more Ca than the POOR site (Table 4.1). Unlike the results from our soil analysis, the Al concentration and the Ca:Al molar ratios were not significantly different between sites. Just as in the soil, the foliage Ca concentrations were above the 5000 mg kg-1 threshold deemed to be sufficient for tree growth (Schaberg et al. 2006).

Dendrochemical Analyses

Wood chemistry was also found to be significantly different between samples taken from RICH and POOR trees. However, the analysis of wood chemistry differs in many ways from previous chemical analyses. The most important difference is that we analyzed trends in Ca and Al over time by sampling from individual tree rings, instead of only measuring the current conditions. When the chemical compositions of the rings are compared pairwise between 1934 and 2009, the common period between the two ring series, the concentrations of Ca and Al were significantly different. They were also significantly and positively correlated (Table 4.1 & Fig. 4.4). This means that the concentrations of both Ca and Al fluctuated similarly in the RICH and POOR site over time. However, the concentrations of Ca and Al were significantly higher in the RICH samples than the POOR ones. Despite having a higher concentration of Al, wood samples from the RICH tree maintained a significantly higher Ca:Al ratio than did the POOR tree during its our study period (Table 4.1). Additionally, we see that over time, the concentrations of Ca and Al within the wood of trees at each site decline. Correspondingly, the Ca:Al ratios for RICH and POOR sites also trend slightly downward over time (Fig. 4.3).

In addition to providing information on the chemical condition of our trees, our data also suggest that our LA-ICP-MS procedure is accurately capturing and quantifying Ca and Al in tree rings. The clustered points that represent consecutive years' chemical composition indicate that Ca and Al change gradually year to year as we would expect (Fig. 4.3 & 4.4). Therefore, we are likely to be capturing real differences or similarities in the quantity of Ca and Al in the wood.

Tree Ring Analyses: Statistics

Despite many significant differences in the chemical compositions of the soil, wood and foliage in RICH and POOR sites, when aggregated, the tree rings themselves differed very little by site across the entire length of our tree ring record. Though the maximum series length (age) of POOR trees is substantially longer at 126 years than RICH trees, whose maximum series length was 90, the average series lengths were not significantly different (p=0.1724) (Fig. 4.5) (Table 4.2). The sensitivity and the frequency of missing rings were slightly higher for POOR trees than for RICH ones (Table 4.2). However, the series sensitivity statistics are within the desired range for trees to be responsive to their environment, but not overly reactive (Speer 2010). RICH trees exhibited slightly higher average BAIs, and ring widths as well as series inter-correlations and autocorrelations than POOR trees (Table 4.2). Again, the values for inter-correlations and autocorrelations were within the desired range. None of these differences suggests that site had a significant influence on the physical characteristics of tree rings within the time period studied.

Tree Ring Analyses: Dendrochronology

Although there was little difference between the tree ring metrics in our RICH and POOR sites, comparisons of the chronologies for each site did reveal differences in the growth of trees over time. Most of these differences took place within the last 40 years of our study period, while changes in growth before this time were more or less similar across sites.

Similarities in the regional curves that predict age-related growth patterns show that ring widths in RICH and POOR sites are highly correlated for most of our trees' lives (Fig. 4.6). Growth in both sites increases rapidly until approximately age 30 at which point growth begins to decline. One clear difference in the regional curves is the precipitous drop in ring width that RICH maples experience around age 80. A similar, though more gradual decline in ring width is observed in POOR trees, but not until trees are closer to 100 years old (Fig. 4.6).

In addition to highlighting differences in the age/growth relationships of maples in our study, Fig. 4.6 also confirms that detrending methods that assume a negative binomial growth pattern are not appropriate for our data. Figure 4.6 shows that ring widths of young trees are small and increase rapidly. Therefore, detrending using the c-method, for example, would not be able to accurately remove the biological growth trend (Esper et al. 2003, Bunn et al. 2004, Briffa and Melvin 2011).

The trends in the BAI chronologies indicate that growth throughout the SREW followed the same general trajectory, regardless of site. RICH and POOR site BAI chronologies show that growth increased rapidly until approximately 1940. Growth then appears to slow between 1940 and 1960 at which point growth stabilizes somewhat until around 1980. (Fig. 4.7A). In 1985, POOR BAIs begin to generally decline while RICH BAIs fluctuated, but maintained a higher level of growth than POOR trees. This trend seemed to continue through approximately 2005 (Fig 4.7A).

RWI chronologies were similar to BAI chronologies in that they showed a rapid increase in initial growth followed by a leveling out, but the timing of these events was different based on the method used. BAIs indicate that tree growth increased through at least 1983 (Fig. 4.7A), an assertion that is seemingly inconsistent with our RWI analysis, which shows maximum growth occurring around 1965 in both sites (Fig. 4.7B). It is, however, at this point in the mid-1960's that growth became more variable and RICH and POOR chronologies appear to have begun to diverge. These growth declines continued to be similar in both sites until 1990 when the RWIs of RICH trees stabilized, while POOR tree growth continued to decline. This divergence lasted until the end of our study period in 2009. RCS detrended chronologies were similar to BAI chronologies in that they showed RICH trees outperforming POOR trees after the mid-1980's (Fig. 4.7B).

While the results of our BAI and RWI analyses may seem to be contradictory, the BAI chronology actually corroborates and clarifies the results of our RCS analysis. Consider that in our RCS analysis, growth after 1970 appears to decline, however, the BAI analysis indicates that growth in both sites continued to increase for at least another decade. Both scenarios are possible simultaneously because of the geometry governing tree growth. As a tree gets bigger, it must distribute new wood over a larger surface area, consequently, constant annual growth results in smaller annual rings over time. Therefore, a tree may simultaneously be increasing the amount of wood it produces over time, while its annual ring widths get smaller (Johnson and Abrams 2009).

When we examine the frequency of significant differences in BAI between RICH and POOR trees, it becomes clear that the relative growth in the two sites transitioned to favor RICH trees in approximately 1985. Between the beginning of the common period in 1941 and 1985, POOR tree growth significantly exceeded RICH tree growth 6 times. Twice within that same time period, RICH growth was significantly higher than POOR growth. After 1985 however, the only significant differences occurred when RICH growth exceeded annual POOR growth, which it did 9 times (Fig 4.7A).

In addition to examining tree ring chronologies, we identified differences in how RICH and POOR trees related to the factors that controlled their growth over time. These relationships were analyzed in two ways, 1) we used DendroClim2002 to calculate correlations between climatic variables and BAIs, and 2) we built a model to predict tree ring growth using local climate data and compared the results to actual tree ring chronologies. In many instances, we found that the relationships that tree growth had to climate changed over time.

Correlation analyses indicated that the impact that temperatures had on growth (BAI) changed between 1960 and 1975, particularly for POOR maples (Fig. 4.8 & 4.9). Within this period, strong positive correlations to high temperatures that existed prior to 1960 disappeared. After 1975, correlations that had been strongly positive between POOR ring widths and maximum monthly temperatures in October, the previous November and the previous July, became strongly negative (Fig. 4.8A), indicating that high maximum temperatures from this point on were reducing growth in POOR trees. After 1975, RICH tree growth also began to respond negatively to increased maximum October temperatures (Fig. 4.8B). Another transition between growth and maximum monthly temperatures appears to have occurred in the late 1990s. At this time, trees in both sites began to be more positively influenced by hotter maximum temperatures, particularly in the late summer. This trend, though present in POOR trees, is much more pronounced in RICH trees. Relationships between growth and monthly minimum temperatures are not as strong or stable over time as those with maximum temperatures (Fig. 4.9). Precipitation also strongly influenced growth and appears to have been particularly important in the late summer and winter (Fig. 4.10). Unexpectedly, strong negative correlations between RICH growth and September precipitation before 1975 transitioned into a strongly positive correlative relationship by the mid-1990s (Fig. 4.10). This is the only example of a sign reversal in our precipitation correlation analysis.

In addition to examining the impacts of local climate on tree rings, we also investigated the relationship between tree growth and climatic global teleconnection indices. We tested the correlations of RICH and POOR tree growth against the El Nino Southern Oscillation (ENSO), the Pacific Decadal Oscillation (PDO), the North Atlantic Oscillation

(NAO) and the Atlantic Multi-decadal Oscillation (AMO). However, only the NAO produced results with a discernable pattern. Tree growth within the SREW was strongly correlated to many of the seasonal NAO indices, though this relationship was not consistent over time (Fig. 4.12). Like the relationship between tree growth and local climate, there seem to have been transitions in how ring widths correlated to the NAO. Prior to 1950, positive correlations between tree growth and the winter NAO index were dominant. During most of this period, the winter NAO index was in a positive phase, which led to mild, wet winters (Visbeck et al. 2001, NOAA CPC 2012). Positive correlations to the winter NAO returned during the 1990's and corresponded to periods of both negative (1950 – 1970) and positive (1970 – 2000) winter NAO values. Between 1950 and 1970, the negative phase of the winter NAO would have led to stormy, cold conditions, resulting in lower than expected tree growth (Visbeck et al. 2001). Since 1970, the winter NAO has been fixed in a record-breaking positive phase (Visbeck et al. 2001). However, our results clearly show a significant correlation between tree growth and summer NAO values (Fig. 4.12). Between 1955 and 1985, summer NAO values were generally positive (Warren II and Bradford 2010). Negative correlations to these NAO indices indicate that conditions resulting from positive summer NAO values were detrimental to tree growth. There was no evidence that the highly positive summer NAO values between 1995 and 2000 correlated with growth (Fig. 4.12).

Modeled ring widths were calculated by selecting a suite of annual, seasonal and monthly climatic variables that best described tree ring growth between 1920 and 2009. The selected variables highlight the importance of spring low temperatures and winter high temperatures. Out of 26 possible variables, the model selected by step-AIC included eight variables, seven of which were significant ($\alpha = 0.1$) and were used to create an expected ring width chronology (Table 4.3). The selected variables come from every season, include both maximum and minimum temperatures and precipitation and do not suggest that there is any one critical time that is important for determining tree growth. Additionally, many of the variable coefficients are unexpected and seem to be contradictory. For example, the coefficient for March minimum temperature is positive while the April minimum temperature coefficient is negative. This seems to be saying that high minimum temperatures in March helped growth but in April, high minimum temperatures reduced growth. Similarly, our model suggests that high January maximum temperatures resulted in smaller ring widths, while higher overall winter maximum temperatures (DJF) resulted in larger ring widths. Lastly, high summer (JJA) maximum temperatures negatively affected ring widths, while high minimum temperatures in the previous summer (JJA) increased growth (Table 4.3). Annual precipitation also limited growth (Table 4.3), a phenomenon that was not commonly observed in our previous correlation analysis using DendroClim2002, though occasional significant negative correlation values did occur before 1975 (Fig. 4.10). This suggests that too much precipitation within SREW was sometimes a problem between the 1930's and 1970's. The existence of so many seemingly contradictory effects of climate on ring widths underscores the complexities and subtleties involved in tree growth models and the importance of timing in tree growth.

Despite the ambiguities in the model coefficients, growth could be successfully predicted using our model. Modeled and real chronologies were significantly correlated across the entire study period ($\varrho=0.4770$, $p < 0.0001$) (Table 4.4), suggesting that model parameters were able to accurately capture the nature of tree ring growth over time.

The RICH, POOR and modeled RWI chronologies are similar in many respects, but differed most notably in their variance (Fig. 4.11). The observed RWI chronologies for RICH and POOR trees exhibited a much larger variance than did the chronology built using modeled tree ring data. Our model was only able to capture only about one-eighth of the variation in the natural ring width chronologies (Adjusted $R^2 = 13.0\%$). However, over the duration of our study, both the RICH and POOR chronologies were significantly correlated with the modeled data (Table 4.4). That said, Spearman's correlations do not take into account the magnitude of the change, only the direction. This means that the directional changes in annual RWIs were similar throughout the modeled and observed chronologies, despite differences in their amplitude.

When we compared the modeled ring widths to observed ring widths in the early and late 20th century separately, we found that the relationships between POOR tree growth and climate changed significantly, while climate-growth relationships for RICH trees remained constant over time. Between 1920 and 1950, during a period before which we expected to see impacts of acid deposition, RICH and POOR observed RWIs were significantly correlated with modeled ring widths. However, between 1980 and 2009, the correlation between RICH growth and expected ring width remained significant, while POOR growth was no longer correlated (Table 4.4). This means that climate dictated growth patterns in POOR trees prior to 1950, but after 1980, a different factor was limiting growth. We believe that this decoupling of climate and ring widths indicates a transition from climatically limited tree growth into a state of soil nutrient limited tree growth that was caused by acid deposition.

4.5 Discussion

Our tree ring and chemical analyses suggest that only the most recent changes in forest growth that have occured since the 1980's within the SREW are likely to have been brought on by acid depsition. We believe that with the use of dendrochonology we have been able to indentify the potential duration of acid-deposition mediated forest decline and that similar studies could be done in sites throughout the northeastern US and in other parts of the world where acid deposition is causing ecological disruptions, such as in Europe and in China. While we hoped to also present evidence that some natural recovery from the impacts of acid deposition may be taking place within the SREW, no definitive evidence was found. Only very recently have studies suggested a limited recovery is taking place (van Doorn et al. 2011) while most sites are still experiencing decline or suppressed growth (McLaughlin et al. 2002, Juknys et al. 2003, Halman et al. 2008, Halman et al. 2011). We think that this study offers land managers and policy makers a way to identify whether a forest is being affected by acid-mediated decline or to determine the duration of the acid impacts on a site.

Growth Transitions

Our results suggest that the maple trees within SREW underwent three significant shifts in their growth patterns between 1920 and 2009. Each shift was defined by a unique transition in the radial growth of RICH and POOR sugar maples trees. As a result, we believe that each transition was the result of a different process. .

We suggest that climate was likely the driver behind the first growth transition, which occurred between 1960 and 1980, and was characterized by the rise and fall in tree growth in both the RICH and POOR sites simultaneously. We believe that among the possible causes of such shifts, climate is the only variable whose effects would result in our observed trends. Changes to growth patterns, which are shared between both RICH and POOR sites are unlikely to be related to acid deposition since those effects would be regulated by soil environment, which differs significantly between our sites (Table 4.1). It is possible that the trends observed may be related to stand dynamics. With our POOR site being approximately 20 years older than our RICH site, it is possible that age would affect mortality (Taylor et al. 2007). However, healthy maples should live much longer than the 80 or so years at which we begin to see declines of some individuals (Godney et al. 1990). Additionally, stand dynamics are unlikely to have been the driver of this transition since two stands that differ even slightly in site age or history would not respond to density-dependent forces at the exact same time, as they appear to do in Fig. 4.7A. Information on stand age structure can be found in Appendix 4B.

The evidence to support our conclusion that climate is the driver of this growth transition is found within the relationships between BAI and climate between 1960 and 1980. During this time, the relationships between trees and individual climatic variables in both sites changed in a similar fashion. In Fig. 4.8, for example, positive correlations between BAI and maximum monthly temperatures in both sites that existed before 1960, disappeared by 1965, then reappeared in 1975 as negative correlations. We see a similar pattern in the relationships between BAI and minimum temperatures, only less pronounced (Fig. 4.9). The relationship between BAI and precipitation over time appeared to be more stable with fewer abrupt, widespread changes in correlations (Fig. 4.10). Water budgets produced for SREW suggest that water is rarely, if ever limiting in these forests (Hornbeck et al. 1997, Shanley 2000). However, the positive, stable correlations between tree growth and December precipitation (Fig. 4.10) suggest that snow pack can affect tree growth. In each of these examples, the correlations between BAI and climate are very similar across the SREW between 1960 and 1980. It is these similarities in the correlational patterns of the RICH and POOR sites that suggest climate was the driving force behind changes in growth during this time.

In addition to changes in trees' relationships to local climatic conditions, the relationships between BAIs and the NAO also changed significantly between 1960 and 1980. Both RICH and POOR sites exhibited very strong correlations between BAI and seasonal NAO values at various times throughout the 20th century (Fig. 4.12). It was during the transitional period between 1960 and 1980, however, that the trees within the SREW developed a negative corollary relationship to the NAO (Fig. 4.12). Despite the weaker effect that summer NAO indices are thought to have on weather worldwide (Visbeck et al. 2001, Warren II and Bradford 2010), in the mid 1960's, a strong negative correlation developed between tree rings and summer NAO values. Between 1955 and 1985, warm season NAO was in a positive phase (Warren II and Bradford 2010) suggesting that trees responded with reduced growth. However, the mechanism responsible for this loss in tree vigor is difficult to identify because the impacts of summer NAOs on climate in the northeastern US are poorly understood. NOAA reports no significant correlation between July NAO and temperature or precipitation and it is not thought to influence east coast ecology significantly (NOAA CPC 2012). As a result, identifying exactly what our trees are responding to in relation to the summer NAO index is difficult. Based on our findings, we suggest that the strong correlations observed between our trees and the summer NAO index are indicative of a stronger relationship between summer NAOs and Northeastern climate than previously thought. Because of the impact that the NAO appears to have on tree rings, this relationship should receive further investigation.

We suspect that the third and final shift in tree growth that took place between the early 1980's and 1990's, was mediated by acidic deposition because of the incongruous tree growth observed in the RICH and POOR sites. Our observations conform to the pattern of growth we expected to see as a result of acid deposition. First, we predicted that sites with low ANC, like our POOR site, would be most susceptible to acidification and would respond first to accumulated acid deposition with declining growth. Our data indicate that POOR sites experienced reductions in growth beginning in the 1980's or 1990's (Fig. 4.7) that did not correspond to similar reductions in RICH tree growth. These POOR growth declines extended through the end of our study, in 2009. This pattern can be seen most clearly in our analysis of RWIs where similar declines in RICH and POOR RWI chronologies that started in 1970, began to diverge by 1990 (Fig. 4.7B). This divergence was characterized by plateauing RICH tree growth, while POOR growth continued to decline. Our analysis of BAIs exhibited a similar pattern. In 1983, the BAI of POOR trees began to decline, while RICH maple BAI continued to increase, though, it is worth noting, at a slower rate than it had during the previous five decades (Fig. 4.7A).

It was also during this time that RICH tree growth consistently began to overtop POOR tree growth. After 1985 the frequency in which RICH growth was significantly higher than tree growth increased while the POOR BAI did not overtop RICH BAI after this time (Fig. 4.7A). Before 1985, there were periods where both RICH and POOR trees had grown significantly better than trees on the other site. This suggests that a threshold in soil chemistry was reached in the POOR site in which declining pH caused the mobilization and subsequent leaching of soil Ca ions. Once the available Ca dropped below a level sufficient for healthy tree growth, tree growth declined. Given the small size of our research area within SREW (~ 2.25 km^2), climatic conditions are unlikely to have varied significantly enough between our sites to have caused these divergent growth patterns. Instead, these patterns are consistent with those we would expect as a result of acid deposition.

In addition to a decline in growth, our data suggest that between the 1980's and 1990's, trees growing in our Ca poor site experienced a change in their relationship with climate. While this trend had been observed in previous studies of red spruce (*Picea rubens*) (Puckett 1982, Cook and Johnson 1989), a cause was unable to be identified. However, in our study we show that the relationship between tree growth and climate before 1950, had been maintained in RICH trees, but had significantly changed for POOR trees (Table 4.4) (Fig. 4.11). This difference in the relationship between climate and growth by site indicates that acid deposition is the likely cause of this decoupling. Additionally, Fig. 4.8 indicates that after 2000, the correlations between BAI and monthly maximum temperatures were consistently strong for RICH trees, while POOR trees exhibited more sporadic and weak correlations to these same variables than they did before 1960. For RICH trees, it appears that their climatic correlations after 2000 are stronger than they were before the climatic transition of the late 1960's (Fig. 4.8 & 4.9).

Foliar Chemistry

The decline in tree growth we observed in the tree ring records within SREW occurred at foliar Ca levels above those previously thought to be adequate for healthy tree growth. We observed growth declines in trees whose foliar Ca concentrations averaged 6230 mg kg^{-1} (Table 4.1). However, previous studies suggested that foliar Ca levels above 5000 mg kg^{-1} (Schaberg et al. 2006) or 6000 mg kg^{-1} (Hendershot 1991) should be sufficient for maple growth, and would therefore be unlikely to cause decline. Those studies, however, defined decline with external symptoms such as crown health, while decline in our study was based solely on tree ring growth patterns. This difference may explain the disparity in our findings. It is unclear at this point, however, what proportion of trees with reduced tree ring growth will progress into having external symptoms of decline or will ultimately die from decline related causes, since the relative timing of these events is poorly understood (Duchesne et al. 2002). Even if mortality of these trees is fairly low, our study indicates that trees with foliar Ca >5000 mg kg^{-1} may still be susceptible to growth decline due to acid deposition and forests vulnerable to acid-mediated decline may be more widespread than previously thought.

Delayed Effects of Acid Deposition

Although anthropogenic acid deposition has been influencing the northeastern US since at least the mid-1920's (Driscoll et al. 2001b), we observed that any declining growth in POOR trees that may be due to acid deposition did not begin until the mid-1980's or early 1990's and that the RICH sites have yet to experience a similar decline in tree growth. This lag would be expected since the effects of acid deposition on forests are delayed. Growth suppression and decline are most caused by the indirect effects of gradually accumulated acidic compounds in soils, not the acid deposition directly (Driscoll et al. 2001a). As a result, the initial, pre-industrial soil chemistry of a site greatly affects when the effects of acid deposition will be observed. The highest soil Ca concentration we recorded within SREW was 312 g kg-1, which is among the highest values recorded in the northeast (Lawrence et al. 1997, Ross et al. 2009). Since our RICH site within SREW is so high in soil Ca (Table 4.1), models suggest that this site should be capable of neutralizing all acidic inputs, even when they were at their highest levels in the 1970's (Driscoll et al. 2001a, NEG/ECP 2003, Miller 2005b). The soil Ca in our POOR site was significantly lower than in our RICH site (Table 4.1), but was still above the level generally considered adequate to prevent maple decline (Driscoll et al. 2001a). Despite this, our data suggest that after 60-70 years of acidic deposition and accumulation, trees within our POOR site were exposed to acidified soil to the point that tree ring growth began to decline (Fig. 4.7). Given these declines, we suggest that one of two possible scenarios has played out within SREW. First, it is possible that soil Ca levels within the POOR site have, in the past, dipped below the accepted threshold for biological decline to initiate. There is ample evidence that deposition levels have been significantly higher in the past (Driscoll et al. 2001b, NEG/ECP 2003, Lawrence et al. 2012), and some indication that soils in many sites in New England have begun to recover from acid rain by experiencing a decrease in soil Al (Lawrence et al. 2012). It is possible that the same phenomenon is happening within SREW. Alternatively, our data could also suggest that radial growth suppression occurs prior to the emergence of external decline symptoms, which may only present at lower soil Ca levels (Duchesne et al. 2003). If this is true, sugar maples in SREW are experiencing suppressed growth, but only with continued accumulation of acidic deposition will they progress into expressing external decline symptoms.

Dendrochemistry

While our dendrochemical analysis confirms that soil conditions influence Ca concentrations in wood, we were not able to demonstrate definitively that declining wood Ca concentrations over the course of the 20th were the result of an increasingly acidic soil environment or that recent increases in Ca concentrations are evidence of a recovery. POOR wood Ca concentrations were consistently and significantly lower than those found in RICH tree rings (Table 4.1) (Fig. 4.4). This indicates that, overall, our wood samples were able to confer the relative soil Ca concentrations at each site (Bukata and Kyser 2008). However, further extrapolations regarding the concentrations of Ca in tree rings over time are less reliable due to the possibility of radial translocation. In our results, it appears that wood Ca concentrations have been declining since the 1920's. This declining pattern is seen almost identically in both RICH and POOR sites suggesting that this decline is not the result of soil acidification. Reductions in wood Ca that are the result of acid deposition would have occurred the POOR site far earlier and more severely due to its reduced ANC. Instead, as observed in other studies (Momoshima and Bondietti 1990, Shortle et al. 1995, McLaughlin et al. 2002), this pattern is likely associated with the natural translocation of Ca ions and the availability of cation binding sites in wood as it ages.

While we expected that patterns of wood Al concentrations over time would be more useful in soil acidification reconstruction than Ca concentrations due to their relative immobility (Bilodeau-Gauthier et al. 2008), this did not turn out to be the case. Generally, we expected Al concentrations to change inversely with Ca concentrations since toxic Al displaces Ca in acidified environments (Watmough 2002), however, we did not see this pattern emerge in our wood samples. Instead, Ca and Al concentrations were significantly and positively correlated in the wood of both RICH and POOR trees ($\varrho=0.95$, 0.84: p-value <0.0001 for both). This result was unexpected, but not without precedent. Previous studies have observed incidents in which the most mobile fractions of Al in wood (acid and water soluble Al) increase as soil pH drops, while at the same time, total Al decreases (DeWalle et al. 1999, Bilodeau-Gauthier et al. 2011). Since our LA-ICP-MS analysis could not differentiate between the different fractions of Al, this scenario is at least still possible. However, without more information, we cannot determine the nature of the changes in Al concentrations in our trees over time.

4.6 Conclusion

Using dendrochronological and dendrochemical techniques, we were able to identify historical changes in sugar maple tree growth within the SREW that we believe were caused by acid deposition. Prolonged exposure to acid deposition has resulted in soil acidification and has led to Ca being leached from soils of throughout the Northeast and we believe it was this process that led to recent reductions in radial growth of sugar maple trees in our POOR site beginning in the 1970's and 1980's. This theory is supported by the absence of a corresponding growth decline in trees growing in our RICH site. Presumably, the POOR site was particularly susceptible to acidification and Ca loss because of its lower initial ANC. Further evidence that acid deposition may be the cause of these growth changes is found in the relationships between tree rings and climate. RICH trees maintained a consistent relationship with climate throughout the duration of this study, while POOR trees experienced a change in their relationship to climate after 1980. Additionally, after 1980 tree growth in the POOR site appeared less correlated with climate than it was prior to 1950.

While the soil and foliar Ca measurements at both our RICH and POOR sites were above the thresholds previously identified as causing tree health declines, our results suggest that a declines in radial growth can occur at higher levels of soil Ca than expected. As a result, in a forest that is still receiving acid deposition and experiencing soil acidification, radial decline may be expected to precede external decline symptoms. Further monitoring of tree health as well as soil and foliar chemistry is necessary however, to confirm our results. Lastly, we found that despite recent increases in wood Ca in the POOR site, dendrochemistry was not effective at identifying sugar maples' response to recent acidic deposition.

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4.8 Tables and Figures

Tables

Table 4.1: Chemical and physical characteristics of soil, foliage and wood samples from within the RICH and POOR sites in the SREW. Significant differences between RICH and POOR sites are in bold and are the result of a Wilcoxon Rank Sum Test ($\alpha = 0.05$).

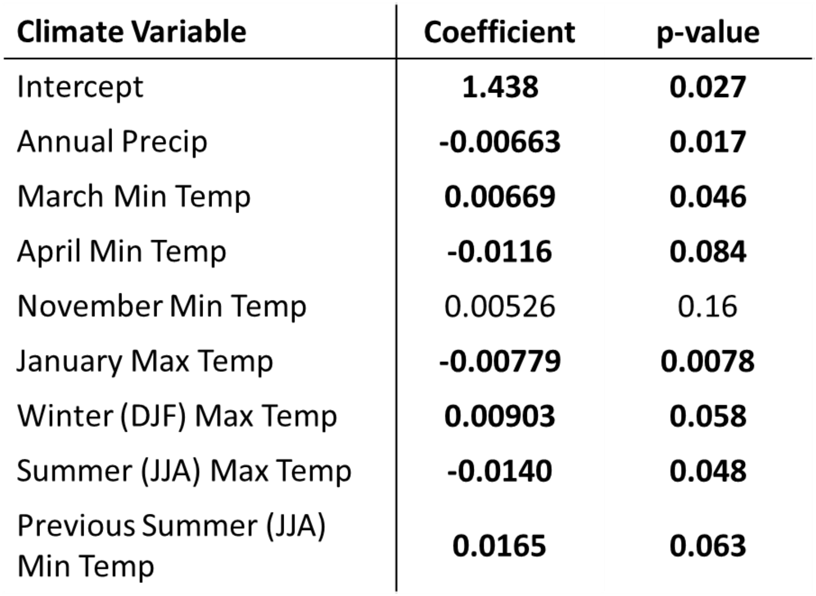
* indicates the results of a Wilcoxon Sign Rank Test.

		Average	RICH Site	POOR Site	p-value (Wilcoxon Rank Sum Test)	Spearman's Correlation	p-value
Site	Elevation	630.58	567.6	691.6	**<0.0001**	NA	NA
Soil (mg kg^{-1})	Calcium	547.0	911.7	303.9	**<0.0001**	NA	NA
	Aluminum	69.8	23.9	100.3	**0.0239**	NA	NA
	Ca:Al Molar Ratio	101.25	248.04	3.39	**0.0055**	NA	NA
Foliage (mg kg^{-1})	Calcium	7895	9559	6230	**0.0289**	NA	NA
	Aluminum	4.95	4.42	5.48	0.783	NA	NA
	Ca:Al Ratio Molar	347.96	375.89	329.35	0.800	NA	NA
Wood (g gC$^{13\ -1}$)	Calcium (^{43}C and ^{44}C)	3.52	4.30	2.97	**<0.0001 ***	**0.980**	**<0.0001**
	Aluminum	0.026	0.028	0.025	**<0.0001***	**0.745**	**<0.0001**
	Ca:Al Ratio	135.02	156.23	120.33	**<0.0001 ***	**0.536**	**0.0045**

Table 4.2: Descriptive tree ring statistics for the RICH and POOR sites within the SREW.

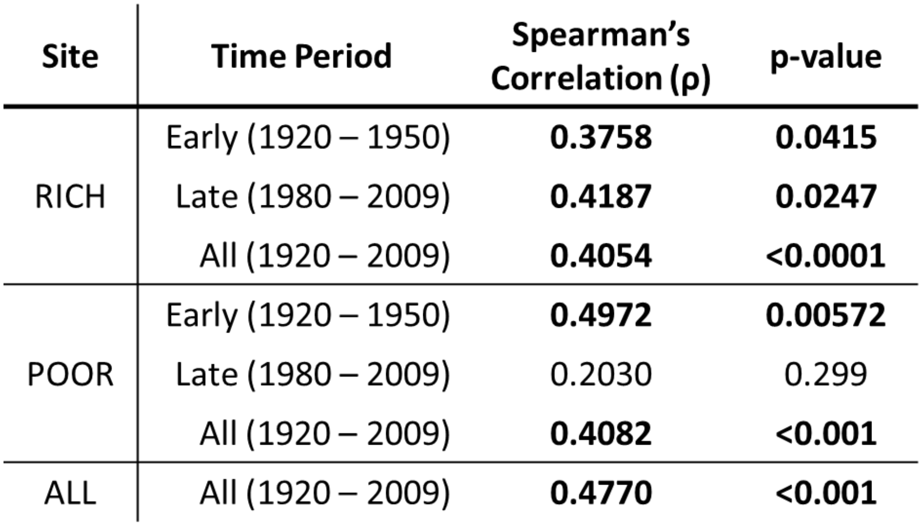
	RICH Site	POOR Site
Number of Series	57	62
Ave Series Sensitivity (raw ring widths)	0.248	0.300
Ave Series Sensitivity (RCS Detrended)	0.244	0.296
Series Inter-correlation	0.510	0.476
Ave Ring Width (mm)	1.738	1.624
Ave BAI (mm^2)	689.2	649.4
Ave Missing Rings (per Series)	0.415	0.581
Ave Series Length (Years)	67.7	72.2
Max Series Length (Years)	90	126
Ave Autocorrelation	0.711	0.701

Table 4.3: Model selected by Step-AIC to best describe tree ring growth for all trees sampled in the SREW between 1920 and 2009. Significant variables (α = 0.1) are in bold, and only those were used to generate an expected ring width chronology.



Climate Variable	**Coefficient**	**p-value**
Intercept	**1.438**	**0.027**
Annual Precip	**-0.00663**	**0.017**
March Min Temp	**0.00669**	**0.046**
April Min Temp	**-0.0116**	**0.084**
November Min Temp	0.00526	0.16
January Max Temp	**-0.00779**	**0.0078**
Winter (DJF) Max Temp	**0.00903**	**0.058**
Summer (JJA) Max Temp	**-0.0140**	**0.048**
Previous Summer (JJA) Min Temp	**0.0165**	**0.063**

Table 4.4: Correlations between our model-generated expected ring width chronology and the measured RICH and POOR ring width chronologies. Significant correlations are in bold ($\alpha = 0.05$).



Site	Time Period	Spearman's Correlation (ρ)	p-value
RICH	Early (1920 – 1950)	**0.3758**	**0.0415**
	Late (1980 – 2009)	**0.4187**	**0.0247**
	All (1920 – 2009)	**0.4054**	**<0.0001**
POOR	Early (1920 – 1950)	**0.4972**	**0.00572**
	Late (1980 – 2009)	0.2030	0.299
	All (1920 – 2009)	**0.4082**	**<0.001**
ALL	All (1920 – 2009)	**0.4770**	**<0.001**

Figures

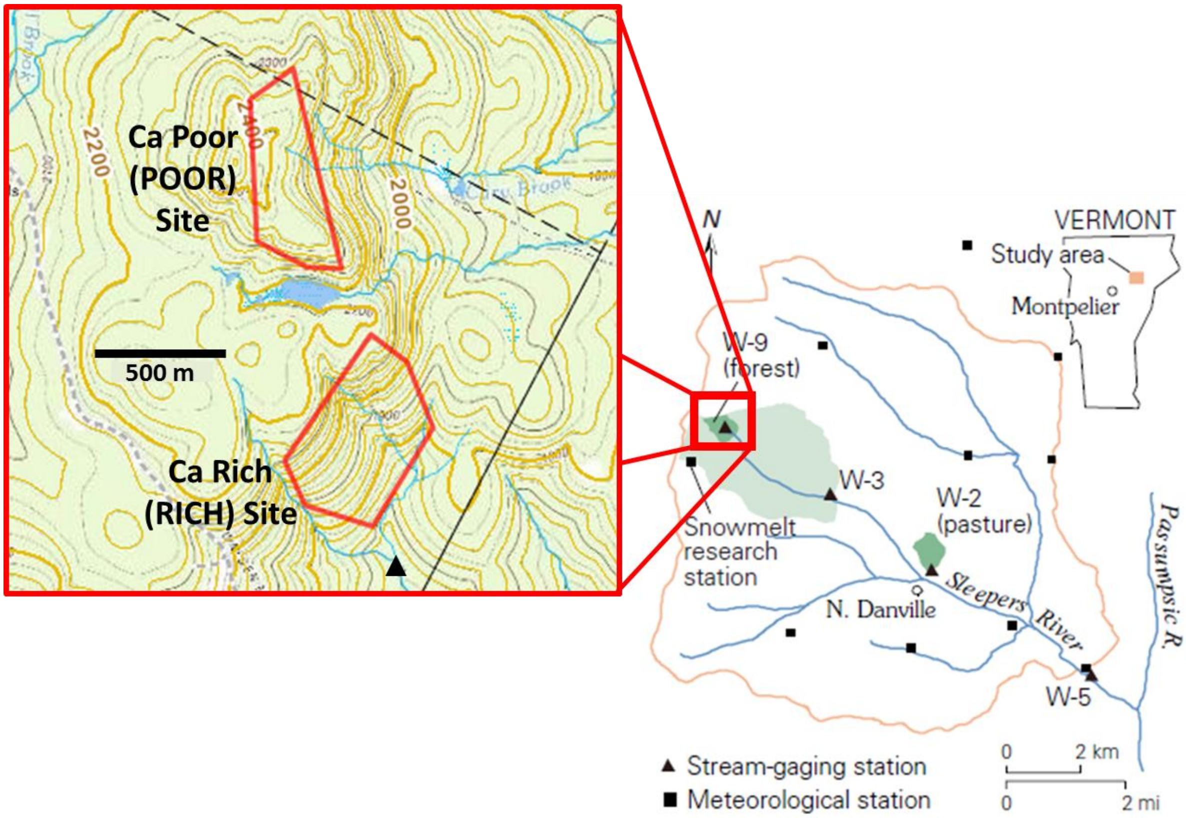


Figure 4.1: Map of Sleeper's River Experimental Watershed (SREW) and the RICH and POOR sites within it. SREW map from Shanley 2000. Inset base map is a USGS topographic map. Contours on the USGS base map are in feet.

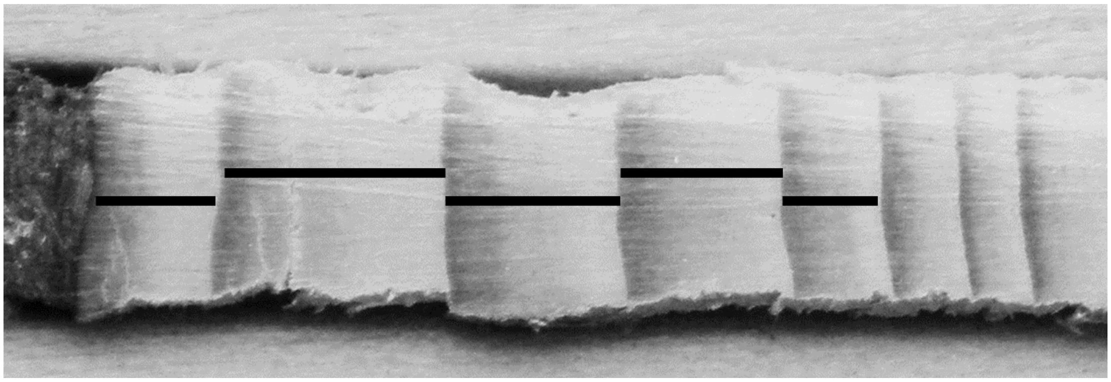


Figure 4. 2: Representation of our LA-ICP-MS sampling scheme on a tree core for the years 2005 – 2009.

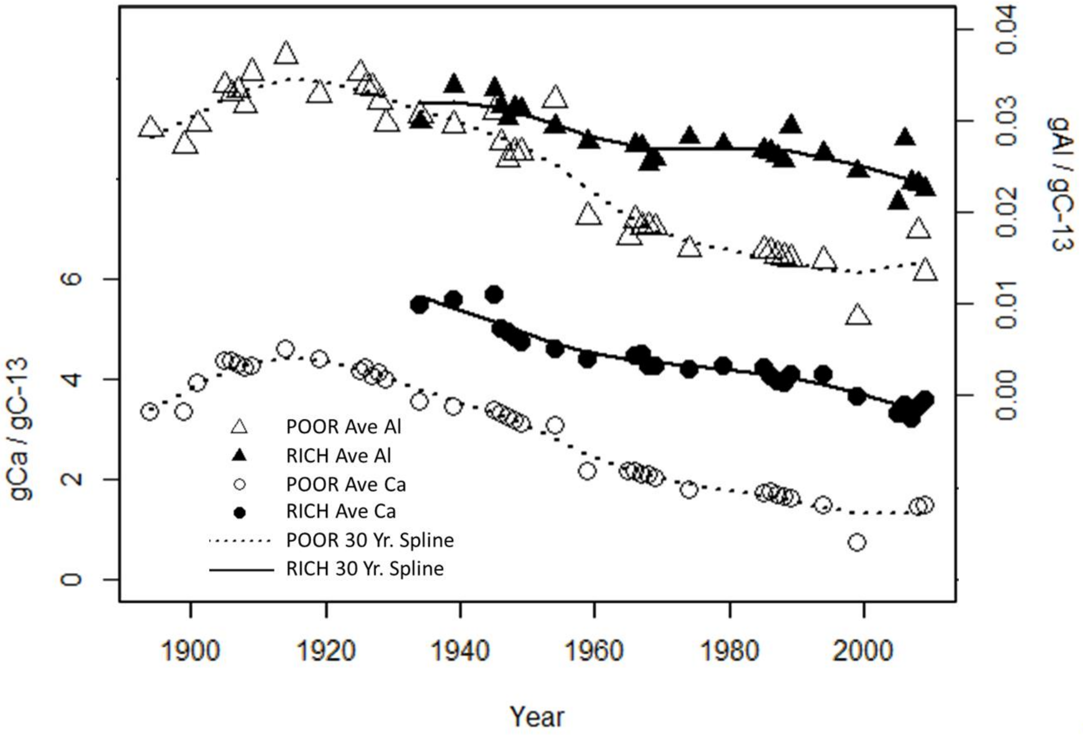


Figure 4. 3: Wood Calcium from a RICH and POOR tree core between 1900 and 2009. LA-ICP-MS was used to collect the chemical data, which was fitted with a 30-year smoothing spline.

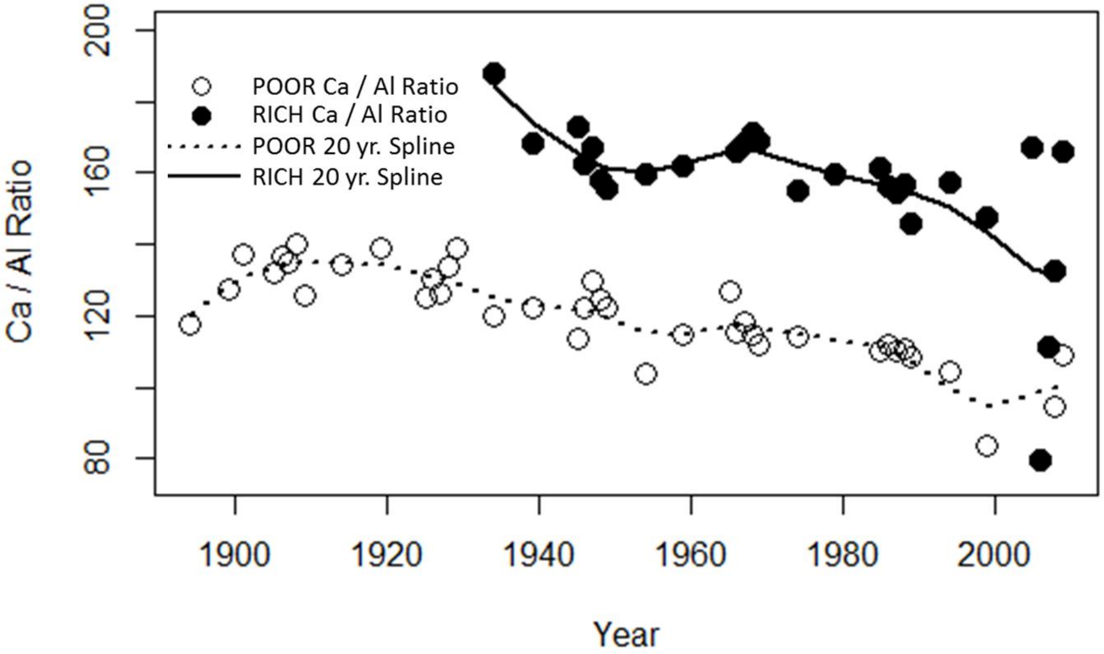


Figure 4. 4: Wood Calcium: Aluminum ratios from a RICH and POOR tree core between 1900 and 2009. LA-ICP-MS was used to collect the chemical data, which was then fitted with a 20-year smoothing spline.

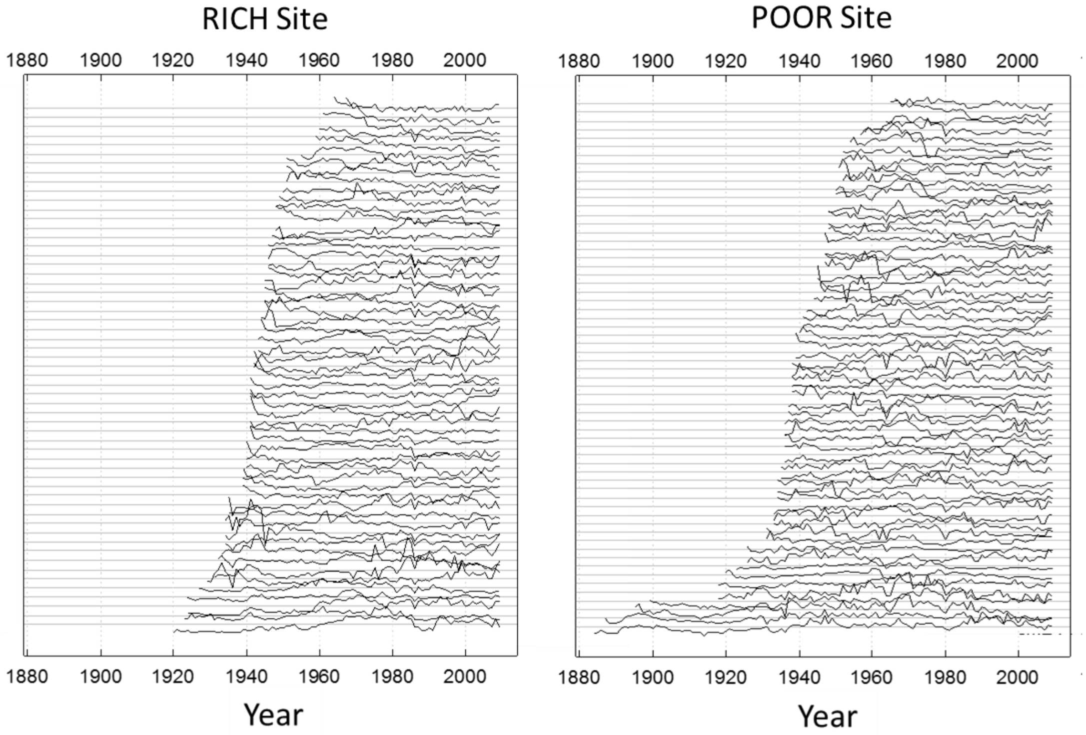


Figure 4. 5: Spaghetti plots for tree cores used in dendrochronological analyses from the RICH and POOR sites within the SREW.

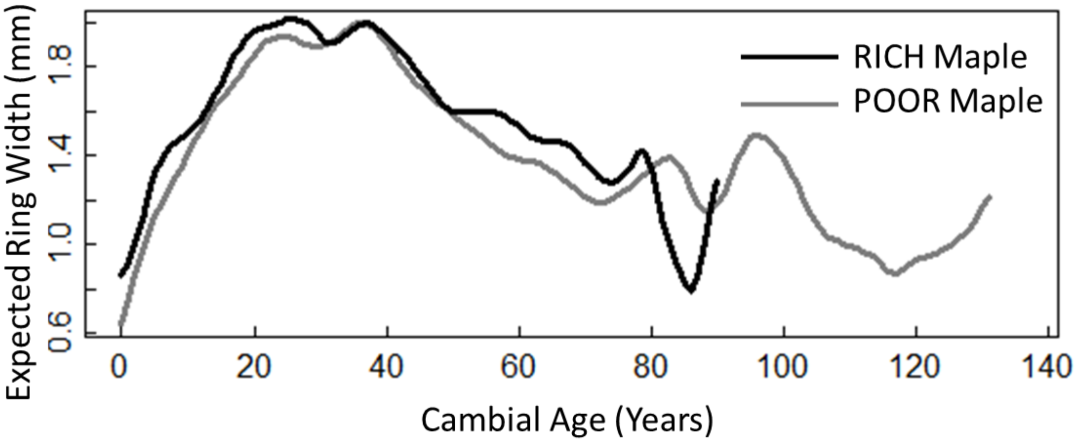


Figure 4. 6: The regional curves generated through RCS detrending identify the expected ring widths for trees in each site by cambial age.

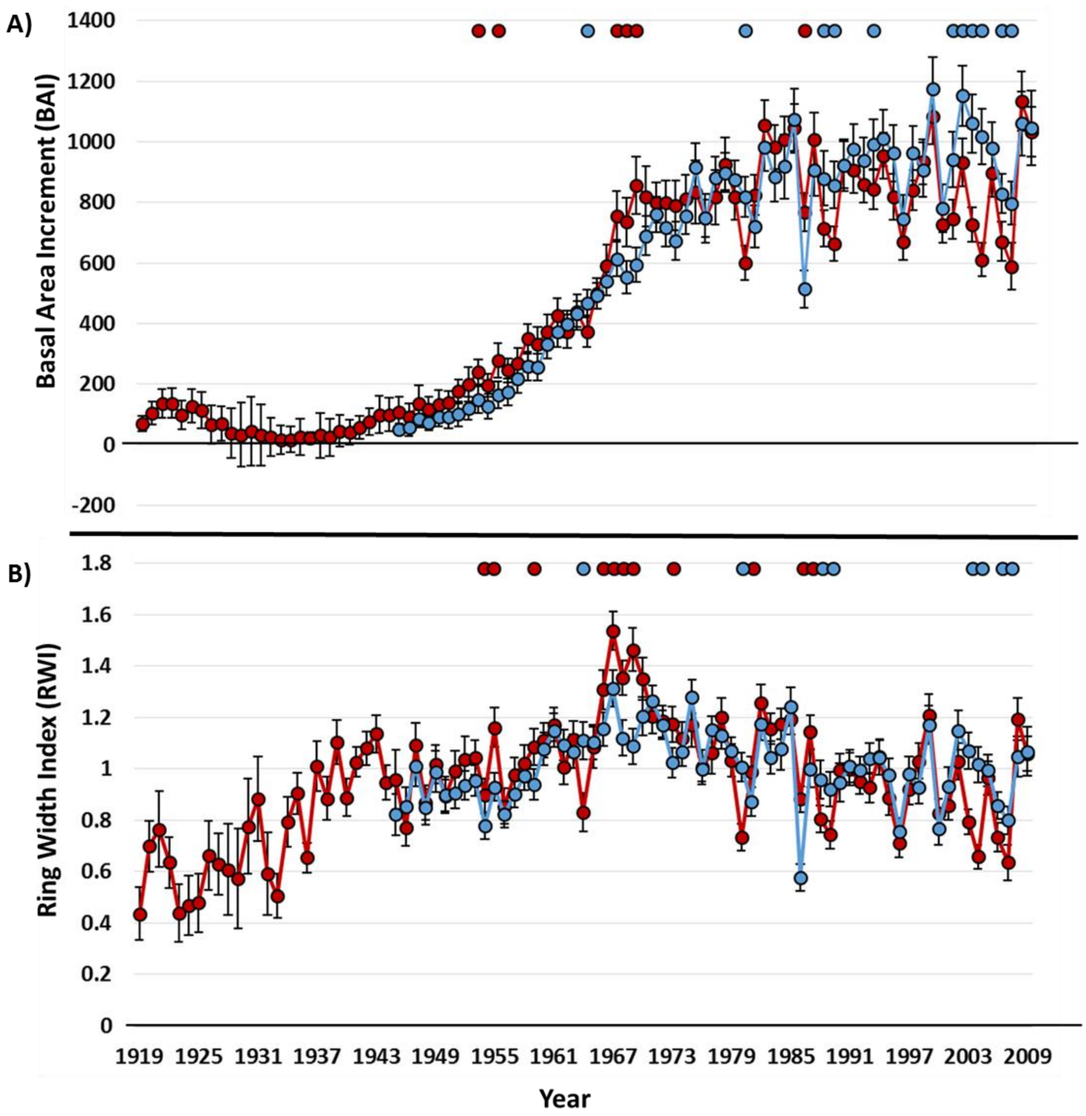


Figure 4. 7: Master chronologies calculated for RICH (Blue) and POOR (Red) sites. Circles along the upper edge of each panel represent years in which POOR growth was significantly higher than RICH growth (Red Circles) or when RICH growth was significantly higher than poor growth (Blue Circles). Error bars represent the standard error associated with each annual growth measurement. A) The Un-detrended BAI chronologies. B) The RCS generated RWI chronologies. Chronology length was determined using an Expressed Population Signal (EPS) threshold of 0.85.

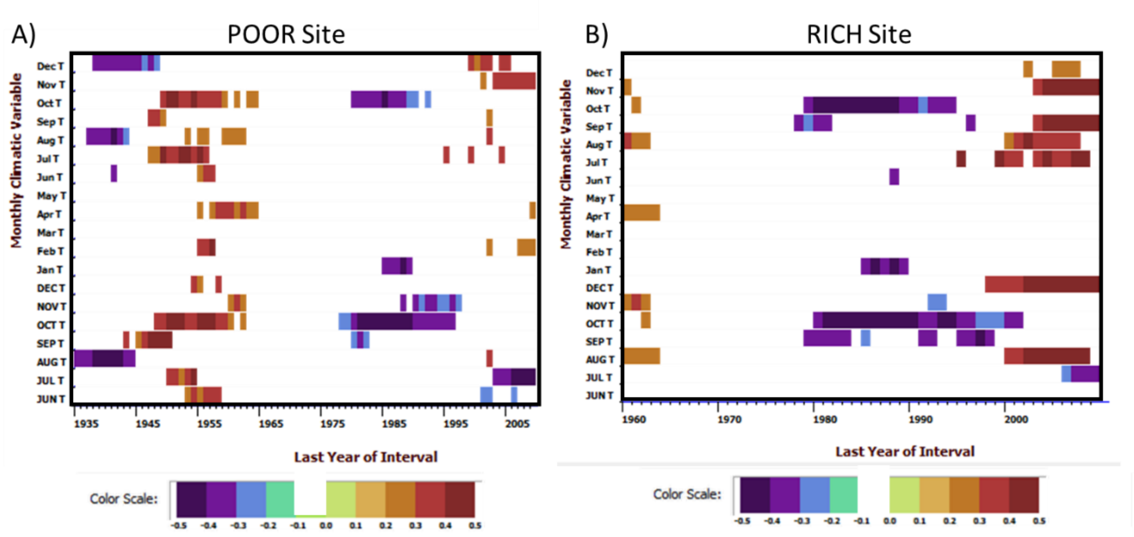


Figure 4. 8: Correlations between the mean-detrended BAI master chronologies for POOR (A) and RICH (B) sites and the mean, ***maximum, monthly temperatures*** between 1895 and 2009 (PRISM). Significant correlations are displayed as colored bars shown in the final year of each 40-year, moving-window. The first 12 rows represent the correlations between tree rings and the monthly temperatures from the same year. The last seven rows represent the correlations between tree rings and the previous year's monthly temperatures.

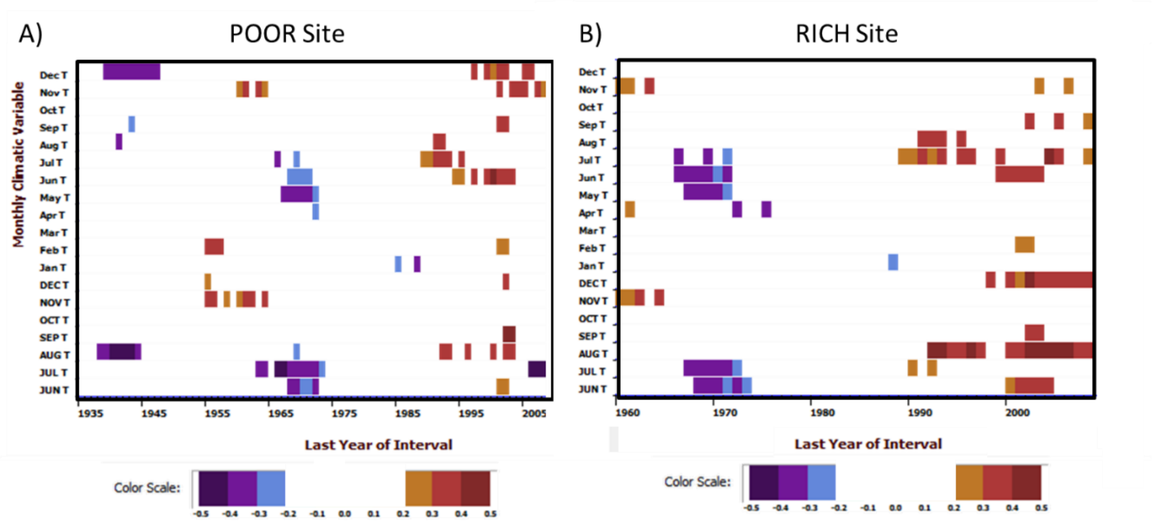


Figure 4. 9: Correlations between the mean-detrended BAI master chronologies for POOR (A) and RICH (B) sites and the mean, ***minimum, monthly temperatures*** between 1895 and 2009 (PRISM). Significant correlations are displayed as colored bars shown in the final year of each 40-year, moving-window. The first 12 rows represent the correlations between tree rings and the monthly temperatures from the same year. The last seven rows represent the correlations between tree rings and the previous year's monthly temperatures.

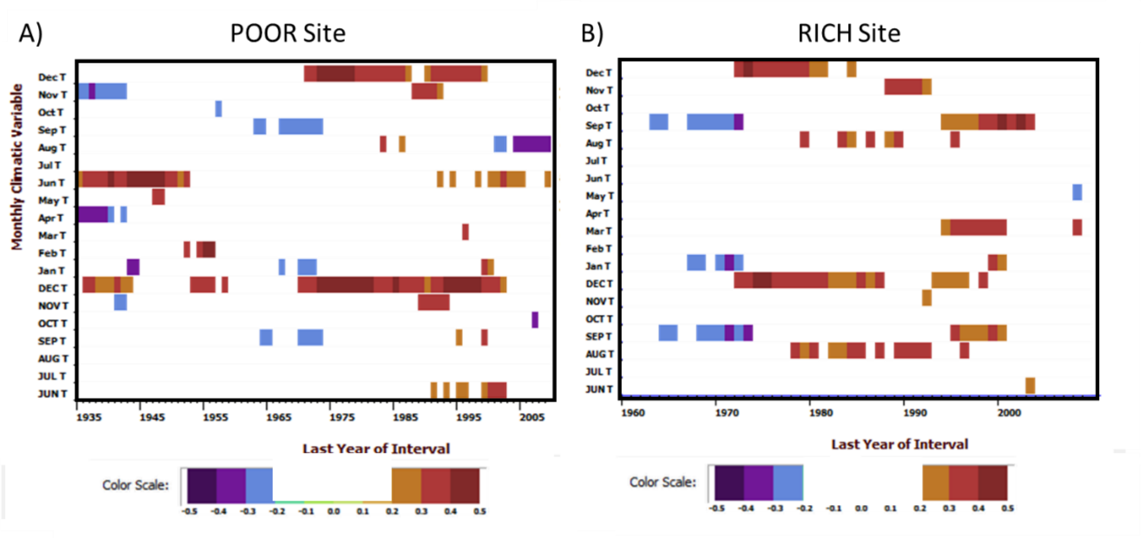


Figure 4. 10: Correlations between the mean-detrended BAI master chronologies for POOR (A) and RICH (B) sites and the total ***monthly precipitation*** between 1895 and 2009 (PRISM). Significant correlations are displayed as colored bars shown in the final year of each 40-year, moving-window. The first 12 rows represent the correlations between tree rings and the monthly precipitation from the same year. The last seven rows represent the correlations between tree rings and the previous year's monthly precipitation.

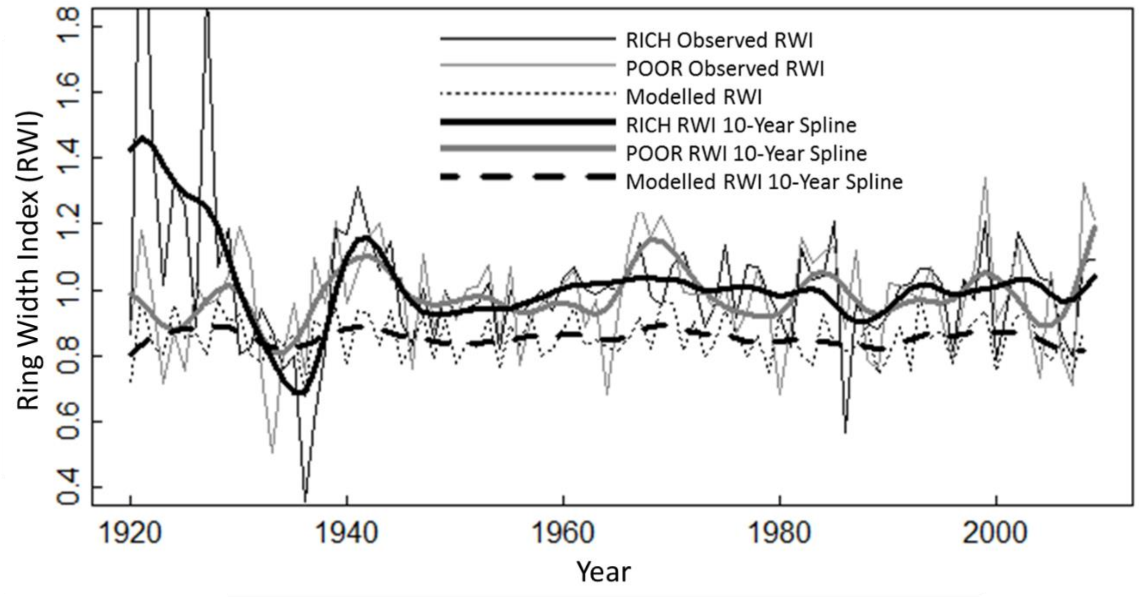


Figure 4. 11: Measured and modeled tree ring RWI chronologies between 1920 and 2009. Each chronology is fitted with a 10-year smoothing spline.

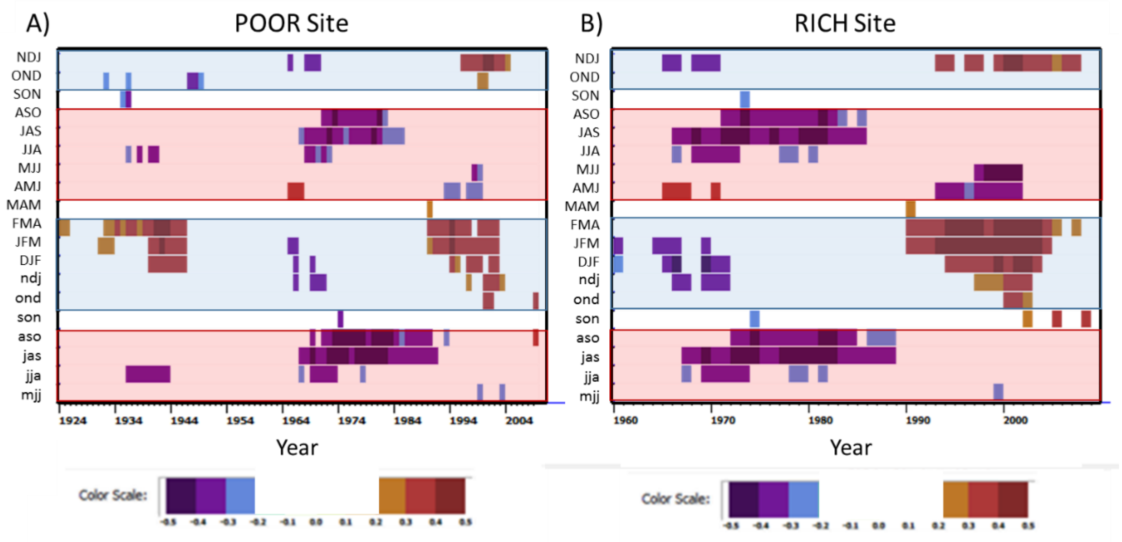


Figure 4. 12: Correlations between the un-detrended BAI master chronologies for POOR (A) and RICH (B) sites and 3-month average NAO indices 1885 and 2009 (NCAR). Significant correlations are displayed as colored bars shown in the final year of each 40-year, moving-window. The first 12 rows represent the correlations between tree rings and the NAO indices from the same year. The last seven rows represent the correlations between tree rings and the previous year's NAO indices. Summer NAO indices are shaded in red and winter NAO indices are shaded in blue.

4.9 Supplemental Information

Appendix 4A: Tree-ring Model Details

Table 4A. 1: Climatic Variables Considered in step-AIC model selection

Annual / Seasonal Variables	Average Monthly Maximum Temperatures	Average Monthly Minimum Temperature
Annual Precip	January Tmax	March Tmin
Spring (MAM) Precip	April Tmax	April Tmin
Summer (JJA) Precip	June Tmax	July Tmin
Fall (SON) Precip	July Tmax	October Tmin
Spring (MAM) Tmax	August Tmax	November Tmin
Summer (JJA) Tmax	October Tmax	December Tmin
Fall (SON) Tmax	November Tmax	
Fall (SON) Tmin	December Tmax	
Winter (DJF) Tmax		
Previous Summer Tmax		
Previous Fall Tmax		
Previous Summer Tmin		

These variables were chosen from a full suite of monthly, seasonal and annual precipitation, maximum and minimum temperature variables. The number of variables used in the step-AIC analysis is limited by the software and was dependent on the length of the tree ring chronology (response variable). Selections were made based on their significance in a set of preliminary model runs. All variables are taken or derived from PRISM interpolated data (PRISM Climate Group 2010).

Appendix 4B: Information on Stand Structure

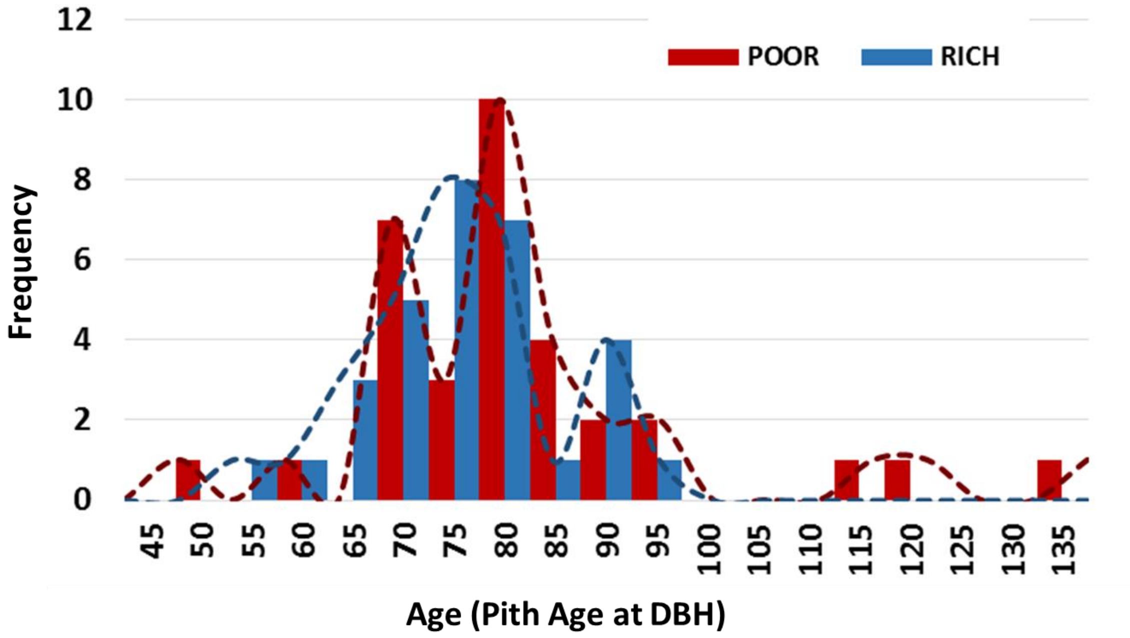


Figure 4B.1: Age Structure for RICH and POOR sites. Histogram of tree ages for RICH and POOR sites. Age was determined by subtracting the pith-offset estimate from the innermost measured ring.

CHAPTER 5: SUMMARY / CONCLUSION

The work presented in this dissertation has expanded on work done by others to identify how forests, and more specifically ecotonal forests, have changed in the recent past in response to climatic and environmental changes. Most influential was the work published by Beckage et al. (2008) that identified and upslope migration of the northern hardwood range within and around the Boreal-Deciduous Ecotone (BDE) since the 1960's. The extent of this shift was estimated to be between 90 and 120 m (Beckage et al. 2008). My work aimed to better understand this observed shift by identifying the mechanisms responsible for it, and examining how this shift was exhibited in the sub-canopy and forest floor communities.

Throughout this dissertation, I have examined the forests of the Green Mountains and their responses to recent simultaneous anthropogenic disturbances. With the goal of better understanding how and why northeastern forests have responded to changing conditions, I have observed and quantified changes in plant communities, identified the physical conditions that control tree seedling establishment and examined the responses of forest species to interacting anthropogenic disturbances such as climate change, acidic deposition and invasive species. What made my work unique were the variety of methods used to examine forest change and the range of species that were studied. As a result, I have developed an in-depth understanding of these montane forests, which provides a multi-faceted perspective of recent changes that have taken place within the BDE of the Green Mountains. This research is important because an in-depth understanding of past change in these forests will make it easier to predict future forest location and composition through the use of bioclimatic models. Models that are more accurate can better anticipate future changes to ecosystems as they continue to experience climate change and other anthropogenic disturbances.

In Chapter 2, I examined plant communities on Camels Hump and found that changes in composition since 1965 varied by guild (i.e. understory vs. canopy), elevation, exposure to anthropogenic disturbance and proximity to the BDE. In and above the BDE, the greatest compositional change occurred within the understory. In this area, I identified novel communities that formed since 1965 (Figure 2.2). These communities were the result of the combined influence of climate change and acidic deposition on an area that naturally contained a high number of species boundaries. The least amount of understory compositional change occurred within the northern hardwood forest below approximately 600 m.a.s.l.. However, individual species in these forests such as *Arisaema triphillim* and *Cardamine diphylla,* did experience large changes in abundance that were likely in response to localized earthworm invasion (Figure 2.4). Above the BDE, exposure to acid deposition and a relatively low influence of warming temperatures resulted in only moderate changes in understory composition. As a group, with the exception of *Arisaema triphillim* and *Cardamine diphylla,* understory species on Camels Hump responded similarly in terms of elevational shift and change in abundance over time. This indicates that, in general, understory communities are shifting as intact units. The most notable exception takes place just above the BDE where a few species are migrating upslope faster than the others, creating novel communities. As climate change continues, we expect the observed patterns of migration to continue as well.

In Chapter 3, I identified factors responsible for limiting the growth and establishment of tree seedlings across the BDE. For northern hardwoods, the most important factors that determine success above the BDE differ depending on species. For the shade-intolerant yellow birch, light was primarily responsible for survival, while temperature more closely controlled growth (Figures 3.3 and 3.5). For sugar maple, survival above the BDE was elevated with increased temperature regardless of light conditions (Figures 3.2 and 3.5). Promotion of northern hardwood in the boreal forest is going to be dependent on the rate of warming at high elevations as well as the level and type of disturbance in the future. Large disturbances that produce large gaps (multiple-tree sized gaps) will promote birch regeneration. The seedlings of both focal northern hardwood species will also be affected by short- term climatic fluctuations and weather events. Differences between the distributions of naturally occurring seedlings and planted seedlings suggests that dispersal or germination limitations may also be affecting seedling distribution and ultimately, will impact the ability of species to migrate upslope.

I examined the interactions between acid deposition and climate change on tree growth in Chapter 4 by comparing tree rings in trees growing in calcium-rich and calcium-poor soils. This comparison allowed me to examine the impact of acid deposition on long-term sugar maple growth. As a result, we identified a growth decline in sugar maples that began between 1970 and 1990 (Figure 4.7). These declines emerged prior to the emergence of external symptoms of decline and occurred at a higher soil calcium levels than expected given previous studies. This may indicate that growth declines can precede external decline symptoms or that soil and foliar calcium levels in the past were lower than they are presently. In addition, my results suggest that increased stress due to prolonged exposure to acid deposition may also cause changes in the relationships between tree growth and climate. No significant recent increase in growth was detectable in our data however, despite recent evidence that acid deposition-mediated decline of red spruce may itself be on the decline in some locations (van Doorn et al. 2011).

Taken as a whole, the work presented in this dissertation provides a broad perspective on how montane forests in Vermont have changed in the past 50 years. It may also provide insight into how we can expect these forests to change in the future as they continue to be impacted by anthropogenic disturbances such as climate change, introduction of invasive species and the continued influence of acid deposition. In terms of past responses to climate change, my work demonstrates that it is not the canopy alone that migrates in response to environmental changes. Understory communities also respond to anthropogenic impacts and by some measures, change even faster than canopy species. Changes in the canopy have been the result of prolonged exposure to acid deposition, which has reduced the radial growth of sugar maple at soil calcium concentrations once thought to be sufficient. Continued mortality resulting from acid-mediated decline is among the factors that will influence seedling establishment in the future and lead to changes in canopy composition because, as canopy trees die, the gaps created allow seedlings to establish. The temperature and light environment within those gaps will determine the species able to capture it. Increased light resulting from large gaps will favor yellow birch survival, while increased temperatures will enhance its growth rate. Sugar maple seedlings will be more likely to establish above the BDE under a closed canopy and elevated temperatures. As a result, any gap-creating disturbance, will increase the rate of birch migration and the larger the disturbance, the more likely establishment will be.

Given what we have observed regarding the rate of upslope migration of northern hardwoods in response to recent climate change, it seems possible that many understory and canopy species will, in the short-term, be able to migrate upslope fast enough to keep pace with changing climate. However, in the longer-term, once climate changes to the point where elevational refugia are no longer sufficient, the probability of long-term survival decreases. For most species, in the absence of observed extremely long distance dispersal and given their current rates of migration, it does not seem probable that they will be able to migrate within their optimal climatic zones without human intervention (IPCC 2014). While this may seem grim, there have been instances in earth's past, such as following the last ice age, where the rate of forest expansion and migration has exceeded expectations (Clark 1998, Phillips et al. 2008). This provides at least a glimmer of hope that the resilience of natural systems can overcome detrimental human behavior.

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