

Flyleaf

An abstract of the thesis of Jordan R. Christ for the degree of Master of Science in Biology presented on August 7th, 2012.

Title: Winter climate change and the hydraulic properties of the northern hardwood forest.

Abstract approved:

Michele L. Pruyn

Currently sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*) are in decline in the northeast U.S. This decline disease is caused by multiple stressors which weakens the tree, making it more vulnerable to acute stress events or disturbances. Stressors affecting the northern hardwood forest include atmospheric deposition, insect pests and pathogens, invasive species, fragmentation, and climate change. Of these stressors, much is uncertain about the effects of climate change on tree species physiology, health and future distributions in New England. Winter climate change is especially important because many trees species in the northern hardwood forest are not very cold hardy and rely on snowpack over winter as insulation which protects roots from soil frost damage. Furthermore, recent temperature increases have been greater over the winter season compared to summer, providing a greater emphasis on the winter season. A better understanding of the impacts of winter climate change will allow for improved land management practices for forest industries, like timber and maple sugaring, which can provide economic longevity for New England. Sap velocity can be directly linked to productivity in tree individuals as the flow of sap is closely correlated to the rate of transpiration, a by-product of photosynthesis. We present the heat dissipation method for calculating tree sap velocity in two experiments under the general theme of winter climate change and the hydraulic properties of the northern hardwood forest. The experiments in this document include 1) comparing root percent embolism and sap velocity in yellow birch stands over natural gradients and 2) the pre-bud break sap velocities of sugar maple trees in response to winter variability, air temperature fluxes and sapwood aspect and depth.

Chapter 1 Results: Snowpack variation over natural gradients of aspect and elevation was greatest over winter 2010/2011 compared to 2009/2010 at the HBEF and differences in root percent embolism using a repeated measured ANOVA with elevation and aspect as factors were significant in 2011 ($p=0.05488$); however no significant differences were found in 2010. Overall snowpack depth (80-130cm) and duration (18 weeks) was greatest over winter 2010/2011 compared to 2009/2010 (40-70cm and 16 weeks) and root percent embolism was greatest at all plots in 2010, with the exception of the Kineo Mid plot. These results suggest that annual snowpack variation in depth and duration influences root embolism patterns in yellow birch trees. In comparing average root percent embolism to average sap velocity we found that within class of aspect all plots with the greatest average root percent embolism had the lowest average sap velocity and vice-versa for both years, with the exception of

Kineo Low and WS 3 High in 2010, likely due to drought during 1 of the 2 days when sap velocities were compared. This trend suggests that root embolism may be limiting sap flow in yellow birch trees.

Chapter 2 Results: Sap velocities of sugar maple trees during the early spring sugaring season in 2011 and 2012 were influenced by thaw-freeze cycling and temperature fluctuations, where these conditions were important in producing the greatest sap velocities. After two days of above freezing night temperatures in 2011 xylem pressure was greatly reduced. Sap velocity was greatest at 2cm sapwood depth and south aspect (up to 3,000 g/m²/s), where stem temperature fluctuation was likely the greatest due to sun exposure. Sapwood depth had a greater influence on flow rates than sapwood aspect. Sugar maple trees had later and greater pre-bud break sap velocities in 2011 (Julian day 96, 3000 g/m²/s) compared to 2012 (Julian day 80, 120 g/m²/s) where the winter prior to the sugaring season in 2012 was very mild with little snowpack compared to winter conditions prior to the sugaring season in 2011.

© Copyright by Jordan R. Christ

(August 7th, 2012)

All Rights Reserved

WINTER CLIMATE CHANGE AND THE HYDRAULIC PROPERTIES OF THE NORTHERN
HARDWOOD FOREST

BY

Jordan R. Christ

THESIS

Submitted to Plymouth State University

In Partial Fulfillment of

The Requirements for the Degree of

Master of Science

in

Biology

August 7th, 2012

Master of Science thesis of Jordan R. Christ presented on August 7th, 2012.

APPROVED:

Michele L. Pruyn, representing Biological Sciences

Mark B. Green, representing Center for the Environment

Geoff F. Wilson, representing the Hubbard Brook Research Foundation

Kerry L. Yurewicz, Head of Biological Sciences

I understand that my thesis will become part of the permanent collection of Plymouth State University, Lamson Library. My signature below authorizes release of my thesis to any reader upon request.

Jordan R. Christ, Author

ACKNOWLEDGEMENTS

Thank you to the following for making this research possible...

- * Michele L. Pruyn (Primary Thesis Advisor)
- * Mark B. Green, Thomas R. Boucher, Geoffrey F. Wilson (Thesis Committee Members)
- * REU (Research Experience for Undergraduates) program
- * Nathan Phillips (Boston University)
- * RAC grant
- * Plymouth State University College of Graduate Studies
- *Hubbard Brook Experimental Forest (WMNF)
- *Hubbard Brook Research Foundation (HBRF)
- * Plymouth State University Biology Department
- * REU's Kristin Greiner and Darrius Harrison (2010) for help with data collection

TABLE OF CONTENTS

1	Patterns in the hydraulic properties of yellow birch (<i>Betula alleghaniensis</i>) stands over natural gradients in a northern hardwood forest	1
1.1	Abstract.....	1
1.2	Introduction	2
1.3	Methodology	7
1.4	Results.....	11
1.5	Discussion	18
1.6	Conclusions	20
2	Factors influencing the pre bud-break sap velocities of sugar maple (<i>Acer saccharum</i>) trees in central, New Hampshire	22
2.1	Abstract.....	22
2.2	Introduction	23
2.3	Methodology	26
2.4	Results.....	27
2.5	Discussion	32
2.6	Conclusions.....	33
3	Bibliography	34

LIST OF FIGURES

1.1 Snowpack depth and duration 2009/2010.....	12
1.2 Snowpack depth and duration 2010/2011.....	12
1.3 Plot average root percent embolism 2010.....	13
1.4 Plot average root percent embolism 2011.....	13
1.5 Plot average sap velocity 2010.....	15
1.6 Plot average sap velocity 2011.....	16
2.1 Air Temperature 2011.....	28
2.2 Sap velocity sugar maple tree 1.....	29
2.3 Sap velocity sugar maple tree 2.....	29
2.4 Sap velocity sugar maple tree 3.....	30
2.5 Sap velocity HBEF HQ 2012.....	30
2.6 Sap velocity HBEF HQ 2012.....	31
2.7 Sap velocity HBEF HQ 2012.....	31

LIST OF TABLES

1.1 Level 1 and level 2 thaw-freeze events.....	11
1.2 Repeated measures ANOVA (Root % Embolism).....	14
1.3 Root % embolism v. Sap velocity.....	17
1.4 Plot average DBH.....	18

LIST OF APPENDICES

Individual DBH (Chapter 1).....	42
Average sap velocities of sugar maple (<i>Acer saccharum</i>), American beech (<i>Fagus grandifolia</i>), and yellow birch (<i>Betula alleghaniensis</i>) at Bartlett, Hubbard Brook, and Jeffers Brook Forests, New Hampshire.....	43-45

LIST OF APPENDIX FIGURES

Baseline sap velocities in sugar maple, American beech, and yellow birch (HBEF control v. calcium).....	76
Baseline sap velocities in sugar maple, American beech, and yellow birch (Jeffers Brook control v. calcium).....	77
Baseline sap velocities in sugar maple, American beech, and yellow birch (Bartlett control v. calcium).....	78

FLYLEAF

Chapter 1: *Patterns in the hydraulic properties of yellow birch (*Betula alleghaniensis*) stands over natural gradients in a northern hardwood forest*

Abstract: This study investigated the potential impacts of winter climate change (reduced snowpack depth and duration and increasing soil frost depth and frequency) on yellow birch distributions in the northern hardwood forest. We established plots over north and south-facing elevation transects as a gradient of susceptibility to winter soil frost induced root damage in yellow birch stands at the Hubbard Brook Experimental Forest (HBEF) during the growing season of 2010 and 2011. Air temperature and snowpack data were used from the HBEF hydrometeorological database from weather stations near our plots as a proxy for determining vulnerability differences and frequency and intensity of winter thaw-freeze events for each year. We compared average root percent embolism and sap-flux densities across plots to determine (1) Does susceptibility to soil frost induced damage influence root embolism patterns under natural conditions, and (2) is root embolism a factor limiting sap velocity (transpiration)?

The frequency of thaw-freeze events based on air temperature fluxes for both years revealed that south-facing slopes had greater level 1 (109) and level 2 (6) thaw-freeze events compared to north-facing slopes (83 and 4 for levels 1 and 2 respectively). Snowpack depth was approximately twice as deep and snow cover duration was 2 weeks longer for winter 2010/2011 compared to winter 2009/2010. In general root percent embolism was highest in 2010 compared to 2011. For both years, all north-facing plots had lower (15-20%) average root percent embolism than south-facing plots, with the exception of our north-facing mid plot in 2011. All middle elevation plots in their class of aspect, had the greatest (5-30%) root percent embolism compared to their respective high and low elevation plots during both years. All plots with the greatest average root percent embolism exhibited the lowest sap velocity (J_s) in 2010 and 2011 within class of aspect, but not across class of aspect. A repeated measures ANOVA indicated that there were significant differences in root percent embolism across gradients of aspect and elevation in 2011 (when snowpack variability was greater across plots) ($p=0.05$), but not in 2010 ($p=0.91$). This supports the idea that susceptibility to winter thaw-freeze events and soil frost damage influences root embolism in yellow birch stands. This means an increasing number of thaw/freeze events caused by warming winters with less snowpack, may limit transpiration and photosynthesis. Responses of decreased water flow in sites strongly impacted by winter climate change raises interesting questions regarding future shifts in the distribution of the northern hardwood forest and interactions among ecotones in the northeast United States.

Introduction

The result of colder soils due to winter warming in the northern hardwood forest ecosystem is a fascinating phenomenon which raises many questions regarding the impact of soil frost and thaw-freeze cycles on current and future tree health and distributions. We measured root percent embolism and sap velocity of yellow birch (*Betula alleghaniensis*), stands over natural gradients of susceptibility to soil frost induced damage as a proxy of root health and productivity. Past research on potted yellow birch saplings indicates that yellow birch is susceptible to root embolism as a result of soil freezing and thaw-freeze cycles (Zhu et al. 2000; Zhu et al. 2001; Cox and Zhu, 2003). Other studies suggest that soil thaw-freeze cycles are a powerful mechanism causing crown dieback in yellow birch stands by disrupting the hydraulic pathway (Braatne, 1996; Bourque et al. 2005). Our objective was to reveal patterns in root percent embolism based on natural occurrences of thaw-freeze effects recommended by previous studies under controlled experiments. Furthermore, we hope that our in situ assessment of the relationship between root embolism and sap velocity of yellow birch stands can help us understand how winter root damage may disrupt the hydraulic pathway which can lead to crown dieback. The results of this experiment could provide valuable insights on the future health and distribution of the northern hardwood forest under changing winter climatic conditions in the northeast United States.

Importance of the Hydraulic Pathway in relation to Winter Climate Change

Water transport in the xylem vessels from the roots to the shoots is vital for the growth and survival of tree species, as evaporation of water from the stomates is a considerable cost in acquiring CO₂ during photosynthesis (Maherali et al. 2004). Drought has been considered the main cause of crown dieback in tree species through disrupting the hydraulic pathway (Houston, 1987). Soil freezing induced damage as a result of winter climate change has recently been getting more attention as a possible cause of dieback (Auclair et al. 2002), as it also disrupts the hydraulic pathway. Freezing temperatures can cause injury to plant tissues which alters the ability of the plant to transport water, and in some cases can even be lethal (Cavendar-Bares, 2005; Lianhong et al. 2008). Vulnerability to soil freezing damage and the hydraulic properties of trees show biogeographical patterns based on cold hardiness (Auclair et al. 2002), which suggests that freezing induced embolism is likely to be a critical factor limiting species ranges (Cavendar-Bares, 2005).

Winter Climate Change in New England

Northern temperate areas have experienced greater increases in surface air temperature (1°C) compared to the global average (0.75°C) in the last century, with most of this temperature increase occurring over the winter season (Houghton et al. 2001; Huntington et al. 2004; Campbell et al. 2009). By the end of the century, climate models suggest that New England will warm by 2.1 – 5.3°C, with increasing precipitation occurring over winter (Dukes et al. 2009; Campbell et al. 2009), depending on future land management, emission scenarios, and other various positive and negative feedbacks (IPCC, 2007). The details of predicted change in forest ecosystems on a regional scale is not certain because GCM's (General Circulation Models) only predict major changes over forest biomes

(Noss, 2001). A SHAW model, using downscaled climate projections, predicted a 67% reduction in snow cover and a 70% reduction in snow covered days by the year 2100 at the HBEF (Campbell et al. 2010). Many flora and fauna rely on snow cover, and a change of this degree may affect species composition and biodiversity (Campbell et al. 2010). Similarly, reduction in winter snowpack may delay or reduce plant reproduction, which may diminish future abundance of animal pollinators and seed dispersers (Mohan et al. 2009).

Biologic and hydrologic responses to warming trends are occurring in New England, such as the timing of phenological events (Schwartz and Reiter, 2000), bird and anadromous fish migration dates (Dunn and Winkler, 1999; Huntington et al. 2003), earlier spring lake and river ice out dates (Hodgkins et al. 2002; Dudley and Hodgkins, 2002), lengthening of the growing season (Campbell et al. 2010) and annual spring runoff patterns driven by snowmelt (Huntington et al. 2004; Campbell et al. 2009). Beckage et al. (2008) found over the last 40 years, that the northern hardwood/boreal forest ecotone has shifted upslope by approximately 100m in response to warming in Vermont (Huntington et al. 2008). The areas of tropical and temperate forests are predicted to increase up to 20%, while boreal forests may experience a 50% decline in area (Krankina and Dixon, 1993; Noss, 2001). Most climate projections predict reductions of spruce-fir habitat and a decline in the area suitable for northern hardwood habitat in New England (Iverson et al. 2008; Huntington et al. 2009). This may consequently lead to replacement by oak, hickory, and pine species, however, lag times are expected and the rate of these changes is not certain (Iverson et al. 2008; Huntington et al. 2009). Warmer temperatures will increase growing season length (GSL), however this allows for a greater risk of frost damage and susceptibility to thaw-freeze events due to earlier bud break and later senescence (Richardson et al. 2006).

The Relationship between Snowpack and Soil Frost

Because average winter air temperatures in the New England region are near the freezing point, slight warming has caused considerably more rain with less snow (Campbell et al. 2005). Over the last 50 years, significant trends in decreasing snowpack to total precipitation ratios have been observed in northern New England (Huntington et al. 2004) regardless of a significant increase in annual precipitation (Campbell et al. 2010). Soil freezing events in the northern hardwood forest ecosystem will occur more frequently if snow cover is becoming reduced at northern latitudes (Cooley, 1990) unless or until winters warm to the point where soil frost can no longer occur (Campbell et al. 2010). A measureable snowpack insulates the soil from freezing air temperatures throughout the winter and is particularly valuable in moderating soil temperature fluxes by increasing surface albedo (Huntington et al. 2009; Campbell et al. 2005). The timing of snowpack is crucial in determining soil frost severity (Cleavitt et al. 2008), as soils with an early and deep snowpack can remain unfrozen throughout the duration of winter, and a late snowpack can render the soil frozen through the duration of winter (Cleavitt et al. 2008; Goodrich, 1982; Huntington et al. 2009).

Scenarios of predicted climate change effects reveal that winters will get warmer, snowpack will decrease, and the duration and frequency of winter soil thaw/freeze events will increase (Zhu et al. 2000). The relationship between snowpack depth and duration, soil frost severity and thaw/freeze events are becoming increasingly vital in understanding how winter climate change will affect the northern hardwood ecosystem (Dunne et al. 2004;

Campbell et al. 2005; Tierney et al. 2001). Snow removal experiments studying the relationship between snowpack, soil frost and fine root mortality at the Hubbard Brook Experimental Forest (HBEF) found significantly higher mortality of fine roots in treated plots (where snow was removed) versus reference plots due to frost induced damage (Tierney et al. 2001; Campbell et al. 2005). Soil frost induced damage to fine roots restricts nutrient and water uptake by damaging the semi-permeable characteristics of the plasma membrane and active transport mechanisms, which results in an ion efflux, disrupting osmotic potential and weakening root pressure (Kramer, 1983; Tierney et al. 2001; Zhu et al. 2002). This is the mechanism behind reduced transpiration and productivity with compromised root health. Severe late frosts, occurring once the tree has become metabolically active, can be especially detrimental (high risk of xylem embolism) and occur over large areas (Lianhong et al. 2008; Bourque et al. 2005).

Root damage, Thaw-freeze Events and Winter Embolism

Widespread diebacks of yellow birch, white birch, and red spruce in Eastern North America have been linked to freeze injuries from thaw-freeze cycles or fluctuations (Lianhong et al. 2008; Bourque et al. 2005; Lazarus et al. 2006). Past research indicates that roots are more vulnerable to freezing induced embolism than shoots (Zimmerman, 1983; Langan et al. 1997; Gill and Jackson, 2000). Winter embolism occurs when air bubbles are pulled into the xylem during thaw/freezing cycles (water is frozen in soil matrix) over winter which often leads to hydraulic conductivity loss of the vessels (Cochard and Tyree, 1990; Ewers et al. 2001; Sakr et al. 2003; Hacke et al. 2001). In addition, bubbles can form in the xylem sap upon thawing after a freeze (air is more soluble in liquid water than ice) and can either re-dissolve in the sap or grow larger until embolism occurs within the conduits (Martinez-Vilalta and Pockman, 2002; Bourque et al. 2005). The fate of the bubble is dependent on the balance between surface tension and xylem pressure (Sperry and Sullivan, 1992; Martinez-Vilalta and Pockman, 2002). Initial cavitation (small air bubble) of water inside a vessel is followed by air entrapment from the surrounding tissues until the vessel becomes embolized (large air bubble limiting water movement) or air-filled (Tyree and Sperry, 1989; Martinez-Vilalta and Pockman, 2002; Bourque et al. 2005). Reduced photosynthesis and growth is a result of xylem embolism unless refilling of the vessel can exert pressure in the xylem near atmospheric pressure under high tension to remove emboli (Tyree et al. 1999; Martinez-Vilalta and Pockman, 2002). In addition, it is possible that flowering times may be interrupted as a result of xylem cavitation from winter climate change (Miller-Rushing and Primack, 2008).

Soil thaw-freeze severity and occurrence are limited geographically in the eastern United States, where greater severity is common in the southern half of the region, while interestingly the northern states are subject to more damage and dieback due to soil frost and thaw-freeze events (Auclair et al. 2002). This occurrence can be explained by reliance of northern species on winter snowpack as insulated protection from soil frost, which consequently limits the hardening of fine roots at more northern latitudes in preparation for winter (Auclair et al. 2002). Where snowpack is infrequent and thin, the species in the southern portion of the United States have greater cold hardiness and require warmer temperatures to initiate dehardening (Auclair et al. 2002). Species ability to deal with freezing stress can explain much about their geographic distributions (Cavendar-Bares, 2005;

Tyree and Cochard, 1996). Winter embolism is likely an important element limiting species ranges due to patterns of freezing injury in relation to hydraulic properties (Cavendar-Bares, 2005).

Why Yellow Birch?

Over the last century, periodic occurrences of dieback have been observed in yellow birch populations (USDA Forest Service, 2007; Halman et al. 2011). Dieback in yellow birch linked to the widespread thaw-freeze events from the mid-1930s and early 1940s led to an estimated loss of timber volume from 1935-1955 valued at \$60 billion (value of CND funds in 1987) (Bourque et al. 2005). Yellow birch trees are one of the most susceptible of the northern hardwoods to freezing induced damage and thus a valuable indicator species of the potential changes of the northern hardwood forest in certain areas under future climate conditions. A study in the Maritime Provinces of Canada revealed that cold hardiness of yellow birch is barely enough to prevent freezing injury under average weather temperatures (Bourque et al. 2005; Zhu et al. 2002). Any reduction in cold hardiness due to thaw-freeze events or atmospheric deposition can cause yellow birch to be more prone to freezing injury (Bourque et al. 2005). Yellow birch is significantly affected by soil freezing under conditions of no snowpack due to their shallow root systems (Cox and Zhu, 2003; Miller-Rushing and Primack, 2008; Fahey and Hughes, 1994; Yanai et al. 2008; Bourque et al. 2005). Past studies have shown that yellow birch species show reduced root pressure and a lack of complete recovery from embolism if winter root damage occurs (Zhu et al. 2000; Zhu et al. 2001; Cox and Zhu, 2003; Cox and Malcolm, 1997). Yellow birch generates root pressure in the spring to refill xylem vessels and emboli before leaf out (Zhu et al. 2002; Strati et al. 2003) unlike sugar maple (*Acer saccharum* Marsh.), which generates stem pressure during refilling (Cirelli et al. 2008). Without sufficient root pressure due to root damage from soil frost over winter, incomplete refilling may occur, which increases the risk of branch dieback (Zhu et al. 2002; Bourque et al. 2005; Zhu et al. 2000) due to disruption of the hydraulic pathway.

Yellow birch relies on early phenological development as a technique of competitive advantage, and this strategy is dependent on the ability of the xylem to conduct water and nutrients to the developing foliage (Bourque et al. 2005). This reliance on early phenological development may explain why yellow birch is not particularly cold hardy compared to other species in the region. Furthermore, the regenerative success of yellow birch could be reduced with a reduction in snowpack because this species has a better seed dispersal mechanism on snow (Greene and Johnson, 1997). Winter embolism has been found to reduce xylem conductivity up to 90% and delay the timing of early phenological development in yellow birch (Bourque et al. 2005). The success of yellow birch is determined by a balance between early leaf out, late frost damage, and susceptibility to soil thaw-freeze cycles (Cox and Malcolm, 1997; Cox and Zhu, 2003; Bourque et al. 2005). Winter thaw-freeze cycles experimentally applied to yellow birch saplings have shown associations between branch dieback, reduced xylem conductivity and root pressure, residual embolism (embolism acquired over time), and thaw durations (Braathe, 1995; Braathe, 1996; Zhu et al. 2000; Zhu et al. 2002; Bourque et al. 2005). However, this phenomenon has not yet been studied *in situ* with mature individuals and natural climatic conditions.

The timing and duration of winter thaws are critical in the development of xylem embolism throughout winter (Zhu et al. 2000). Thaw duration has impacts on the cold hardiness of yellow birch, where increased frequency of winter thaw-freeze events can reduce cold hardiness and lower fitness (Zhu et al. 2002; Bourque et al. 2005). Prolonged thaws followed by late spring frosts have been recognized as a fundamental mechanism which leads to shoot dieback in yellow birch trees (Braathe, 1995; Bourque et al. 2005). Laboratory experiments have suggested that soil freezing and winter root thaw-freeze events are responsible for extensive winter embolism and dieback observed in yellow birch individuals (Zhu et al. 2000; Bourque et al. 2005; Zhu et al. 2002), and in other birch species, such as mountain paper birch (*Betula cordifolia* Regel), water birch (*Betula occidentalis* Hook.) and paper birch (*Betula papyrifera* Marsh.) (Sperry, 1993; Sperry, 1994; Cox and Zhu, 2003). Past studies have indicated a range shift for yellow birch trees, that as winter warm, individuals at the northern edge of the range may recruit more capably, while individuals at the southern edge of the range will experience increased mortality due to greater freezing damage (Zhu et al. 2000; Cox and Zhu, 2003). Soil freezing and thaw-freeze cycles play a decisive role in the development of winter xylem embolism in yellow birch (Zhu et al. 2000), and the effects of winter climate change on root embolism and productivity in natural stands deserve further study.

A key approach to understanding the complexity of climate change on forest structure is using natural elevation gradients as a foundation. Natural gradients of aspect and elevation provide differences in temperature and snowpack depth and duration, thus a range of susceptibility to soil frost induced damage and vulnerability to winter soil thaw-freeze cycles. Gradient analyses can provide valuable predictions assuming that ecosystems respond to climate over time the same way that ecosystems currently vary in space (Dunne et al. 2004). It is becoming increasingly essential to incorporate key climate-ecosystem interactions on range shift predictions in global climate models or GCM's (Cox et al. 2000). Understanding changes in species physiology with their spatial distributions over time is essential for a better assessment of successional patterns, especially for the future, in response to further anthropogenic stresses (Vadeboncoeur et al. 2012). Different tree species respond separately to changing environmental conditions thus it is vital to understand the species-specific physiology and quantify stand productivity (Harcombe, 1987; Bassow and Bazzaz, 1998; Van Doorn et al. 2011).

The goal of this study was to determine the impact of winter climate change (decreasing snowpack and increasing soil frost depth and duration) by comparing root health and productivity of yellow birch stands over natural gradients during the growing season at the HBEF for 2 years (2010 and 2011). Our objectives were to determine (1) how susceptibility to soil frost damage varies across our plots for each year (2) if plots more vulnerable to soil frost damage showed greater root percent embolism than plots less vulnerable over natural gradients, and (3) if these sites (more vulnerable to soil thaw/freeze) show decreased sap velocity as a result of root embolism disrupting the hydraulic pathway. Based on the long-term climatic trends observed over space at the HBEF, we predict that south-facing low elevation plots should be more susceptible to soil frost damage than the north-facing high elevation plots due to decreased snowpack depth and duration and greater temperature fluctuation over winter. Furthermore, because we predicted the south-facing plots had greater soil frost severity, we expected root percent embolism was highest at our south-facing plots if soil frost damage is linked to root embolism. Finally, sites with the

greatest root percent embolism may reveal the lowest sap velocity and *vice-versa*, if embolism is currently a factor limiting water transport in yellow birch.

Methodology

Study Site Attributes and Experimental Design

We conducted this study in the southwest portion of the White Mountain National Forest in central New Hampshire at the Hubbard Brook Experimental Forest (HBEF), 43°56'N, 71°45'W (Likens, 1985; Bailey et al. 2003). The HBEF is a site which is characteristic of the northern hardwood forest ecosystem in terms of climate and vegetation (USDA Forest Service, 1996). Current forest vegetation is dominated by yellow birch (*Betula alleghaniensis* Brit.), sugar maple (*Acer saccharum* Marsh.), and American beech (*Fagus grandifolia*) with high elevation red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*) habitat found primarily on the north-facing slope due to the topography of the Hubbard Brook Valley (Bailey et al. 2003). Based on the natural topography of the valley, south-facing plots were chosen at an overall lower elevation transect than our north-facing plots, which should render the south-facing plots even more susceptible to winter soil freezing. We established low, middle, and high elevation plots along a north-facing slope (Mt. Kineo) and south-facing slope (WS 3) during the growing season of 2010 and 2011 at the HBEF to provide a spatial gradient of soil frost susceptibility and vulnerability to thaw/freeze events.

Long-term HBEF hydrometeorological data indicated that the north-facing slope received more annual precipitation than the south-facing slope by approximately 150 mm, with much of this precipitation occurring over winter as snow (Bailey et al. 2003). Furthermore, differences in precipitation among north and south-facing watersheds were smallest during the summer months and largest during the winter and spring, which implies that snowfall varied more than rainfall (Bailey et al. 2003). High elevation rain gauges received more annual precipitation than low elevation gages over a 300m elevation gradient on both north and south-facing slopes by 40mm and 70mm respectively (Bailey et al. 2003). Soil frost was a rare occurrence during the late 1950s and early 1960s, and it wasn't until the late 1960s that soil frost was detected at the HBEF (Bailey et al. 2003). Since the 1970s, soil frost has exceeded 10 cm in depth for heavy frost years (Bailey et al. 2003). Over the last half century (1955-2005), the mean annual snow depth at the HBEF has decreased by 243 mm, and snow cover duration by 23 days near watershed #1 (south-facing aspect) (USDA Forest Service, 2007). In contrast, the north-facing slope of the Hubbard Brook valley (42 year record) does not show significant changes in maximum snowpack depth or duration (Campbell et al. 2010). In the fall dates of first frost and measureable snow depth have occurred later in the season, by 10 and 8 days respectively (Hamburg et al. 2012).

Climate change is one of many variables that are currently driving vegetation composition. Land-use history of the study site is an important factor to consider when determining future forest composition, along with other anthropogenic disturbances such as atmospheric deposition, introduction of exotic pests and pathogens, and fragmentation. The HBEF was utilized for logging from 1880 until 1920 and then briefly for salvage logging (fallen biomass removed) following the hurricane of 1938. The main soil type at the HBEF are spodosols, which are typic haplorthods derived from glacial till (Campbell et al. 2010). These

soils have a sandy loam texture, which is well drained and shallow, with bedrock about 1-2 meters underneath (Campbell et al. 2010).

Quantifying Snow Depth

Weekly snow depth data (Campbell and Bailey, 2012) from the 4 snow-course stations at the HBEF were used to assess the variability in snow depth across plots for each winter. Snow course station 2 (560m) and station 9 (760m) are on the south-facing slope while snow course station 17 (890m) and station 19 (595m) are on the north-facing slope of the valley at the HBEF. We graphed the weekly data from these snow-course stations to determine snowpack depth and duration for each winter season (2009-2010 and 2010-2011).

Quantifying Winter Thaw-Freezing Events

Daily maximum and minimum air temperatures from the HBEF hydrometeorological database (Campbell and Bailey, 2012) at weather stations near our plots on Mt. Kineo (High and Low) and WS 3 (High and Low) were used to develop the frequency and intensity of thaw/freezing events for 2009-2010 and 2010-2011 from December 1st through March 31st. Definitions of level 1 and level 2 thaw-freezing events were derived from (Auclair et al., 2002) to determine the intensity of thaw-freezing events. Level 1 thaw-freezing events for this study were defined as average maximum daily temperature greater than or equal to 1°C followed by a daily average minimum temperature less than or equal to -10°C for one day within the succeeding 10 days since the last day of thaw. Level 2 thaw-freezing events were defined as average maximum daily temperature greater than or equal to 5°C for 2 consecutive days followed by daily average minimum temperature less than or equal to -15°C for at least 1 day within the succeeding 6 days since the last day of thaw. We developed a code to run a function using the program *R* to filter the frequency of level 1 and level 2 events based on these parameters for each high and low elevation plot per transect per year (*R* Development Core Team, 2012).

Native Hydraulic Conductivity

Coarse yellow birch roots were sampled for xylem hydraulic conductivity in 2010 and 2011 at plots established along gradients of north and south-facing aspect and elevation throughout the growing season. In 2010, 5 yellow birch trees were selected per plot on the north-facing elevation transect Kineo Low (610m), Kineo Mid (730m), and Kineo High (820m), and our south-facing elevation transect, WS 3 Low (480m), WS 3 Mid (540m), and WS 3 High (590m). Sampling dates for 2010 include early June, July, early September, and late September. In 2011, 5 yellow birch trees were selected at new plots on the north-facing elevation transect, Kineo Low (590m), Kineo Mid (740m), and Kineo High (830m), and our south-facing elevation transect, WS 3 Low (490m), WS 3 Mid (550m), and WS 3 High (630m). Sampling dates for 2011 include early June and September.

Small holes were dug (up to 20 cm in depth and approximately 10 – 15 cm in diameter) in the soil about 1m from the base of the tree using a trowel to locate coarse root samples at each of the plots. Once an adequate root sample was found, pruning shears were used to cut the root to between 12 and 16 cm in length and then root samples were labeled and stored in plastic bags and kept in a cooler with ice packs before returning to the lab to prevent desiccation. Root samples were washed in the lab with distilled water to remove soil particles and approximately 2cm were cut from each end using pruning shears and then immediately recut with a sharp razor blade under water. Individual root samples were attached to the tubing manifold of our hydraulic conductivity apparatus after cutting. Hydraulic conductivity (K_s) was calculated at the water flow rate through a root divided by the pressure gradient across it (Sperry et al. 1988), where K_s = the volume flow rate (V , mL/s) through the root length (L , m) divided by the pressure gradient (P , MPa). We used the gravitational method to create water pressure (P), where we measured the water temperature (T , °C) to calculate water density (D , kg/m³), the height of the water column (H , m) and D were used to calculate P (kPa). Native hydraulic conductivity measurements were taken at approximately 5kPa of water pressure to avoid removing air emboli (Sperry et al. 1988) using a distilled water solution containing 0.095M of concentrated hydrochloric acid (HCl) to prevent the growth of bacteria. Root length and diameter were measured to calculate specific native hydraulic conductivity (K_s native) per unit cross-sectional area of the root segment. The units for specific native conductivity (K_s native) are m²/s/MPa. Roots were then placed in a distilled water solution containing 0.095M HCl under vacuum for 48 hours in a clean sealed chamber to remove air emboli.

Maximum Hydraulic Conductivity

After 48 hours under vacuum, maximum hydraulic conductivity was calculated in the same manner as native hydraulic conductivity. Root ends were recut using a sharp razor blade under water to provide a clean cross-sectional surface. Root length and diameter were re-measured to calculate specific maximum hydraulic conductivity (K_s max).

Calculating Root Percent Embolism

Individual root xylem embolism was quantified by expressing the difference between maximum specific root conductivity (K_s max) and native specific root conductivity (K_s native) as a percentage of the maximum specific root conductivity (K_s max) (Sperry et al. 1988). Root percent embolism in the 5 individual yellow birch trees at each plot were averaged for each sampling date to obtain plot average root percent embolism. Finally, the plot averages from each sampling date were combined for each year (2010 and 2011) yielding average annual root percent embolism for each plot.

Sap Velocity Measurements

Total sap-flow variation within tree classes (trees of the same species and roughly the same DBH) is much greater due to differences in sapwood cross-sectional area among

crown classes therefore sap velocity (J_s) was used to compare the rates of water flow (Granier et al. 1987). The heat dissipation method was used to calculate sap velocity (J_s) in grams of water per square meter of sapwood area per second ($\text{g}/\text{m}^2/\text{s}$) as described in more detail by Grainer (1987) to quantify water transport in the xylem during the growing season. Heated and reference sap-flow sensors (2 cm in length) were constructed manually using type-T thermocouple pairs inserted halfway (1cm) into the sensor casing (hypodermic needle). Heated sensors were each wrapped with 50cm of constantan heating wire and heated to a constant temperature throughout the experiment by adjusting the trim-potentiometers on the power-boards to set the amperage supply to each sensor at 0.125 amps.

The same individual trees that were chosen for root samples were used for sap velocity measurements to compare the effects of root percent embolism on transpiration rates (sap velocity) across plots. In 2010, we had 4 plots with 5 trees per plot at Kineo High (820m), Kineo Low (639m), WS 3 High (630m), and WS 3 Low (480m). In 2011, we established 5 plots at Kineo High (826m, $n=5$), Kineo Low (589m, $n=5$), WS 3 High (630m, $n=5$), WS 3 Mid (547m, $n=5$), and WS 3 Low (487m, $n=3$). Each plot contained two 12V deep cell marine batteries in water proof battery boxes which were transported to the plots via external frame packs, and daisy chained to a solar charge controller with 40-80 watts of solar panel capacity to recharge the system. The powerboards were attached to the charge controller to help maintain a constant supply of power to the sensors over a variation of sunny and cloudy days during measurement. The copper constantan wires of the heated sap-flux sensors were connected to the powerboards, while the type-T thermocouple wires from each sensor (heated and reference) were connected to a Campbell Scientific, Inc. (Logan UT, USA) data-logger (models CR1000 and CR800 with a multiplexer).

Sensors were inserted radially into the sapwood at breast height with the heated sensor directly 10 cm above the reference sensor. The temperature difference between the heated and reference sensor was recorded as differential voltage to the data-loggers using a program derived from *Short Cut* (Campbell Scientific, Inc. (Logan UT, USA) to store averages every 15 minutes from measurements being recorded at 30 second intervals. The differential voltage data was retrieved from the data-loggers and converted to a comma delimited (.csv) data-file and opened using the program *Baseliner* to set the baseline conditions of no flow and convert differential voltage to sap velocity using Grainers' empirical equation $J_s = 119(\Delta T_b/\Delta T - 1)^{1.23}$ as derived from (Granier, 1987; Oren, 2001). The units for sap velocity are $\text{g}/\text{m}^2/\text{s}$.

Results

Table 1: Frequency and intensity (level 1/level 2) of thaw-freeze events for winter 2009/2010 and 2010/2011 (12/1 – 3/31) at HBEF weather stations across similar gradients of aspect and elevation as our plots.

HBEF Weather Station #	Weather Station Elevation and Aspect	Plot	Plot Elevation and Aspect	Year	Level 1: T/F events	Level 2: T/F events	Total Level 1 T/F events	Total Level 2 T/F events
1	Low - S	WS 3 Low	480m-S	09-10	26	0		
1	Low - S	WS 3 Low	490m-S	10-11	32	4	58	4
6	High -S	WS 3 High	590m-S	09-10	29	0		
6	High - S	WS 3 High	630m-S	10-11	22	2	51	2
South Aspect Totals							109	6
23	Low - N	Kineo Low	610m-N	09-10	22	1		
23	Low - N	Kineo Low	590m-N	10-11	17	1	39	2
17	High - N	Kineo High	820m-N	09-10	17	1		
17	High - N	Kineo High	830m-N	10-11	27	1	44	2
North Aspect Totals							83	4

Note: frequency and intensity were determined strictly from daily maximum and minimum air temperatures. Sites with greater snow accumulation are less susceptible to soil thaw-freeze induced damage as snow insulates the soil protecting it from frost.

Frequency and Intensity of Thaw-Freeze Events

For the 2009-2010 winter season the south-facing plots had a greater frequency of level 1 thaw-freeze events than the north-facing plots (55 vs. 39 events respectively), however the north-facing plots each had one level 2 thaw-freeze event while the south-facing plots had none (Table 1). Kineo High at 820m had the lowest frequency of level 1 thaw-freeze events (17), while WS 3 High at 590m had the highest frequency (29 events) for 2009-2010 (Table 1). For the 2010-2011 winter season the south- vs. north-facing plots had 54 vs. 44 Level 1 thaw-freeze events and 6 vs. 2 for level 2 events. Kineo Low at 590m had the lowest frequency of level 1 thaw-freeze events (17), while WS 3 Low at 490m had the highest frequency of level 1 and level 2 events (32 vs. 4, respectively) (Table 1). In general, south-facing plots had the greatest frequency of level 1 and level 2 thaw-freeze events (109 and 6, respectively) compared to north-facing plots (83 and 4 events) based on air temperature for 2009-2010 and 2010-2011 combined (Table 1).

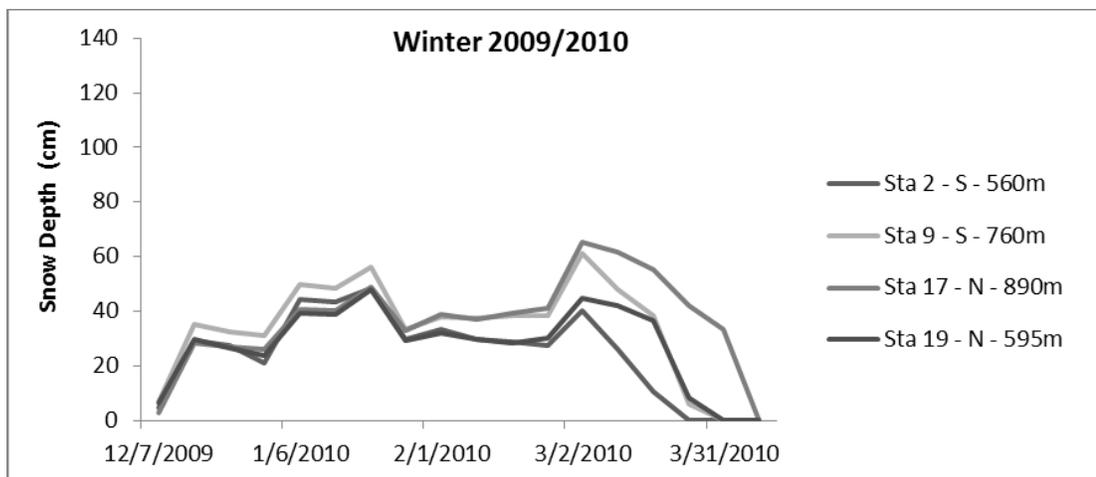


Figure 1: Snow depth in centimeters (cm) (recorded weekly) from the 4 snow-course stations at the HBEF for the winter of 2010. Station 2 (560m) and Station 9 (760m) are on the south-facing slope and Station 17 (890m) and Station 19 (595m) are on the north-facing slope of the Hubbard Brook valley.

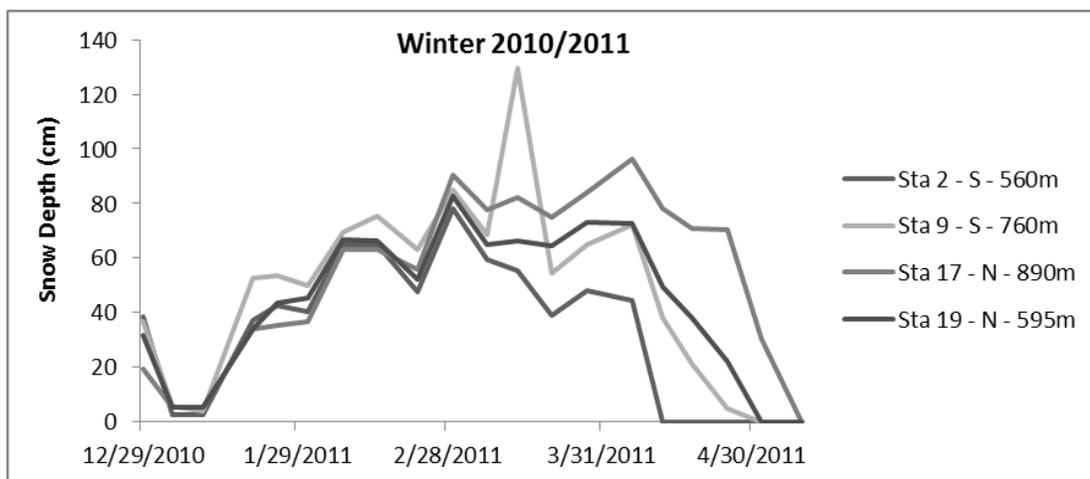


Figure 2: Snow depth data in centimeters (cm) (recorded weekly) from the 4 snow-course stations at the HBEF for the winter of 2011. Station 2 (560m) and Station 9 (760m) are on the south-facing slope and Station 17 (890m) and Station 19 (595m) are on the north-facing slope of the Hubbard Brook valley.

Snowpack depth and duration

Snowpack depth and duration over winter was greater for the 2010-2011 season (Figure 2) compared to the 2009-2010 season (Figure 1). Snow depth was approximately twice as deep for 2010/2011 (Figure 2) compared to 2009/2010 (Figure 1) and snow cover duration was approximately a month longer in 2010/2011 (Figure 2). Variability in snowpack depth and duration between snow-course stations was also greater for the 2010-2011

season (Figure 2) compared to the 2009-2010 season (Figure 1) as indicated by greater spaces between the lines, especially during the second half of winter. During both years, station 2 had the shallowest snow depth earliest snowmelt and station 17 had the highest snow depth and latest snowmelt (Figures 1 and 2). The difference in the timing of snowmelt between station 2 and station 17 was greater for 2010-2011 (Figure 2) compared to the 2009-2010 season (Figure 1), further indicating greater variability of snow cover depth and duration across our plots for the 2010/2011 season.

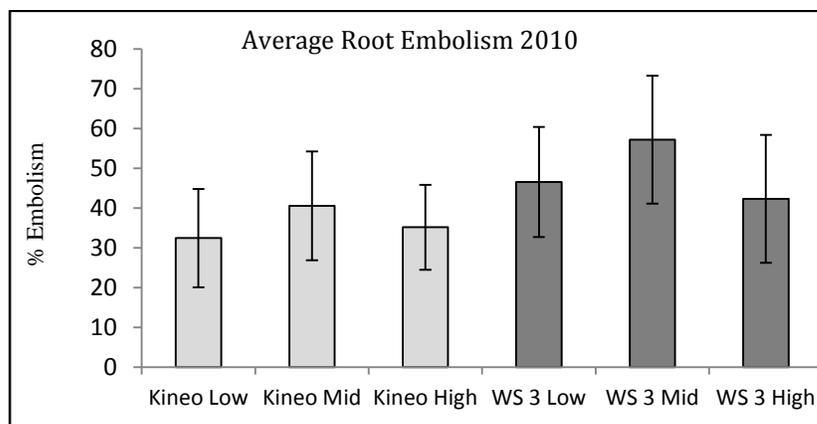


Figure 3: Average root percent embolism for 2010 at Kineo Low (610m), Kineo Mid (730m), Kineo High (820m), WS3 Low (480m), WS3 Mid (540m), and WS3 High (590m). Kineo plots (N-facing) are light gray and WS 3 plots (S-facing) are dark gray. For the four sampling dates (6/7, 7/8, 9/8, and 9/24), the sample size per plot is $n=20$ roots ($n=5$ for each sampling date).

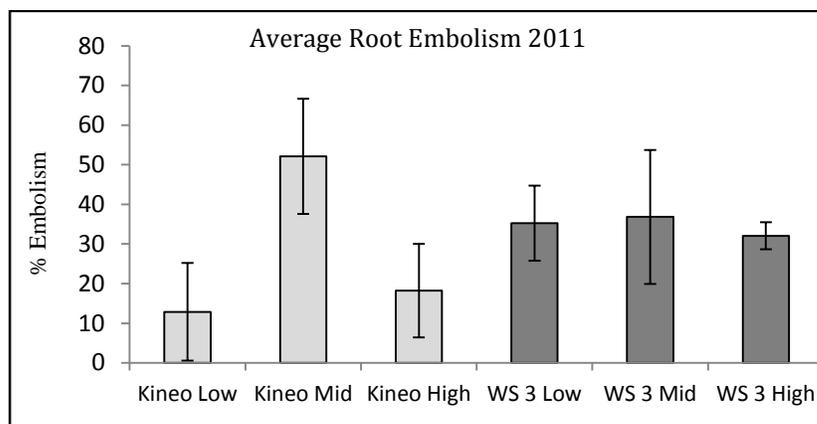


Figure 4: Average root percent embolism for 2011 at Kineo Low (589m), Kineo Mid (737m), Kineo High (826m), WS3 Low (487m), WS3 Mid (547m), and WS3 High (630m). Kineo plots (N-facing) are light gray and WS 3 plots (S-facing) are dark gray. For the two sampling dates (6/21 and 9/18), the sample size per plot is $n=10$ roots ($n=5$ for each sampling date).

Average Root Percent Embolism

A repeated measures ANOVA found no significant differences in root percent embolism with elevation and aspect as factors for 2010, but did find significant differences in 2011 ($p=0.05$) (Table 2). WS 3 Mid had the greatest, while Kineo Low had the lowest average root percent embolism for 2010 (Figure 3). Within class of aspect, all middle elevation plots had the greatest average root percent embolism compared to their respective high and low plots (Figure 3). Kineo Mid had the greatest, while Kineo Low had the lowest root percent embolism for 2011 (Figure 4). All south-facing plots had greater average root percent embolism than north-facing plots with the exception of Kineo Mid in 2011 (Figure 4). All middle elevation plots had the greatest average root percent embolism within their class of aspect compared to their respective high and low elevation plots for 2010 and 2011 (Figures 3 and 4). Root percent embolism was greater for 2010 compared to 2011 at all plots, with the exception of Kineo Mid (Figures 3 and 4).

Table 2: Repeated measures ANOVA for root % embolism with elevation and transect (aspect) as factors during 2010 and 2011. The differences in root % embolism across gradients of aspect and elevation were not significant for 2010 ($p=0.91$), but were for 2011 ($p=0.05$).

Repeated Meas. ANOVA 2010	df	Sum Sq.	Mean Sq.	F value	P value
Elevation	1	7	6.73	0.0056	0.9404
factor(Aspect)	2	2250	1125.09	0.9441	0.3963
Elevation:factor(Aspect)	2	207	103.74	0.0871	0.9168
Residuals	47	56009	1191.69		
Repeated Meas. ANOVA 2011	df	Sum Sq.	Mean Sq.	F value	P value
Elevation	1	211	210.9	0.2006	0.6562
factor(Aspect)	2	1840	920.1	0.875	0.42315
Elevation:factor(Aspect)	2	6473	3236.4	3.0778	0.05488 (.)
Residuals	50	52578	1051.6		

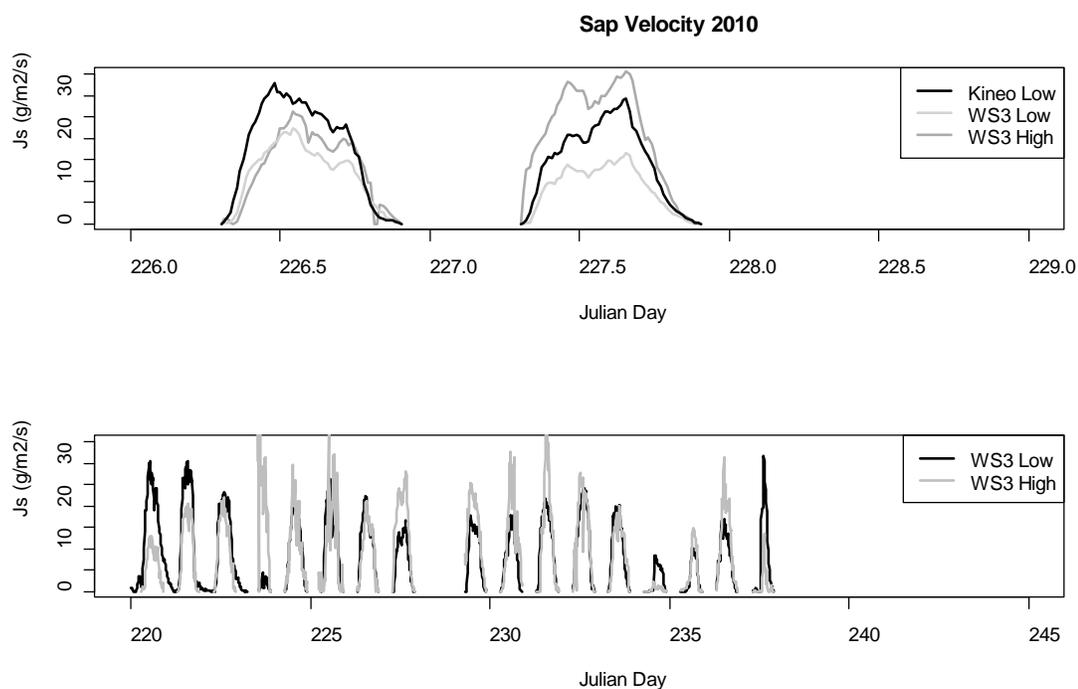


Figure 5: Diurnal variation in average sap velocity (J_s) for Yellow Birch trees at Kineo Low ($n=5$), WS 3 Low ($n=3$), and WS 3 High ($n=3$) plots for 2010. (Top) Average sap-flux densities for Kineo Low (15.91), WS 3 Low (9.78), and WS 3 High (16.63) for ordinal dates 226-228 (August 14th-August 16th). (Bottom) Average sap-flux densities (J_s) for WS 3 Low (9.13) and WS 3 High (10.10) for ordinal dates 220-239 (August 8th-August 27th).

Plot Average Sap Velocity

For 2010, the average sap velocity of all plots with overlapping time is graphed in figure 5. The top graph shows the plot averages of Kineo Low (black), WS 3 Low (red), and WS 3 High (blue) for Julian days 226-228 (Figure 5). As you can see for Julian day 226, Kineo Low had the greatest sap velocity, followed by WS 3 High and WS 3 Low had the lowest (Figure 5). On Julian day 227, the dip in the curve at mid-day is evidence of mid-day heat stress, where the stomates close to avoid desiccation, induced by drought (Figure 5). Drought may cause a situation where root embolism may not be limiting transpiration because soil water is limited. The bottom graph shows the plot averages for WS 3 low (red) and WS 3 high (blue) for Julian days 220-239 (Figure 5). WS 3 High had slightly higher sap velocities over the 18 day period compared to WS 3 Low (Figure 5). For 5 of the days however, WS 3 Low had greater peaks in sap velocity than WS 3 High (Figure 5). This alternation is likely due to slight variance in environmental stimuli and also local site specific factors such as soil water storage and nutrient variation, making it difficult to see the effect of embolism on sap velocity.

For 2011, the average sap velocity of all plots with overlapping time is graphed in figure 6. The top graph shows the plot averages of Kineo Low (black), Kineo High (light gray),

WS 3 High (dark gray), and WS 3 Mid (gray) for Julian days 200-203 (Figure 6). The bottom graph shows the plot averages for Kineo Low (black) and Kineo High (gray) for Julian days 154-162 and 197-202 (Figure 6). Sap velocity was highest for WS 3 High (dark gray) and lowest for WS 3 Mid (gray) for Julian days 200-203 in 2011 (Figure 6). Kineo High (black) and Kineo Low (light gray) were similar in sap velocity, with a slight edge going to Kineo Low for Julian days 200-203 in 2011 (Figure 6). In a 14 day comparison between Kineo High and Kineo Low, Kineo Low had slightly greater peaks in sap velocity compared to Kineo High (Figure 6) for Julian days 154-162 and 197-202 in 2011 (Figure 6).

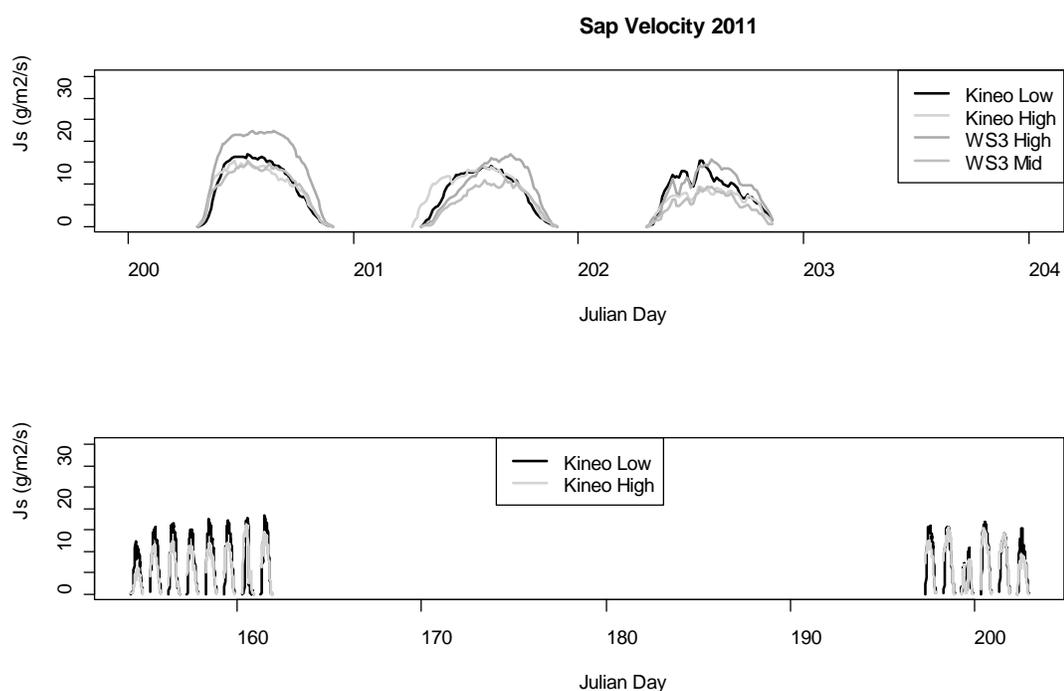


Figure 6: Diurnal variation in average sap velocity (J_s) for yellow birch trees at Kineo Low ($n=5$), Kineo High ($n=5$), WS 3 Mid ($n=4$), and WS 3 High ($n=3$) plots for 2011. (Top) Daily average sap velocities for Kineo Low (8.74), Kineo High (8.15), WS 3 High (11.16), and WS 3 Mid (6.82) for ordinal dates 200-203 (July 19th-July 22nd). (Bottom) Average sap velocity for Kineo Low (8.10) and Kineo High (7.22) for ordinal dates 154-162 (June 3rd – June 11th) and 197-202 (July 16th - July 21st).

Table 3: *The relationship between average root % embolism and average sap velocity for plots with overlapping times for 2010 and 2011. Gray bars separate overlapping time for sap velocity and the year of measurement. Comparisons can only be made over the same Julian days. The units of average sap velocity (J_s) are grams of $H_2O/m^2/second$. Class of aspect can be described under plot, where Kineo = north-facing and WS 3 = south-facing.*

Year	Plot	Elev.	Avg. Sap Velocity	Avg. % Embolism	% Embolism SE	Julian Days
2010	Kineo Low	610	15.91	32.44	12.35	226-228
2010	WS 3 Low	480	9.78	46.55	13.83	226-228
2010	WS 3 High	590	16.63	42.28	16.07	226-228
2010	WS 3 Low	480	9.13	46.55	13.83	220-239
2010	WS 3 High	590	10.07	42.28	16.07	220-239
2011	Kineo Low	590	8.74	12.88	12.33	200-203
2011	Kineo High	830	8.15	18.22	11.81	200-203
2011	WS 3 Mid	550	6.82	36.84	16.93	200-203
2011	WS 3 High	630	11.16	32.08	3.42	200-203
2011	Kineo Low	590	8.09	12.88	12.33	154-162, 197-202
2011	Kineo High	830	7.22	18.22	11.81	154-162, 197-202

The Relationship between Average Root % Embolism and Sap Velocity

For both years, there may be a pattern linking average sap velocity (J_s) to average root percent embolism within class of aspect but not across aspect classes (Table 3). In 2010, WS 3 Low had the lowest J_s (9.78) and the highest percent embolism (46.55%) compared to WS 3 High (16.63 and 42.28% respectively) for Julian days 226-228 (Table 3). Kineo Low had a J_s of 15.91 and the lowest average root percent embolism for Julian days 226-228 in 2010 (Table 3). Again, for Julian days 220-239, WS 3 Low had the lowest J_s (9.13) and the highest percent embolism (46.55%) compared to WS 3 High (10.07 and 42.28 respectively) (Table 3). In 2011, Kineo Low had a greater sap velocity (8.74) compared to Kineo High (8.15) and lower root percent embolism (12.88 to 18.22% respectively) while WS 3 high had a greater sap velocity (11.16) than WS 3 Mid (6.82) and lower root percent embolism (32.08 to 36.84 respectively) for Julian days 200-203 (Table 3). When we compared Kineo Low and High again over 2011 for Julian days 154-162 and 197-202, Kineo Low still had the greatest sap velocity (J_s) and lowest root percent embolism when compared to Kineo High (Table 3).

Table 4: Individual and plot average DBH (cm) with standard error (SE) of yellow birch trees for 2010 and 2011 at the Hubbard Brook Experimental Forest.

Plot/Year	Kineo Low	Kineo Mid	Kineo High	WS 3 Low	WS 3 Mid	WS 3 High
2010	27.38 (+/- 2.89)	36.26 (+/- 4.49)	27.8 (+/- 2.67)	31.88 (+/- 4.98)	41.1 (+/- 7.87)	26.16 (+/- 4.86)
2011	23.68 (+/- 2.17)	32.1 (+/- 5.03)	33.76 (+/- 3.8)	34.13 (+/- 5.26)	40.94 (+/- 7.01)	24.12 (+/- 4.66)

In 2010, Kineo Mid had the greatest plot average DBH (diameter at breast height) at 36.26 cm compared to Kineo Low (27.38 cm) and Kineo High (27.8 cm), furthermore WS 3 Mid had the greatest plot average DBH at 41.1 cm compared to WS 3 Low (31.88 cm) and WS 3 High (26.16 cm) (Table 4). In 2011, Kineo High had the greatest DBH at 33.76 cm compared to Kineo Low (23.68 cm) and Kineo Mid (32.1 cm) (Table 4). WS 3 Mid had the greatest DBH of the south-facing transect in again in 2011 at 40.94 cm compared to WS 3 Low (34.13 cm) and WS 3 High (24.12 cm) (Table 4). Kineo Low and WS 3 High were very similar in plot average DBH for both years, and were on the smaller end of the plot average DBH spectrum (Table 4).

Discussion

The plots along our south-facing transect (WS 3) had the greatest frequency of thaw-freeze events based on air temperature fluxes compared to our north-facing transect (Kineo) (Table 1). It is likely the south-facing transect was more susceptible to thaw-freeze events due to more direct sunlight during the day, providing for greater temperature fluctuation. In 2010 the south-facing transect had no level 2 events and the north-facing transect had 2 events, while in 2011, the south-facing transect had six level 2 thaw-freeze events and the north-facing transect had two level 2 events (Table 1). These results suggest that the south-facing transect had greater freeze-thaw severity than the north-facing transect in 2011 compared to 2010. South-facing snow-course stations accumulated less snow and experienced earlier snowmelt than north-facing snow-course stations for each year (Figures 1 and 2). These results indicated that our south-facing transect (WS 3) was more susceptible to winter and early spring soil frost than our north-facing transect (Kineo) due to decreased insulation from limited snowpack. South-facing plots had greater average root percent embolism than north-facing plots for each individual year, with the exception of Kineo Mid in 2011 (Figures 3 and 4). It is possible we observed this trend due to greater thaw-freeze severity and decreased snowpack depth and duration at the south-facing low elevation plots. These results support lab studies (Zhu et al. 2000; Zhu et al. 2001; Cox and Zhu, 2003; Cox and Malcolm, 1997) and suggest that under natural conditions, susceptibility to soil frost and thaw-freeze events is a key factor causing embolism in yellow birch trees. These results also support our first and second hypotheses, that susceptibility to thaw-freeze events and soil frost was greater at our south-facing low elevation transect compared to our north-facing

high elevation transect. Because of this south-facing plots had greater root percent embolism than north-facing high elevation plots.

Snowpack variation across our plots was greater for winter 2010/2011 than for winter 2009/2010 (Figure 1) and a repeated measures ANOVA found differences in root percent embolism due to aspect and elevation for 2011 were near significant ($p=0.05$) (Table 2), however no significant differences were found for 2010 ($p=0.91$) (Table 2). It is possible we observed greater variation in root percent embolism with greater variation in snowpack across our plots. Snowpack depth and duration for winter 2009/2010 (Figure 1) was less than winter 2010/2011 (Figure 2). Root percent embolism was greater at all plots for 2010 (Figure 3) compared to 2011 (Figure 4), with the exception of our Kineo Mid plot. These results suggest that annual snowpack variation influences root embolism patterns in yellow birch trees.

Within class of aspect, all middle elevation plots experienced the greatest root percent embolism compared to their respective high and low elevation plots for each year (Figures 3 and 4). Interestingly, a recent study by Vadeboncoeur et al. (2012), comparing presettlement vegetation surveys to current surveys found that yellow birch is now more dominant than during presettlement, however the difference in current distribution is only significant from 200-500m and 800-900m. The significant difference between 800-900m may be explained by the upslope shift in the northern hardwood/boreal forest ecotone as observed by Beckage et al. (2008). This shift in the ecotone is credited to warmer winters in the region (Beckage et al., 2008). However, our finding that middle elevation plots experience the greatest root embolism may be explained by a larger DBH class at the middle elevation sites (Table 4). This larger DBH class at the middle elevations could be attributed to land-use history, that old yellow birch was not selected for cutting due to imperfections compared to the other species during this time. It is likely that greater average DBH at middle plots is due to older individuals instead of more productive individuals since embolism was found to be the greatest during both years at middle elevation plots, which would theoretically lower productivity. In addition, it is possible that if these individuals are older, that they would have greater residual embolism (embolism acquired over the years) compared to younger individuals.

When comparing plot average root percent embolism to average sap velocity, we found that within class of aspect, all plots with the greatest average root percent embolism experienced the lowest sap velocity and vice-versa for both years (Table 3). The only exception to this pattern is Kineo Low and WS 3 High in 2010 (Table 3), where drought conditions may have skewed our sap velocity results on Julian day 227 (Figure 5a) due to water being limited, allowing embolism not to be a factor influencing sap velocity. The link between embolism and sap velocity within class of aspect suggests that root embolism may be a factor which limits sap flows at the HBEF, supporting our second hypothesis. Differences in environmental stimuli, such as photoperiod and temperature, across aspect classes over the growing season may explain why we observed this trend within class of aspect and not across aspect classes.

Our results suggest that current winter climatic conditions are influencing yellow birch root health and sap velocity over natural gradients, and thus warmer winters will likely impact future yellow birch distributions, and alter the dynamic of the northern hardwood forest ecosystem. It has been predicted that yellow birch individuals at the northern edge of

their range may reproduce more capably, while individuals at the southern edge will experience increased mortality (Zhu et al. 2000; Cox and Zhu, 2003) due to changing climatic conditions. Our results support this prediction assuming that yellow birch distributions change over time the way they currently vary in space. Other studies suggest that extended winter thaws play an important role in yellow birch decline (Mohan et al. 2009; Bourque et al. 2005).

Campbell et al. (2009) found in a PnET-BGC model simulation response to 4 climate scenarios that soil water content will decrease by the year 2100 with an 8-15% increase in NPP driven largely by longer growing seasons at the HBEF (Mohan et al. 2009). This increased drought risk during the growing season along with increased winter root injury is likely to increase xylem tension, which can provide further cavitation/embolism (Tyree and Sperry, 1989; Tyree and Ewers, 1991) and if this positive feedback mechanism continues, hydraulic failure is possible (Maherali et al. 2004). In mountainous ecosystems, diversity is relatively limited and decline of 3 main tree species could likely create gaps that would disrupt trophic levels and essential ecosystem services (Halman et al. 2011). It is possible that the rate of climatic change may outpace the adaptive change of some northern hardwood species (Bourque et al. 2005). Empirical and modeling studies that include tree DNA evidence suggest that tree migration since the last glaciation were much slower than is required to keep up with current and future warming (Mohan et al. 2009). Nitrogen and sulfate deposition in the northern hardwood forest has been found to reduce reproductive success and frost hardiness while increasing physical damage to leaf surfaces (Mohan et al. 2009). These interactions may increase future tree declines and disturbances under warming climatic conditions by making it more difficult to adapt to climate change (Mohan et al. 2009).

There is a strong need for information on climate change effects in New England as programs and policies are being readied to reduce greenhouse gas emissions (Campbell et al. 2009). Current effects and future predictions of climate change research give policy makers vital information in making analyses and decisions. Yellow birch is an economically valuable species due to its use as a hardwood lumber, veneer, and wood alcohol, and is ecologically valuable as a preferred browse plant for many wildlife species (Bourque et al. 2005). Climate change could profoundly affect forest ecosystem services in which New England has become reliant, such as biofuel, paper, clean air and water, food products, flood control, carbon sequestration, biodiversity, wildlife habitat, aesthetic benefits, and recreation and tourism (Campbell et al. 2009). We hope this study brings insight to some of the key issues involving the impact of winter climate change on yellow birch trees in the northern hardwood forest.

Conclusions

Air temperature and snowpack depth and duration influences root embolism patterns of yellow birch stands in situ. As winter climate warms and soil frost and thaw-freeze events increase, root health and productivity may decline in yellow birch stands, and thus, future range shifts are possible. Yellow birch is a valuable indicator species of future changes and shifts in the distribution of the northern hardwood forest. Middle elevation plots had the greatest root damage and lowest sap velocity within class of aspect compared to the respective high and low elevation plots. It may be that thaw-freeze and soil frost

susceptibility was greatest at these plots during the 2 years of this study, due to less snowpack than high elevation plots and colder temperatures/ greater temperature fluctuation than low elevation plots. We need to start making connections between the impacts of climate change on ecosystem services including water and carbon balances and budgets (Mohan et al. 2009). Future research on the impacts of winter climate change in the region is needed to inform the public and help to pass climate change legislation and preserve northern hardwood forest habitat in the northeast United States. Fine tuning our ability to predict future forest composition, productivity, and distributions is essential for improving our ecologic, economic, and policy making decisions (Mohan et al. 2009). It is crucial to merge empirical data from field manipulations and natural gradients with modeling efforts to increase our understanding of future forest composition (Mohan et al. 2009).

Chapter 2: *Factors influencing the pre bud-break sap velocities of sugar maple (Acer saccharum) trees in central, New Hampshire*

Abstract: This study is important in understanding how annual winter variation, temperature fluctuation, cardinal direction, and sapwood depth affects early spring sap flows during the “tapping” or “sugaring” season in New England. We focus on the importance of the winter season and air temperature fluxes, which may alter spring sap velocity and greatly influence the maple syrup industry. In this experiment we apply the heat dissipation method (Granier 1985; 1987) to quantify early spring sap flows as sap velocity in grams of H₂O per m² per second (g/m²/s). Three sugar maple trees were chosen in close proximity with nearly the same DBH, crown class and vigor on the campus of Plymouth State University in central New Hampshire during early spring in 2011, following an average winter. Two and 4cm long sap-flux sensors were constructed to provide for differences in sapwood depth and north and south cardinal direction were used when inserting the sensors in the sapwood of the sugar maple trees. We compared sap-flux densities of these sensors to determine (1) how north/south exposure of the stem affects sap flows, (2) how sapwood depth affects sap flows of sugar maples trees in the early spring (pre-bud break), and (3) how temperature fluctuation plays a role in the volume and intensity of the sap flows. In 2012, we measured the pre-bud break sap velocities of 2 sugar maple trees at the HBEF following the mild winter of 2012 to see (4) how annual winter variability influences the timing of sap initiation and peak sap velocity.

We hypothesized that (1) sap flows will be greatest following nights when air temperatures drop below the freezing point then rise above the freezing point during the day, (2) south-facing sensors will have the greatest flows due to greater variation in wood temperature on the south-side, (3) as sapwood depth increases the flow of sap will be reduced, and (4) pre-bud break sap velocity will be reduced in 2012 compared to 2011 due to a very mild winter during the prior 2011/2012 season.

Sap velocity was greatest (up to 1,500 g/m²/s) on the south compared to the north side of the sapwood. Furthermore, sap velocity decreased (500-2,000 g/m²/s) with increasing depth in the sapwood. All sensors at 4 cm depth showed similar patterns where sap velocity increased quickly during the morning and then steadily declined throughout the rest of the day. On Julian day 97, 2cm long sensors on the south side had a large spike in sap velocity compared to the other sensors (up to 3000 g/m²/s). Peak pre-bud break sap velocities occurred earlier and were much less in 2012 (120 g/m²/s) compared to 2011 (3,000 g/m²/s). These results have implications for the maple syrup industry under future climate change scenarios. Methods from this study can be used to provide longevity to the maple syrup industry in the United States.

Introduction

Sugar maple (*Acer saccharum* Marsh.) trees are one of the most important of the northern hardwood tree species for many reasons (Burns and Honkala, 1990). They are a keystone species in forest ecosystems of the Northeast and Midwest United States and Canada (Horsley et al. 2002). Sugar maple currently grows on 12.5 million hectares, or 9% of all hardwood forest land and are an important source of saw-timber and maple sugar (syrup) in the United States (Burns and Honkala, 1990). Sugar maple trees are found at sites with ample organic matter in New Hampshire (Burns and Honkala, 1990). Much of the genetic work on sugar maple trees involves improving the efficiency of maple sap production, as approximately 34-40 gallons of sap from early spring flows are required to make 1 gallon of maple syrup, but these numbers can vary depending on the quality of the sap or sucrose concentration (Burns and Honkala, 1990). Sugar maple individuals vary in sugar content of their sap by 2-3%, even in the same bush (forest stand of sugar maple trees exploited for maple syrup) and a single tree can show variation in sucrose concentration of its sap annually (Taylor, 1956). A tree which produced sap with a high percentage of sap one season cannot be expected to yield sap with the same proportion of sugar to water during the next season (Taylor, 1956). Sugar yields are of the best quality and quantity in the early spring, only if wood temperature rises above the freezing point followed by a couple hours of freezing (Tyree, 1983). Because of the specific temperature requirements needed to produce early spring sap flows, the effects of winter climate change on sugar maple trees deserves further study.

Maple Syrup Production in the United States

Tapping sugar maple trees to create maple syrup is an essential part of New England's economy and character (Rock and Spencer, 2000). Prior to the 1950's, the United States accounted for 80% of worldwide maple syrup production and currently this figure has dropped to 20% of worldwide production due to changing winter climate and the introduction of tubing based methods for sap collection in the 1970's (Rock and Spencer, 2000). Prior to the 1950's snow depth in Canada was often too deep to tap sugar maples and thaw-freeze events rarely occurred (Rock and Spencer, 2000). The New England and New York region comprised of 75% US total maple syrup production in 1997-1999 and the average value for production during this time in the region was \$25 million (Rock and Spencer, 2000). Vermont currently produces the highest volume of maple syrup in the United States which represents over 4,000 seasonal jobs and \$105 million annually (Rock and Spencer, 2000). Sugar maple trees are tapped in the late winter or early spring to capture the first flow of sap, which usually has higher sugar content compared to later flows in the season (Burns and Honkala, 1990). As winter climatic conditions are beginning to change so will regional sugar maple sap-flow timing and velocity in the early spring. For this reason it is important that we understand the mechanism behind pre-bud break pressure generation and how climatic changes may impact pre-bud break sap flows in sugar maple trees. We offer a method to help improve efficiency during the sugaring season to help reduce labor costs and contribute to the longevity of maple syrup production in the United States.

Mechanism of pre-bud break xylem pressure generation in sugar maple

Because sucrose appears in the vessels when the sap season starts, it is suggested that living cells are involved in the process of initiating sap-flows during the early spring (Marvin et al. 1967; Sauter, 1974; Johnson et al. 1987). The high and long term pressurization of maple sap can be explained via an osmotic process (Tyree, 1995; Tyree and Zimmerman, 2002; Cirelli et al. 2008). As the sap season begins, the sucrose concentrations in the xylem vessels become increasingly greater (Sauter et al. 1973). Sucrose, which is derived from starch catabolism, lowers the water potential in sugar maple vessels and is actively transported from ray parenchyma cells into vessels across connecting pit membranes (Sauter, 1974; Sauter et al. 1973; Decourteix et al. 2006). Once sucrose concentrations have been established in the vessels, the pressure and volume of sap flows are positively correlated with sucrose concentrations in the cells, air temperature fluctuation and thaw-freeze cycles or events (Marvin et al. 1967; Johnson et al. 1987; Cirelli et al. 2008). However, we do not fully understand how air temperature fluxes and thaw-freeze events contribute to the high pressure generation (in combination with sucrose concentrations) during pre-bud break in sugar maple trees. Pressures of early spring flows have been recorded up to 200 kPa (kilopascals) in the vessels of sugar maple (Yang and Tyree, 1992) coinciding with high sucrose concentrations. Because of the link between sucrose concentration and sap flows, identifying areas in the sapwood of greatest sap velocity should provide for greater sucrose concentration in the sap, thus more efficient and higher quality maple syrup production.

Spring thaw-freeze cycles in sugar maple and sap flow response

The alternation of above freezing air temperatures during the day followed by below freezing temperatures at night provide conditions of positive stem pressure in sugar maple trees, which results in early spring sap flow (Rock and Spencer, 2000; Wiegand, 1906). Sugar yields from maple sap are greatest when air temperature falls below 0°C at night and rises a few degrees above freezing during the day (Tyree, 1983; Wiegand, 1906). When a few days occur (24-26 hours) where night temperatures do not fall below freezing, sap flow is halted (Rock and Spencer, 2000; Tyree, 1983; Wiegand, 1906). Because of this, the maple sugar industry is largely dependent on the timing of climatic events (Rock and Spencer, 2000). Warmer seasonal temperatures in the United States have caused reduced sap flow, a shorter syrup season and a lower grade product (Rock and Spencer, 2000). The swelling of leaf-buds, which is occurring earlier in the season, indicates the end of the maple syrup season, and is largely controlled by temperature (Wiegand, 1906; Richardson et al. 2006).

Concerns of maple syrup producers in the region

The main concern of many maple syrup producers in the New York, Pennsylvania, and New England region is tree health (Rock and Spencer, 2000). In 1987 a group was formed to address regional decline in sugar maple health, today they are called the National Association of Maple Production (NAMP) (Rock and Spencer, 2000). Abiotic stressors to the sugar maple industry in New England include atmospheric deposition, drought, and freezing injury to roots during times when snow cover is lacking (Rock and Spencer, 2000). Snow

cover is an important climatic condition that functions to protect sugar maple from root soil frost injury during winter (Bertrand et al. 1994). Past research has found a correlation between soil frost stressed trees and ABA (abscisic acid) concentration in the sap, which was significantly higher than drought stressed trees (Bertrand et al. 1994). These results can be applied to sugar maple trees when choosing which individuals to tap for early spring flows. The increased frequency of ice storms is also another major concern associated with climate change. The ice storm of 1998 had significant negative impacts on maple health and syrup production in the region (Rock and Spencer, 2000). The economic impact of the 1998 ice storm in Clinton County, New York was estimated to be \$4.5 million in losses by the Cornell Cooperative Extension Agency (Rock and Spencer, 2000).

Dieback and decline disease of sugar maple

Widespread dieback of sugar maple recently occurred in Quebec and many hypotheses to explain this phenomenon involve the effects of changing winter climatic extremes (Bertrand et al. 1994). Winters preceding a sugar maple dieback in 1932 (Pomerleau, 1991) and 1981 (Auclair, 1989) as well as yellow birch dieback in 1936 (Braathe, 1957) were characterized by abnormally thin snow cover with very low temperatures, which likely resulted in root damage from soil freezing and frost heaving (Bertrand et al. 1994). Sugar maple dieback from mild winters is one stressor that helps perpetuate decline disease. Nutrient deficiencies of *Mg*, *Ca*, and *K* are also considered to be contributing factors of sugar maple decline (Page et al. 2008; Juice et al. 2006; Horsley et al. 2002). A small fraction of total soil calcium is available for plant uptake (>5%) and most of the *Ca* is found in the mineral soil and forest floor of temperate forest ecosystems (Likens, 1998; Page et al. 2008). Sugar maple has a relatively high demand for *Ca* and *Mg* compared to the other northern hardwood species (Horsley et al. 2000). Recent decline in sugar maple health and recruitment at the HBEF (Hubbard Brook Experimental Forest) are linked to calcium depletion and reductions in soil pH (Juice et al. 2006; Kobe et al. 2002). When calcium was added to WS 1 at the HBEF, sugar maple health, growth, and survivorship increased (Juice et al. 2006). Mycorrhizal colonization increased in response to calcium fertilization in both seedlings and mature tree individuals (Juice et al. 2006). Atmospheric deposition can lead to increased tree dieback by causing soil nutrient deficiencies, which weakens trees making them more susceptible to soil frost induced damage (Foster, 1989; Bertrand et al. 1994).

Air temperature fluctuation, cardinal direction and sapwood depth in relation to early spring sap flow rates

As sapwood depth increases, pre-bud break sap flow in sugar maple trees decreases (Hatton et al. 1990; Becker, 1996; Phillips et al. 1996; Wullschleger and King, 2000; James et al. 2002; Delzon et al. 2004; Fiora and Cescatti, 2006). Pre-bud break sap flow rates are a function of temperature, regardless of whether temperatures fall below freezing at night (Tyree, 1983). The southern exposures of the stem usually have the greatest sap flows since temperature extremes are the greatest there (Wiegand, 1906). Maximum xylem pressure on good sap days usually occurs about 90 minutes after the start of flow early in the morning (Wiegand, 1906), when air temperature is increasing at a fast rate. A considerable fluctuation

in temperature without great fluctuation in tension can occur when temperatures do not cross the freezing point (Wiegand, 1906). Flow of maple sap is highest early in the morning and then progressively falls as the day advances and ceases during cold nights (Wiegand, 1906). It is important to capture the first sap flows of the season because they have the highest sugar concentrations and provide the greatest yield and most efficient production process.

Objectives and hypotheses

We compared sap velocities in sugar maple trees in early spring (pre-bud break) to determine how spring sap flows are affected by (1) north/south exposure of the stem, (2) sapwood depth, (3) temperature fluctuation, and (4) winter variability. We hypothesize that (1) sap flows will be greatest following nights when air temperatures drop below the freezing point then rise above the freezing point during the day, (2) south-facing sensors will have the greatest flows due to greater variation in wood temperature, (3) as sapwood depth increases the flow of sap will be reduced, and (4) sap velocity will be decreased following mild winters with low snow accumulation and deeper soil frost penetration.

Methodology

Study site and experimental design

We chose a stand of 3 sugar maple trees (as a pilot study to determine the feasibility of monitoring sap-flow under winter conditions) in 2011 that were approximately the same DBH and health on the campus of Plymouth State University in Plymouth, New Hampshire during the early spring. We measured sap velocity at 1cm (2cm long sensor) and 2cm sapwood depth (4cm long sensor) for determining the effect of sapwood depth on sap velocity. Each sensor had a thermocouple inserted halfway in the sensor casing, so 2 cm long sensors are measuring wood temperature at 1 cm sapwood depth and 4 cm long sensors are measuring wood temperature at 2 cm sapwood depth. Sugar maple tree 1 had a 4cm long sensor set in the north-side and a 2cm long sensor set in the south-side of the sapwood. Tree 2 had 2 cm long sensors set in both the north and south-side of the sapwood and Tree 3 had a 2cm long sensor set in the north-side and a 4cm long sensor set in the south-side of the sapwood (opposite of tree 1).

In 2012 we conducted a similar study in the southwest portion of the White Mountain National Forest in central New Hampshire at the Hubbard Brook Experimental Forest (HBEF), 43°56'N, 71°45'W (Likens, 1985; Bailey et al. 2003). We sampled 2 sugar maple trees at a plot near the snow-course station behind headquarters at the HBEF. Heat dissipation probes were installed at 2cm depth in the sapwood of each tree on the southeast side of the stems to calculate sap velocity. The initial set-up of the plots occurred before bud development in the early spring, following the mild winter of 2012 (air/soil temp. and snow depth data to support this).

Calculating sap velocity (*J_s*)

Sap velocity was measured using the heat dissipation method as described in more detail by Granier (1985; 1987). Each sensor was handmade, consisting of a copper-constantan thermocouple inserted halfway in the sensor casing (19 gage 1-1/2 in. hypodermic needle-cut to size). Pairs of heated and reference sensors were vertically aligned 10 cm apart and inserted at breast height (1.3m) into the sapwood. The upper sensor (heated) was wrapped with constantan wire and warmed to a steady temperature, while the lower sensor (reference) was unheated and recorded the natural wood temperature. The electric current of the power-board was adjusted to 0.125A (Amperes) using a 1k Ohm trim-potentiometer (Newark Scientific, USA) so all heated sensors maintained a consistent temperature. Aluminum tubing (in 2 cm lengths) was used to surround each sensor to allow for sensor longevity and uniform heat dissipation throughout the sapwood. All sensors were covered with an insulated and reflective covering to minimize the error from solar radiation and air temperature. The temperature difference between the thermocouples in each sensor was recorded every 30 seconds using the CR1000 or CR800 data loggers with an AM 16/32 channel multiplexer (Campbell Scientific, USA). Averages were stored every 15 minutes in the data-logger from the 30 second interval measurements. The temperature differences (recorded as differential voltage) were converted to sap velocity (*J_s*) using the program *Baseliner* created by Ram Oren using Graniers calibration equation ($119 \cdot \Delta T_m - \Delta T$) (Granier, 1985; 1987). ΔT_m is the maximum temperature difference, or “baseline”, when flow is considered to be zero (Oren, 2001; Granier, 1985, 1987; Fiora and Cescatti, 2006; Gebauer et al. 2008). The units for sap velocity are g of H₂O/m²/s (Granier, 1985; 1987).

Results

Air temperature fluctuated below freezing at night and above freezing during the day for Julian days 97, 98 and 99 in 2011 (Figure 1). Julian days 100 and 101 did not cross the freezing point (0°C) at night (Figure 1). For Julian day 96, air temperature just reached the freezing point during the night (Figure 1). In sugar maple tree number 1 the south-facing sensor at 2 cm sapwood depth (black line) showed a greater (3,000 g/m²/s) sap velocity (*J_s*) than the north-facing sensor (650 g/m²/s) at 4cm sapwood depth (gray line) (Figure 2). On Julian day 97, the south-facing 2cm long sensor showed a large spike in sap velocity (up to 3,000 g/m²/s) following the first freeze-thaw event, while the north-facing 4cm long sensor was just beginning to detect flow (Figure 2). The south-facing 2cm long sensor on Julian day 96 shows a quick spike in the morning and a gradual decline throughout the rest of the day, similar to the shape of the curve for the north-facing 4cm long sensor for Julian days 98 and 99 (Figure 2). For Julian day 100, sap velocity of both sensors starts to decrease and by Julian day 101, sap velocity is minimal for both sensors (Figure 2). In sugar maple tree number 2 the south-facing sensor at 2cm sapwood depth (gray line) showed a greater spike in sap velocity (*J_s*) (3,000 g/m²/s) than the north-facing sensor at 2cm sapwood depth (black line) for Julian days 97 and 100 (Figure 3). The north-facing 2cm long sensor (black line) showed more consistent patterns in flow rates with the greatest flow occurring on Julian days 96 and 97. By Julian day 101, the south-facing 2 cm long sensor showed a minimal rate of sap flow (Figure 3).

In sugar maple tree number 3 the south-facing sensor at 4 cm sapwood depth (gray line) showed a lower sap velocity ($550 \text{ g/m}^2/\text{s}$) than the north-facing sensor ($1,400 \text{ g/m}^2/\text{s}$) at 2 cm sapwood depth (black line) for Julian days 97 through 101 (Figure 4). This trend suggests that sapwood depth had a greater influence on sap flow rates than sapwood aspect. Both sensors showed a quick spike in sap velocity in the morning with a gradual decline throughout the rest of the day for Julian days 98 and 99 (Figure 4). The greatest sap velocities for both sensors occurred on Julian day 98 and 99 (Figure 4). On Julian day 101, sap velocity of both sensors was reduced to a minimal rate of sap-flow.

Our pre-bud break sap velocity results for 2012 showed that sap flows were initiated earlier in the season (Julian day 80) compared to 2011 (Julian day 96) (Figure 5). Furthermore, sap velocity was much lower ($120 \text{ g/m}^2/\text{s}$) in spring of 2012 compared to spring 2011 ($3,000 \text{ g/m}^2/\text{s}$) (Figure 5). From Julian day 80 – 86 there were no thaw-freeze events, and minimal temperature fluctuation for Julian days 83 – 86 (Figures 5 and 6). On Julian day 87 there was a mild thaw-freeze event, however with minimal temperature fluctuation and a small response from sugar maple tree 2 (Figure 6). From Julian days 95-102, pre-bud break sap flows have ceased (Figure 7).

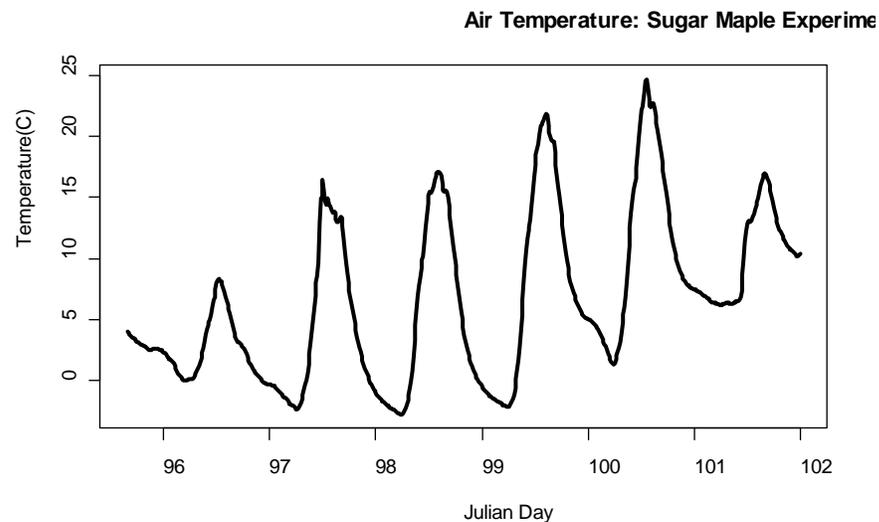


Figure 1: Diurnal air temperature ($^{\circ}\text{C}$) fluctuation over time (Julian day) during the early spring of 2011 in Plymouth, New Hampshire.

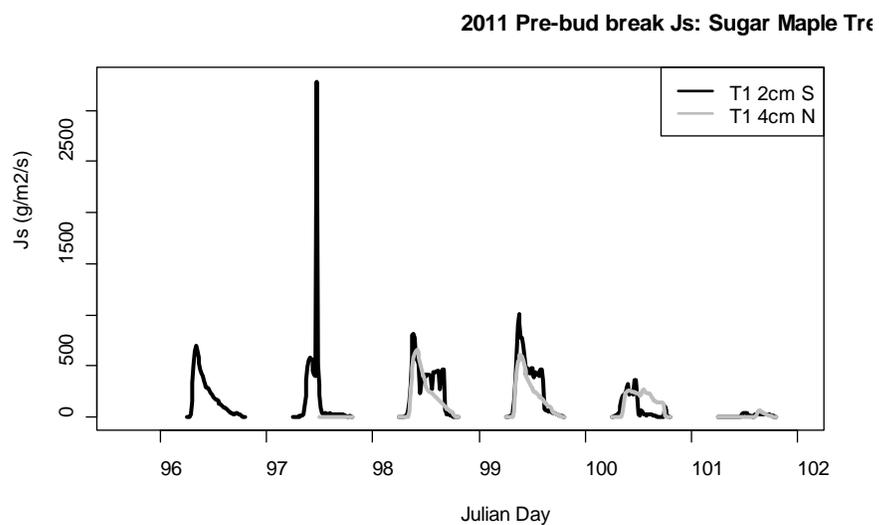


Figure 2: Sap velocity (J_s) over time (Julian Day) for sugar maple tree #1. The black line indicates a 2cm long sensor in the south-facing side of the sapwood and the gray line indicates a 4cm long sensor in the north-facing side of the sapwood.

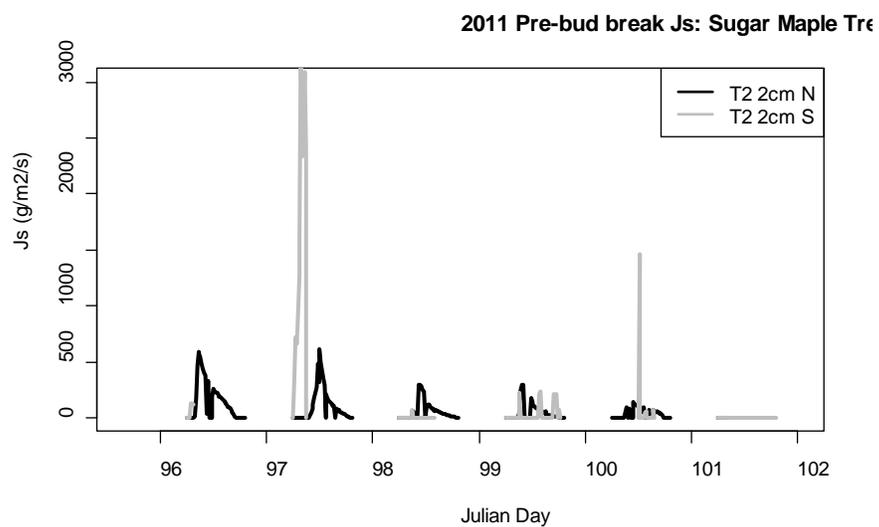


Figure 3: Sap velocity (J_s) over time (Julian Day) for sugar maple tree #2. The black line indicates a 2cm long sensor in the north-facing side of the sapwood and the gray line indicates a 2cm long sensor in the south-facing side of the sapwood.

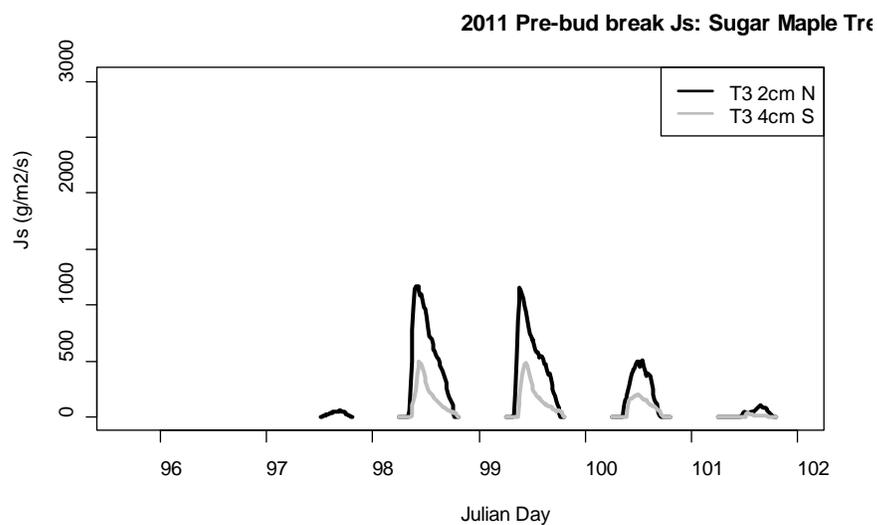


Figure 4: Sap velocity (J_s) over time (Julian Day) for sugar maple tree #3. The black line indicates a 2cm long sensor in the north-facing side of the sapwood and the gray line indicates a 4cm long sensor in the south-facing side of the sapwood.

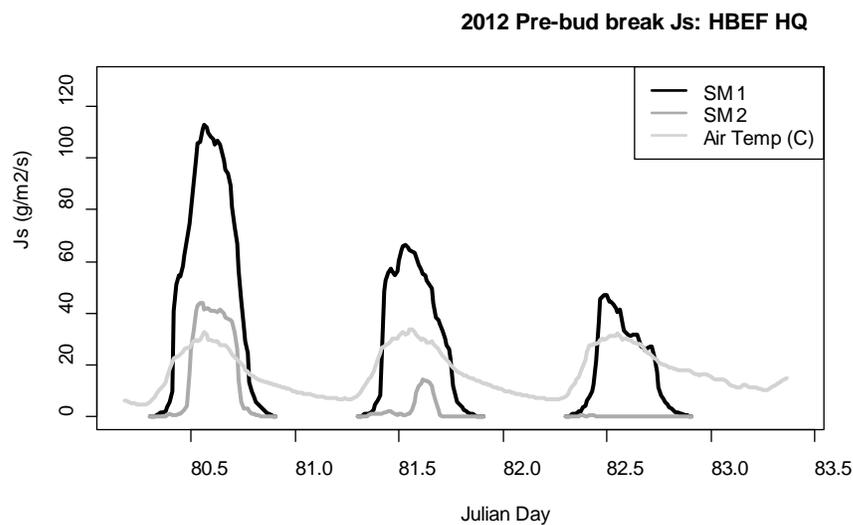


Figure 5: Pre bud-break sap velocities (2 cm long sensors, 1 cm sapwood depth) for Julian days 80-82 during 2012 at the HBEF in 2 sugar maple (SM 1-black and SM 2-dark gray) trees. Air temperature ($^{\circ}\text{C}$) is shown by the light gray line.

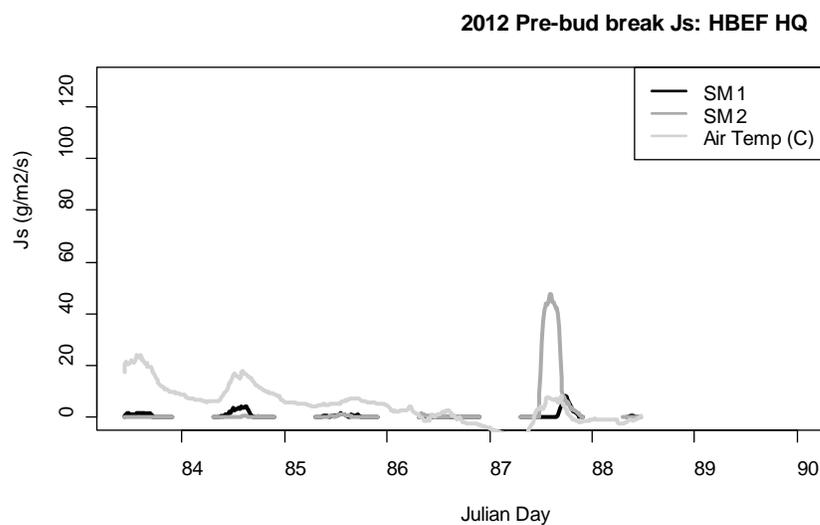


Figure 6: Pre bud-break sap velocities for Julian days 83-88 during 2012 at the HBEF 2 sugar maple (SM 1-black and SM 2-dark gray) trees. Air temperature ($^{\circ}\text{C}$) is shown by the light gray line.

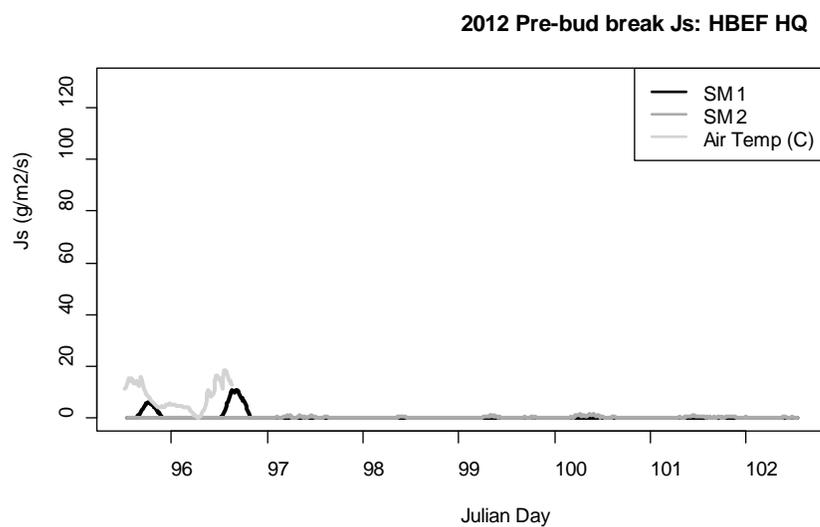


Figure 7: Pre bud-break sap velocities for Julian days 95-102 during 2012 at the HBEF in 2 sugar maple (SM 1-black and SM 2, dark gray) trees. Air temperature ($^{\circ}\text{C}$) is shown by the light gray line.

Discussion

Our results indicated that sap flow rates were greatest following the first thaw-freeze event on the south side of the sapwood at 1 cm sapwood depth (2 cm long sensor) compared to 2 cm sapwood depth (4 cm long sensor). Our results supported the findings of Wiegand (1906) that maximum xylem pressure on good sap days usually occurs about 90 minutes after the start of flow early in the morning and that a considerable fluctuation in temperature without great fluctuation in tension can occur when temperatures do not cross the freezing point. Our results support past research that stem pressure in sugar maple is highly dependent on air temperature, and several freeze-thaw cycles are needed to initiate sap ascent and pressure (Cirelli et al. 2008; Tyree and Zimmerman, 2002).

Our results suggested that tapping on the south-facing side could result in higher sap yield. Typical commercial taps are 2.5 to 3 inches long and can be inserted at the depth the tapper chooses. Our results indicated that flows are much greater at 1 cm sapwood depth compared to 2 cm sapwood depth. In light of this, it may be beneficial to tap shallower into trees to reduce risk of injury and scarring or to collect higher quality sap. This conservation effort may allow the tapper to get more tapping seasons out of the south aspect of the stem. Temperature fluctuation is vital in determining the volume and intensity of sap-flows, especially when temperatures fall below the freezing point at night and rise above freezing during the day. Our hypothesis was supported that south-facing sensors had the greatest sap flows due to greater temperature variation and that as sapwood depth increased, the flow of sap was reduced.

Total stem sap flow is calculated from the product of sap velocity and the cross sectional area of the sapwood for each individual tree (Fiore and Cescatti, 2006; Granier, 1985). These estimates assume equal sap velocity across the entire radius of the sapwood, and can lead to large errors if sap velocity is unequal across the radius of the sapwood (Fiore and Cescatti, 2006). Our results suggest that sap velocity varies greatly in response to aspect and sapwood depth, and in order to achieve accurate total stem sap-flow, these parameters must be taken into consideration. Although this study occurred during pre-bud break, past literature has shown this to be true when transpiration is driving sap flow (Fiore and Cescatti, 2006). Many maple syrup producers would like to understand how climate change will affect sap flows and sap quality (Rock and Spencer, 2000). The maple syrup industry is an important part of New England's character and economy and ecological models predict that changes in climate could potentially extirpate the sugar maple from New England.

A study at Cornell University which measured the relationship between sugar maple sap flow and temperature over the last several decades to model projected sap flow in the future, found that the number of sap flow days may not change in New England, but the timing of peak production will shift earlier in the spring (USFS Press Release, no. 1022). We observed an earlier tapping season in the spring of 2012 following a very mild winter compared to 2011, which supports this claim. By adapting to an earlier tapping season, states in New England may be able to sustain their maple syrup production over the next 100 years, however more southern states, such as Pennsylvania may have production reduced sooner (USFS Press Release, no. 1022). Sugar maple mortality in Pennsylvania since the early to mid-1980s has reached abnormally high levels across northern parts of the state (Horsley et al. 2000). Currently, levels of mortality and crown dieback of sugar maple in Pennsylvania

are unusually higher than other areas of the Northeast United States and Canada (Horsley et al. 2000).

Conclusions

Early spring sap flows in 2012 were greatly reduced compared to 2011, due to a mild winter with lacking snow cover, which likely led to increased frost damage, and a lack of thaw-freeze events during the sugaring season in 2012. The mild winter of 2011/2012 allowed for an earlier initiation of sap flows in 2012 compared to 2011 in central, New Hampshire. Sap flows were greatest at 2cm sapwood depth and on the south side of the stem where temperature fluctuation was greatest. After several days of temperatures not falling below the freezing point at night, xylem pressure was reduced. The first flows had the highest sap velocity and likely had the greatest sucrose concentration, which can be explained by the osmotic process and starch catabolism. Furthermore, the link between thaw-freeze events and temperature fluctuation in relation to sap flows was supported; however the mechanism behind this is not fully understood. Some studies suggest that upon freezing ice and compressed gas form in the fiber lumen and as the ice melts upon thawing, the compressed gas pushes the liquid water out (O' Malley, 1979; Tyree, 1983). This physical model for pre-bud break sap flow is not favored over the vitalistic model (nor the vitalistic model favored over the physical model) mentioned in the introduction as we do not have enough evidence to support/refute either.

Bibliography

- Auclair, A.N.D. 1989. **Climate change theory of forest decline**. In Proc. IUFRO Conference on woody plant growth in a changing physical and chemical environment. Ed. D.P. Lavender. Univ. British Columbia, Vancouver, BC, Canada, pp. 1-29.
- Auclair, A.N.D.; Heilman, W.E.; Busalacchi, P. 2002. **Monitoring the effects of extreme climate disturbances on forest health in the northeast U.S.** USDA Forest Service (6.12).
- Bailey, A.S.; Hornbeck, J.W.; Campbell, J.L.; Eagar, C. 2003. **Hydrometeorological Database for Hubbard Brook Experimental Forest: 1955-2000**. Gen. Tech. Rep. NE-305.
- Bassow, S.L and Bazzaz, F.A. 1998. **How Environmental Conditions Affect Leaf-Level Photosynthesis in Four Deciduous Tree Species**. Ecology 79(8): 2660-2675.
- Beckage, B.; Osborne, B.; Gavin, D.G.; Pucko, C.; Siccama, T.; and Perkins, T. 2008. **A rapid upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont**. PNAS 105(11):4197-4202.
- Becker, P. 1996. **Sap flow in Bornean health and dipterocarp forest during wet and dry periods**. Tree Physiology (16): 295-299.
- Bertrand, A.; Robitaille, G.; Nadeau, P.; Boutin, R. 1994. **Effects of soil freezing and drought stress on abscisic acid content of sugar maple sap and leaves**. Tree Physiology (14): 413-425.
- Bourque, C.P.-A.; Cox, R.M.; Allen, D.J.; Arp, P.A., and Meng, F-R. 2005. **Spatial extent of winter thaw events in eastern North America: historical weather records in relation to yellow birch decline**. Global Change Biology (11): 1477-1492.
- Braathe, P. 1957. **Is there a connection between the birch dieback and the March thaw of 1936?** Forestry Chronicle (33): 358-363.
- Braathe, P. 1995. **Birch dieback – caused by prolonged early spring thaws and subsequent frost**. Norwegian Journal of Agricultural Sciences (20): 59 p.
- Braathe, P. 1996. **Birch dieback- the effects of artificial spring frost on budburst and foliage**. Norwegian Journal of Agricultural Sciences 10 (1): 1-6.
- Burns, R.M. and Honkala, B.H. 1990. **Silvics of North America: Volume 2**. USDA Agriculture Handbook 654.
- Campbell, J. L. and Bailey A.S. 2012. **Snow Depth Data**. Hubbard Brook Research Foundation. snod.txt.
- Campbell, J.L. and Bailey, A.S. 2012. **Daily Maximum/Minimum Temperature Data**. Hubbard Brook Research Foundation. Weather_-_min,_max_temperature.txt.
- Campbell, J.L.; Driscoll, C.T.; Eagar, C.; Likens, G.E.; Siccama, T.G.; Johnson, C.E.; Fahey, T.J.; Hamburg, S.P; Holmes, R.T.; Bailey, A.S.; Buso, D.C. 2007. **Long-term trends from ecosystem research at the Hubbard Brook Experimental Forest**. Gen. Tech. Rep. NRS-17.

Campbell, J.L.; Mitchell, M.J.; Groffman, P.M.; Christenson, L.M.; Hardy, J.P. 2005. **Winter in northeastern North America; a critical period for ecological processes.** *Frontiers in Ecology and the Environment*. 3(6): 314-322.

Campbell, J.L.; Ollinger, S.V.; Flerchinger, G.N.; Wicklein, H.; Hayhoe, K.; Bailey, A.S. 2010. **Past and projected future changes in snowpack and soil frost at the Hubbard Brook Experimental Forest, New Hampshire, USA.** *Hydrological processes* (24): 2465-2480.

Campbell, J.L.; Rustad, L.E.; Boyer, E.W.; Christopher, S.F.; Driscoll, C.T.; Fernandez, I.J.; Groffman, P.M.; Houle, D.; Kieckbusch, J.; Magill, A.H.; Mitchell, M.J.; Ollinger, S.V. 2009. **Consequences of climate change for biogeochemical cycling in forests of northeastern North America.** *Canadian Journal of Forest Research* (39): 264-284.

Cavendar-Bares, J. 2005. **Impacts of Freezing on Long-Distance Transport in Woody Plants.** 401-424.

Cirelli, D.; Jagels, R.; Tyree, M.T. 2008. **Toward and improved model of maple sap exudation: the location and role of osmotic barriers in sugar maple, butternut and white birch.** *Tree Physiology* (28): 1145-1155.

Cleavitt, N.L.; Fahey, T.J.; Groffman, P.M.; Hardy, J.P.; Henry, K.S.; Driscoll, C.T. 2008. **Effects of soil freezing on fine roots in a northern hardwood forest.** *Canadian Journal of Forest Research* 38(1): 82-91.

Cochard, H. and Tyree, M.T. 1990. **Xylem dysfunction in *Quercus*: vessel sizes, tyloses, cavitation and seasonal changes in embolism.** *Tree Physiology* (6): 393-407.

Cooley, K.R. 1990. **Effects of CO₂-induced climatic changes on snowpack and streamflow.** *Hydrological Sciences Journal* 35 (5): 511-522.

Cox, P.M.; Betts, R.A.; Jones, C.D.; Spall, S.A.; and Totterdell, I.J. 2000. **Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model.** *Nature* 408 (9): 184 – 187.

Cox, R.M. and Malcolm, J.W. 1997. **Effects of duration of a simulated winter thaw on dieback and xylem conductivity of *Betula papyrifera*.** *Tree Physiology* (17): 389-396.

Cox, R.M. and Zhu, X.B. 2003. **Effects of simulated thaw on xylem cavitation, residual embolism, spring dieback and shoot growth in yellow birch.** *Tree Physiology* (23): 615-624.

Decourteix, M.; Alves, G.; Brunel, N.; Ameglio, T.; Guilliot, A.; Lemoine, R.; Petel, G.; Sakr, S. 2006. **JrSUT1, a putative xylem sucrose transporter, could mediate sucrose influx into xylem parenchyma cells and be up-regulated by freeze/thaw cycles over the autumn-winter period in walnut tree (*Juglans regia* L.).** *Plant Cell and the Environment* (29): 36-47.

Delzon, S; Sartore, M.; Granier, A.; Loustau, D. 2004. **Radial profiles of sap flow with increasing tree size in maritime pine.** *Tree Physiology* (24): 1285-1293.

Dudley, R.W. and Hodgkins, G.A. 2002. **Trends in streamflow, river ice, and snowpack for coastal river basins in Maine during the 20th century.** U.S. Geological Survey, Water-Resources Investigations Rep. 02-4245, 26 pp.

- Dukes, J.S.; Pontius, J.; Orwig, D.; Garnas, J.R.; Rodgers, V.L.; Brazee, N.; Cooke, B.; Throharides, K.A.; Strange, E.E.; Harrington, R.; Ehrenfeld, J.; Gurevitch, J.; Lerdau, M.; Stinson, K.; Wick, R.; Ayres, M. 2009. **Responses of insect pests, pathogens, and invasive plant species to climate change in the forests of northeastern North America: What can we predict?** Canadian Journal of Forest Research (39): 231-248.
- Dunn, P.O. and Winkler, D.W. 1999. **Climate change has affected breeding date of tree swallows throughout North America.** Royal society for the protection of birds, London (B266): 2487-2490.
- Dunne, J.A.; Saleska, S.R.; Fischer, M.L.; Harte, J. 2004. **Integrating experimental and gradient methods in ecological climate change research.** Ecology 85 (4): 904-916.
- Ewers, B.E.; Oren, R.; Phillips, N.; Stromgren, M.; Linder, S. 2001. **Mean canopy stomatal conductance responses to water and nutrient availabilities in *Picea abies* and *Pinus taeda*.** Tree Physiology (21): 841-850.
- Fahey, J.H.; Hughes, J.W. 1994. **Fine root dynamics in a northern hardwood forest ecosystem, Hubbard Brook Experimental Forest, NH.** Journal of Ecology (82): 533-548.
- Flora, A. and Cescatti, A. 2006. **Diurnal and seasonal variability in radial distribution of sap flux density: implications for estimating stand transpiration.** Tree Physiology (26): 1217-1225.
- Foster, N.W. 1989. **Acidic deposition: what is fact, what is speculation, what is needed?** Water, Air, and Soil Pollution. (48): 299-306.
- Gebauer, T.; Horna, V.; Leuschner, C. 2008. **Variability in radial sap flux density patterns and sapwood area among seven co-occurring temperate broad-leaved tree species.** Tree Physiology (28): 1821-1830.
- Gill, R.A.; Jackson, R.B. 2000. **Global patterns of root turnover for terrestrial ecosystems.** New Phytologist (147): 13-31.
- Goodrich, L.E. 1982. **The influence of snow cover on the ground thermal regime.** Canadian Geotechnical Journal (19): 421-432.
- Granier, A. 1985. **Une nouvelle method pour la mesure du flux de seve brute dans le tronc des arbres.** Annual Science and Forestry (42): 193-200.
- Granier, A. 1987. **Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements.** Tree Physiology (3): 309-320.
- Greene, D.F. and Johnson, E.A. 1997 **Secondary dispersal of tree seeds on snow.** Journal of Ecology (85): 329-340.
- Groisman, P.Y. and Knight, R.W. 2007. **Prolonged dry episodes over North America: new tendencies emerging during the last 40 years.** Advanced Earth Science (22): 1191-1207.

- Hacke, U.G.; Sperry, J.S.; Pockman, W.T.; Davis, S.D.; McCulloh, K.A. 2001. **Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure.** *Oecologia* (126): 457-461.
- Halman, J.M.; Schaberg, P.G., Hawley, G.J.; Hansen, C.F. 2011. **Potential role of soil calcium in recovery of paper birch following ice storm injury in Vermont, USA.** *Forest Ecology and Management* (261): 1539-1545.
- Hamburg, S.P.; Vadeboncoeur, M.A.; Richardson, A.D.; Bailey, A.S. 2012. **Climate change at the ecosystem scale: A 50-year record in New Hampshire.** *Climatic Change* In review.
- Harcombe, P.A. 1987. **Tree Life Tables – Simple birth, growth, and death data encapsulate life histories and ecological roles.** *BioScience* (37): 557-568.
- Hatton, T.J.; Catchpole, E.A.; Vertessy, R.A. 1990. **Integration of sap flow velocity to estimate plant water use.** *Tree Physiology* (6): 201-209.
- Hodgkins, G.A.; James, I.C.; Huntington, T.G. 2002. **Historical changes in lake ice-out dates as indicators of climate change in New England.** *International Journal of Climatology* (22): 1819-1827.
- Horsley, S.B.; Long, R.P.; Bailey, S.W.; Hallett, R.A.; Hall, T.J. 2000. **Factors associated with the decline disease of sugar maple on the Allegheny Plateau.** *Canadian Journal of Forest Research* (30): 1365-1378.
- Horsley, S.B.; Long, R.P.; Bailey, S.W.; Hallett, R.A.; Wargo, P.M. 2002. **Health of eastern north American sugar maple forests and factors affecting decline.** *Northern Journal of Applied Forestry* 19 (1): 34-44.
- Houghton, J.T; Ding, Y.; Griggs, D.J.; Noguer, M.; van der Linden, P.J.; Dai, X.; Maskell, K.; Johnson, C.A. 2001. **Climate Change 2001: The Scientific Basis. Contribution of Working Group 1 to the Third Assessment Report of the Intergovernmental Panel on Climate Change.** Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 881pp.
- Houston, D.R. 1987. **Forest tree declines of past and present: current understanding.** *Canadian Journal of Plant Pathology* 9(4): 349-360.
- Huntington, T.G. and Hodgkins, G.A. 2004. **Changes in the Proportion of Precipitation Occurring as Snow in New England (1949-2000).** *Journal of Climate* (17): 2626-2636.
- Huntington, T.G.; Hodgkins, G.A.; Dudley, R.W. 2003. **Historical trend in river ice thickness and coherence in hydroclimatological trends in Maine.** *Climatic Change* (61): 217-236.
- Huntington, T.G.; Richardson, A.D.; McGuire, K.J.; Hayhoe, K. 2009. **Climate and hydrological changes in the northeastern United States: recent trends and implications for forested and aquatic ecosystems.** *Canadian Journal of Forest Research* (39): 199-212.
- IPCC, 2007: **Climate Change 2007: The Physical Science Basis. Contribution of the Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.** *oChange* (446): pp. 104.

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

James, S.A.; Clearwater, M.J.; Meinzer, F.C.; Goldstein, G. 2002. **Heat dissipation sensors of variable length for the measurement of sap flow in trees with deep sapwood.** Tree Physiology (22): 277-283.

Johnson, R.W.; Tyree, M.T.; Dixon, M.A. 1987. **A requirement for sucrose in xylem sap flow from dormant maple trees.** Plant Physiology (84): 495-500.

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

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

Kramer, P.J. 1983. **Water relations in plants.** Academic Press, New York.

Krankina, O.N. and Dixon, R.K. 1993. **Forest management options to conserve and sequester terrestrial carbon in Russia.** World Resource Review (6): 88-101.

Langan, S.J.; Ewers, F.W., Davis, S.D. 1997. **Xylem dysfunction caused by water stress and freezing in two species of co-occurring chaparral shrubs.** Plant, Cell and Environment (20): 425-437.

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

Lianhong, G.U.; Hanson, P.J.; Mac Post, W.; Kaiser, D.P.; Yang, B.; Nemani, R.; Pallardy, S.G. and Meyers, T. 2008. **The 2007 eastern US spring freeze: Increased cold damage in a warming world?** BioScience 58 (3): 253-262.

Likens, G.E. 1998. **Some perspectives on long-term biogeochemical research from the Hubbard Brook Ecosystem Study.** Ecology 85 (9): 2355-2362.

Madsen, T. and Figdor, E. 2007. **When it rains, it pours: global warming and the rising frequency of extreme precipitation in the United States.** Technical Report, Environment Maine. Available from <http://www.environmentamerica.org/home/reports/report-archives/global-warming-solutions/global-warming-solutions/when-it-rains-it-pours>.

Maherali, H.; Pockman, W.T.; Jackson, R.B. 2004. **Adaptive variation in the vulnerability of woody plants to xylem cavitation.** Ecology (8): 2184-2199.

Martinez-Vilalta, J. and Pockman, W.T. 2002. **The vulnerability of freezing-induced xylem cavitation of *Larrea tridentata* (Zygophyllaceae) in the Chihuahuan desert.** American Journal of Botany (89): 1916-1924.

- Marvin, J.W. and Greene, M.T. 1951. **Temperature-induced sap flow in excised stems of Acer**. *Plant Physiology* (14): 565-580.
- Marvin, J.W.; Morselli, M.F.; Laing, F.M. 1967. **Rapid low temperature hydrolysis of starch to sugars in maple stems and maple tissue cultures**. *Cryobiology* (8): 339-351.
- Miller-Rushing, A.J. and Primack, R.B. 2008. **Effects of winter temperatures on two birch (*Betula*) species**. *Tree Physiology* (28): 659-664.
- Mohan, J.E.; Cox, R.M.; Iverson, L.R. 2009. **Composition and carbon dynamics of forests in northeastern North America in a future, warmer world**. *Canadian Journal of Forest Research* (39): 213-230.
- Noss, R.F. 2001. **Beyond Kyoto: Forest management in a time of rapid climate change**. *Conservation Biology* 15 (3): 578-590.
- O'Malley, P.E.R. 1979. **Xylem sap flow and pressurization in *Acer pseudoplatanus* L.**, Ph.D. Thesis, University of Glasgow, Glasgow, Scotland.
- Oren, R. and Pataki, D.E. 2001. **Transpiration in response to variation in microclimate and soil moisture in southeastern deciduous forests**. *Oecologia* (127): 549-559.
- Page, B.D.; Bullen, T.D.; and Mitchell, M.J. 2008. **Influences of calcium availability and tree species on Ca isotope fractionation in soil and vegetation**. *Biogeochemistry* 88: 1-13.
- Phillips, N.; Oren, R.; Zimmermann, R. 1996. **Radial patterns of xylem sap flow in non-, diffuse-, and ring-porous tree species**. *Plant, Cell, and the Environment*. (19): 983-990.
- Pomerleau, R. 1991. **Experiences sur les mecanismes du deperissement des forets de feuillus**. Rapport d'information II, Forets Canada, Sainte-Foy, Quebec, Canada, 48 p.
- R Development Core Team (2012). **R: A language and environment for statistical computing**. **R Foundation for Statistical Computing**, Vienna, Austria. ISBN 3-90005 1-07-0, URL <http://www.R-project.org/>.
- Rhoads, A.G.; Hamburg, S.P.; Fahey, T.J.; Siccama, T.G.; Hane, E.N.; Battles, J.; Cogbill, C.; Randall, J.; and Wilson, G. 2002. **Effects of an intense ice storm on the structure of a northern hardwood forest**. *Canadian Journal of Forest Research* (32): 1763-1775.
- Richardson, A.D.; Bailey, A.S.; Denny, E.G.; Martin, W.C.; O'Keefe, J. 2006. **Phenology of a northern hardwood forest canopy**. *Global Change Biology* (12) 1174-1188.
- Rock, B. and Spencer, S. 2000. **The maple sugar industry: Case Study 2**. *Climate Change Issues*. 39-42.
- Sakr, S.; Alves, G.; Morillon, R.; Maurel, K.; Decourteix, M.; Guilliot, A.; Fleurat-Lessard, P.; Julien, J-L.; and Chrispeels, M.J. 2003. **Plasma membrane aquaporins are involved in winter embolism recovery in walnut tree**. *Plant Physiology* (133): 630-641.
- Sauter, J.J. 1974. **Maple**. In *Yearbook of Science and Technology*. McGraw-Hill, New York, pp. 280-281.

- Sauter, J.J.; Iten, W.; Zimmermann, M.H. 1973. **Studies on the release of sugar into the vessels of sugar maple (*Acer saccharum*)**. Canadian Journal of Botany. (51): 1-8.
- Schwartz, M.D. and Reiter, B.E. 2000. **Changes in North American spring**. International Journal of Climatology (20): 929-932.
- Sperry, J.S. 1993. **Winter xylem embolism and spring recovery in *Betula cordifolia*, *Fagus grandifolia*, *Abies balsamea*, and *Picea rubens***. Water transport in plants under climatic stress. pp. 86-98.
- Sperry, J.S. and Sullivan, J.E. 1992. **Xylem embolism in response to freeze-thaw cycles and water stress in ring-porous, diffuse-porous, and conifer species**. Plant Physiology (100): 605-613.
- Sperry, J.S.; Donnelly, J.R.; Tyree, M.T. 1988a. **A method for measuring hydraulic conductivity and embolism in xylem**. Plant, Cell, and Environment (11): 35-40.
- Sperry, J.S.; Nichols, K.L.; Sullivan, J.E.M.; Eastlack, S.E. 1994. **Xylem embolism in ring-porous, diffuse-porous, and coniferous trees of northern Utah and interior Alaska**. Ecology 75(6) 1736-1752.
- Strati, S.; Patino, S.; Slidders, C.; Cundall, E.P.; Mencuccini, M. 2003. **Development and recovery from winter embolism in silver birch: seasonal patterns and relationships with the phenological cycle in oceanic Scotland**. Tree Physiology (23): 663-673.
- Taylor, F.H. 1956. **Variation in sugar content of maple sap**. Agricultural Experiment Station, Bulletin 587. 3-39.
- Tierney, G.L.; Fahey, T.J.; Groffman, P.M; Hardy, J.P, Fitzhugh, R.D.; Driscoll, C.T.2001. **Soil freezing alters fine root dynamics in a northern hardwood forest**. Biogeochemistry (56): 175-190.
- Tyree, M.T. 1983. **Maple sap uptake, exudation, and pressure changes correlated with freezing exotherms and thawing endotherms**. Plant Physiology (73): 277-285.
- Tyree, M.T. 1995. **The mechanism of maple sap exudation**. In Tree Sap. Eds. M. Terazawa, C.A. McLeod and Y. Tamai. Hokkaido University Press, pp. 37-45.
- Tyree, M.T. and Ewers, F.W. 1991. **The hydraulic architecture of trees and other woody plants**. New Phytologist (119): 345-360.
- Tyree, M.T. and Sperry, J.S. 1989. **Vulnerability of xylem to cavitation and embolism**. Annu. Rev. Plant Physiology and Molecular Biology (40): 19-38.
- Tyree, M.T. and Yang, S. 1992. **Hydraulic conductivity recovery versus water pressure in xylem of *Acer saccharum***. Plant Physiology (100): 669-676.
- Tyree, M.T. and Zimmerman, M.H. 2002. **Xylem structure and the ascent of sap**. 2nd Edition. Springer-Verlag, New York, 250 p.
- Tyree, M.T.; and Cochard, H. 1996. **Summer and winter embolism in oak**. Impact on water relations. Ann Sci For. 53: 173-180.

- Tyree, M.T.; Salleo, S.; Nardini, A.; Assunta Lo Gullo, M.; Mosca, R. 1999. **Refilling of embolized vessels in young stems of laurel. Do we need a new paradigm?** *Plant Physiology* 120 (1): 11-22.
- USDA Forest Service. 2010. **Climate change may impact maple syrup production.** News Release No. 1022. Washington, D.C.
- Vadeboncoeur M.A.; Hamburg, S.P.; Cogbill, C.V.; Sugimura, W.Y. 2012. **A comparison of presettlement and modern forest composition along an elevation gradient in central New Hampshire.** *Canadian Journal of Forest Research*. 42 (1) 190-202.
- Van Doorn, N.S.; Battles, J.J.; Fahey, T.J.; Siccama, T.G.; Schwarz, P.A. 2011. **Links between biomass and tree demography in a northern hardwood forest: a decade of stability and change in Hubbard Brook valley, New Hampshire.** *Canadian Journal of Forest Research* (41): 1369-1379.
- Wiegand, K.M. 1906. **Pressure and flow of sap in the maple.** *The American Naturalist* 40 (474): 409-453.
- Wullschleger, S.D. and King, A.W. 2000. **Radial variation in sap velocity as a function of stem diameter and sapwood thickness in yellow-poplar trees.** *Tree Physiology* (20): 511-518.
- Yanai, R.; Fisk, M.C.; Fahey, T.J.; Cleavitt, N.L.; Park, B.B. 2008. **Identifying roots of northern hardwood species: patterns with diameter and depth.** *Canadian Journal of Forest Research* (38): 2862-2869.
- Zhu, X.B.; Cox, R.M.; Arp, P.A. 2000. **Effects of xylem cavitation and freezing injury on dieback of yellow birch (*Betula alleghaniensis*) in relation to a simulated winter thaw.** *Tree Physiology* (20): 541-547.
- Zhu, X.B.; Cox, R.M.; Bourque, C.-P.A., Arp, P.A. 2002. **Thaw effects on cold-hardiness parameters in yellow birch.** *Canadian Journal of Botany*. (80): 390-398.
- Zhu, X.B.; Cox, R.M.; Meng, F.-R., Arp, P.A. 2001. **Responses of xylem cavitation, freezing injury and shoot dieback to a simulated winter thaw in yellow birch seedlings growing in different nursery culture regimes.** *Forest Ecology and Management* (145): 243-253.
- Zimmerman, M.H. 1983. **Xylem structure and the ascent of sap.** Springer-Verlag, Berlin.

Appendix

Individual DBH (Chapter 1)

YEAR	PLOT	INDIV	DBH	SE	PLOT	INDIV	DBH	SE
2010	KL	1	33.8	2.886798	3L	1	39.4	4.983312
		2	23.5			2	42.2	
		3	25.5			3	23.2	
		4	19.7			4	37.7	
		5	34.3			5	16.9	
	KM	1	26.6	4.494174	3M	1	19.1	7.869879
		2	51.8			2	32.7	
		3	39.4			3	66	
		4	34.8			4	48.8	
		5	28.7			5	38.9	
	KH	1	32.6	2.676079	3H	1	18.6	4.863599
		2	27.1			2	23.2	
		3	23.3			3	31.1	
		4	20.9			4	42.5	
		5	35			5	15.4	
2011	KL	1	30.1	2.168271	3L	1	40.5	5.258749
		2	16.8			2	38.2	
		3	25.7			3	23.7	
		4	22.6					
		5	23.2					
	KM	1	34.7	5.0316	3M	1	30.5	7.012175
		2	44			2	28.5	
		3	25.1			3	65.4	
		4	40.2			4	32.4	
		5	16.5			5	47.9	
	KH	1	33	3.795866	3H	1	27.6	4.66073
		2	47			2	19.5	
		3	23.3			3	23.1	
		4	32.1			4	39.3	
		5	33.4			5	11.1	

Baseline average sap velocities of sugar maple, American beech, and yellow birch at control and calcium addition plots at Bartlett, Jeffers Brook, and Hubbard Brook forests

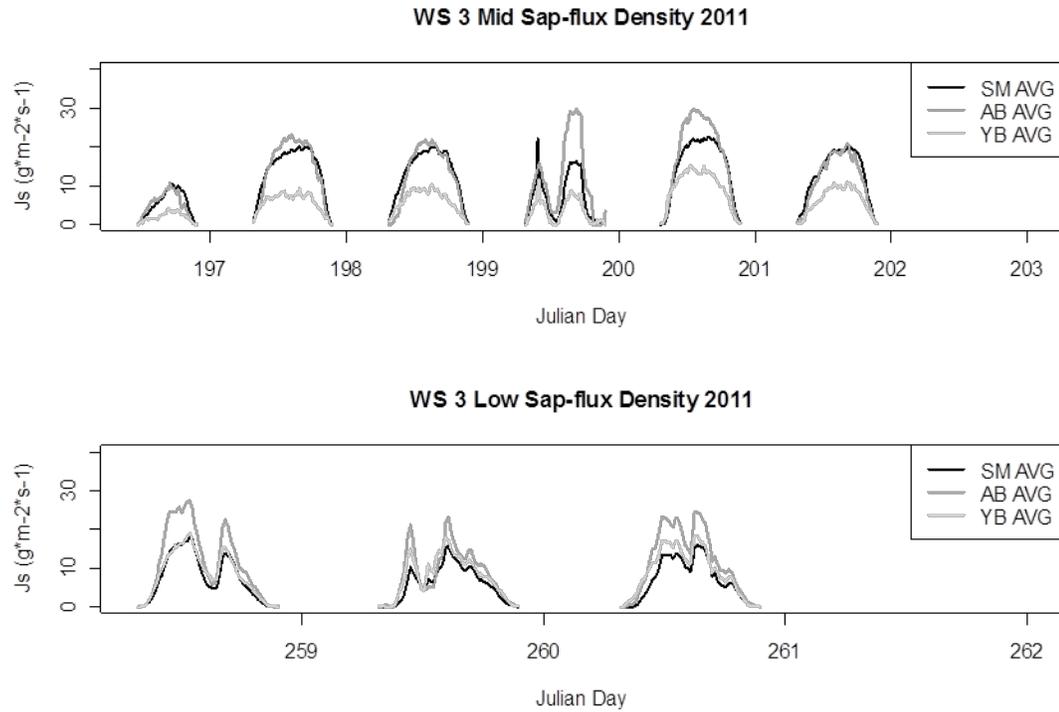


Figure 1: Average post bud-break sap-flux densities in sugar maple ($n=4$), yellow birch ($n=3$), and American beech ($n=1$) for Julian days 196-201 at WS 3 Mid (Top). Average post bud-break sap-flux densities in sugar maple ($n=5$), yellow birch ($n=5$), and American beech ($n=1$) for Julian days 258-260 (Bottom) at the Hubbard Brook Experimental Forest in 2011 at WS 3 Low.

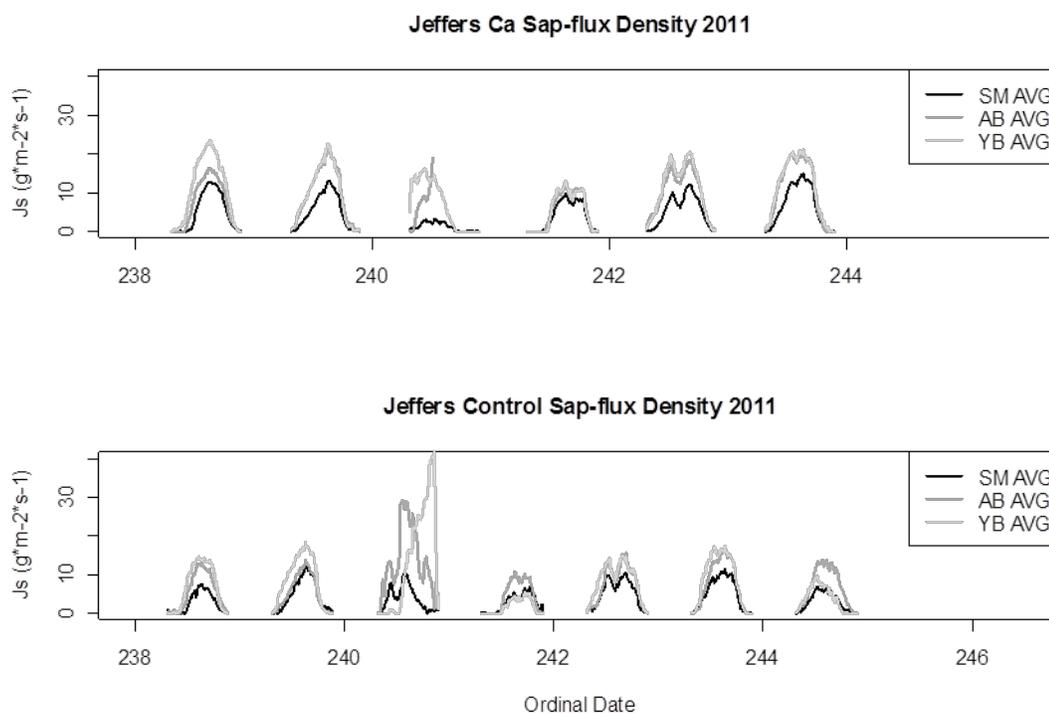


Figure 2: Average post bud-break sap-flux densities in sugar maple ($n=5$), yellow birch ($n=1$), and American beech ($n=1$) for Julian days 238-243 (Top). Average post bud break sap-flux densities in sugar maple ($n=5$), yellow birch ($n=1$), and American beech ($n=1$) for Julian days 238-244 (Bottom) at the Jeffer's Brook Experimental Forest in 2011. Julian day 241 shows the response of tropical storm Irene in 2011.

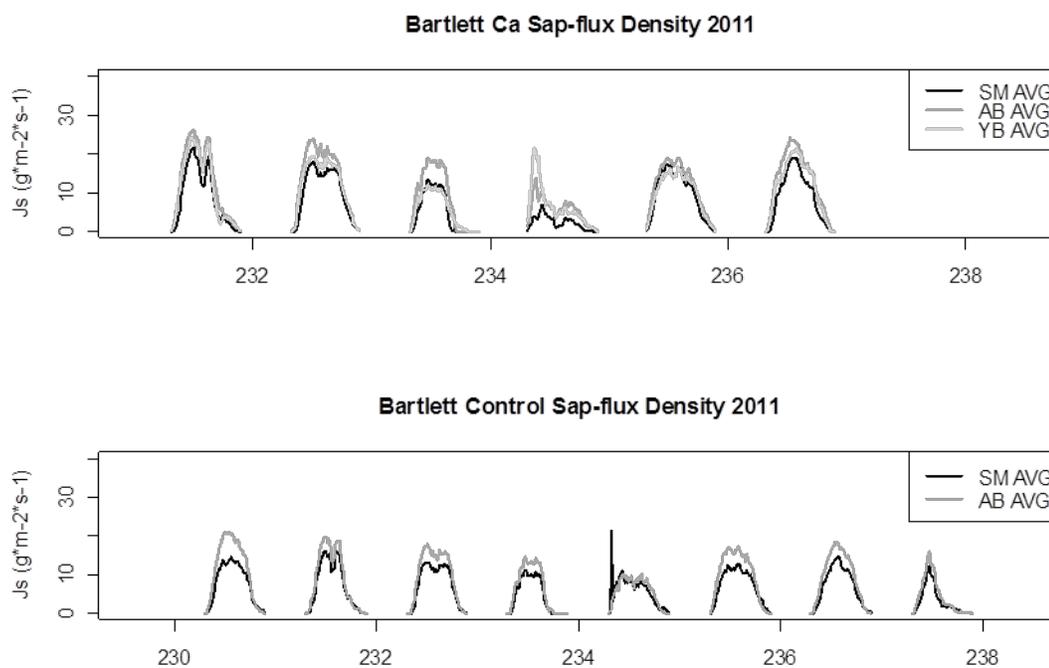


Figure 3: Average post bud-break sap-flux densities in sugar maple ($n=3$), yellow birch ($n=3$), and American beech ($n=3$) for Julian days 231-237 (Top). Average post bud-break sap-flux densities in sugar maple ($n=5$) and American beech ($n=3$) for Julian days 231-237 (Bottom) at the Bartlett Experimental Forest in 2011.