THE WATER USE DYNAMICS OF TEMPERATE PINE PLANTATION FORESTS AND THEIR RESPONSE TO THINNING AND CLIMATE VARIABILITY.

By RACHEL SKUBEL, B.SC.

A Thesis Submitted to the School of Graduate Studies in Partial Fulfillment of the Requirements for the Degree Master of Science

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MASTER OF SCIENCE (2015)  
MCMASTER UNIVERSITY
(EARTH AND ENVIRONMENTAL SCIENCE)  
HAMILTON, ONTARIO

TITLE: The Water Use Dynamics of Temperate Pine Forest Plantations and their Response to Thinning and Climate Variability

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NUMBER OF PAGES: ix, 96
ABSTRACT

Forest plantations have been long-employed to reverse land degradation and support biodiversity, and are now recognized to both take in atmospheric carbon dioxide, reducing the intensity of the greenhouse effect, and moderate local weather. It is important to consider the impact forest aging and management will have on provisioning of these services under climate change and extreme weather events such as drought. This study encompasses a chronosequence of three Eastern White Pine stands planted in 1939, 1974 and 2002, situated in Turkey Point, Ontario, Canada. The oldest forest received two selective thinning treatments, removing 30% of trees, in 1983 and 2012.

Forest water use efficiency (WUE), which represents the amount of gross ecosystem productivity (GEP) per unit of water released through evapotranspiration (E), was compared among the three sites over 2008-2013. The youngest forest’s annual WUE increased over the study period, surpassing that of the older sites by 2013. When bulk surface conductance (Gs), representing gas exchange, was compared across the sites for the same years, the youngest site had the lowest Gs, particularly during drought. Gs at the oldest forest was highest and the most variable. Statistical analysis showed that across all the sites, E was more responsive to air temperature than atmospheric demand, soil moisture, and incident radiation. This study indicated that younger plantations may be more water-conservative during drought, and that air temperature is important to consider in projections of temperate coniferous forests’ carbon and water exchange.

To assess the impact of the 2012 selective thinning on tree-level and ecosystem-level water use at the oldest forest, sapflow velocity (Js), transpiration (Et) and E were compared between the two stands planted in 1939 and 1974, from 2011 to 2013. A relatively severe drought over the 2012 growing season led to a decline in Et at the unthinned site for that year, however the Et decline was more pronounced at the older, thinned site. From 2011 to 2012, Js increased at the thinned site, converse to the unthinned site – wherein Js was low as expected during drought. Hydraulic redistribution and lag time from sapflow at 1.3 m height to canopy evapotranspiration were seemingly unaffected by the thinning, indicating that low-level selective harvesting was not detrimental to the hydrological functionality of the stand, and may have been beneficial in allowing more soil moisture access per tree. As such, the stand may be better positioned to withstand recurrent dry spells resulting from precipitation variability, as predicted with climate change.
ACKNOWLEDGEMENTS

Funding was provided by the Natural Sciences and Engineering Research Council (NSREC), Ontario Ministry of Environment (MOE), Canadian Foundation of Innovation (CFI) and Ontario Research Fund. Support from the Ontario Ministry of Natural Resources (OMNR), Natural Resources Canada (NRCan), Environment Canada (EC), Long Point Region Conservation Authority (LPRCA) and St. Williams Conservation Reserve Community Council is also acknowledged. I am also thankful to Jing Chen’s research group (University of Toronto) for leaf area index measurements, Zoran Nesic (T.A Black’s group at UBC) for his tremendous assistance with instrument design and continuing technical support, and to Steve Williams and Ken Elliott (Ontario Ministry of Natural Resources) for their help with biometric measurements, and providing me with an ecological background of the research sites.

I am immensely grateful to my supervisor Dr. Altaf Arain for providing me with the support and resources to both succeed in my Masters, and develop myself as a researcher and scholar. I would also like to express my gratitude for committee members Dr. Sean Carey and Dr. Mike Waddington.

To the current and past members of the McMaster Hydrometeorology and Climatology Research Group, I am grateful for the support, teaching and guidance so essential to success throughout my degree. I wish to particularly thank Myroslava Khomik for her invaluable contributions to my research projects, and for always encouraging me to achieve ambitious goals. Robin Thorne was vital in field operations and data collection, and Jason Brodeur was both the foundation of data processing and management for our research group, and an ever-helpful resource for any ideas or questions. To Katey Daly, Felix Chan, Sean McKenzie, and Jung Lee, thank you for helping to make the last year of this degree so enjoyable and productive.

I am also thankful for the ongoing support of Mary and James Skubel, and Taylor Reid, throughout all my academic endeavors.
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<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
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<tbody>
<tr>
<td>TPFS</td>
<td>Turkey Point Flux Station</td>
</tr>
<tr>
<td>TP39</td>
<td>Turkey Point research forest planted in 1939</td>
</tr>
<tr>
<td>TP74</td>
<td>Turkey Point research forest planted in 1974</td>
</tr>
<tr>
<td>TP02</td>
<td>Turkey Point research forest planted in 2002</td>
</tr>
<tr>
<td>OMNR</td>
<td>Ontario Ministry of Natural Resources</td>
</tr>
<tr>
<td>IPCC</td>
<td>International panel on climate change</td>
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<tr>
<td>CO$_2$</td>
<td>Carbon dioxide</td>
</tr>
<tr>
<td>Gs</td>
<td>Surface conductance</td>
</tr>
<tr>
<td>EC</td>
<td>Eddy covariance</td>
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<tr>
<td>CPEC</td>
<td>Closed path eddy covariance</td>
</tr>
<tr>
<td>CSI</td>
<td>Campbell Scientific</td>
</tr>
<tr>
<td>BA</td>
<td>Basal area</td>
</tr>
<tr>
<td>LAI</td>
<td>Leaf area index</td>
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<tr>
<td>NPP</td>
<td>Net primary productivity</td>
</tr>
<tr>
<td>GEP</td>
<td>Gross ecosystem productivity</td>
</tr>
<tr>
<td>$E$</td>
<td>Evapotranspiration</td>
</tr>
<tr>
<td>WUE</td>
<td>Water use efficiency</td>
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<tr>
<td>PAR</td>
<td>Photosynthetically active radiation</td>
</tr>
<tr>
<td>Ta</td>
<td>Air temperature</td>
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<tr>
<td>P</td>
<td>Precipitation</td>
</tr>
<tr>
<td>WTD</td>
<td>Water table depth</td>
</tr>
<tr>
<td>REW</td>
<td>Relative extractable water</td>
</tr>
<tr>
<td>$\theta$</td>
<td>Soil volumetric water content</td>
</tr>
<tr>
<td>$\theta_{wp}$</td>
<td>Soil volumetric water content at plant wilting point</td>
</tr>
<tr>
<td>$\theta_{fc}$</td>
<td>Soil volumetric water content at field capacity</td>
</tr>
<tr>
<td>PDSI</td>
<td>Palmer drought severity index</td>
</tr>
<tr>
<td>LE</td>
<td>Latent heat flux</td>
</tr>
<tr>
<td>VPD</td>
<td>Vapor pressure deficit</td>
</tr>
<tr>
<td>u</td>
<td>Wind speed</td>
</tr>
<tr>
<td>ANOVA</td>
<td>One-way analysis of variance</td>
</tr>
<tr>
<td>$J_s$</td>
<td>Sapflow velocity</td>
</tr>
<tr>
<td>$E_t$</td>
<td>Individual tree transpiration</td>
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<tr>
<td>$Et$</td>
<td>Stand transpiration</td>
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<tr>
<td>HR</td>
<td>Hydraulic redistribution</td>
</tr>
<tr>
<td>PCA</td>
<td>Principal component analysis</td>
</tr>
<tr>
<td>SWC</td>
<td>Soil water content (in mm)</td>
</tr>
<tr>
<td>Mg</td>
<td>Magnesium</td>
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</table>
CHAPTER 1: INTRODUCTION

1.1 Rationale and structure of the thesis

As a connection of the carbon, energy and water cycles, forests play an important role in sequestering carbon, maintaining biodiversity, and regulating local climates. Given the potential of current and predicted global forces of change to challenge the functionality of these ecosystems, it is necessary to understand how and why they respond to both environmental variability and management practices.

This thesis encompasses two projects that examined the water dynamics of temperate pine plantations in Turkey Point, Ontario in the context of environmental variability. The first study questions how a forest’s age influences its water use efficiency, with particular reference to climate effects. The second investigates whether a selective thinning treatment affected tree and ecosystem level water use dynamics, with a focus on per-tree transpiration velocity at two adjacent stands.

1.2 The importance of forest ecosystems

Forests provide a vital and unique set of ecosystem services, with knowledge of their importance growing in tandem with that of global environmental change. The long lifespan of trees allows them to sequester considerable quantities of the greenhouse gas carbon dioxide (CO₂) to fuel photosynthesis. This massive intake of CO₂ and complementary production of oxygen through respiration has earned forests the reputation of being the Earth’s lungs (Baldocchi, 1997). Another byproduct of tree respiration is water evaporation; in addition to supplying the water cycle, energy consumed for this process has been found to influence climate at a regional scale.
(Bounoua et al., 2002; Matsumoto et al., 2008). The provisioning of these services is not uniform. For example, a recent study found that old-growth forests had greater weather-moderation capacity than younger and intensively managed stands (Norris et al., 2012).

Worldwide, deforestation for timber and agriculture has led to declines in biodiversity due largely to habitat destruction and fragmentation (Brook et al., 2003; Bradshaw et al., 2009). In the absence of trees’ stabilizing roots, affected areas are often more prone to erosion. Tree removal has led to depleted soil fertility (Merino & Edeso, 1999), and carbon and nitrogen stores (Murty et al., 2002). The rising ubiquity of planted systems to restore degraded landscapes and supplement forestry material (Figure 1) suggests a necessity for their study, especially in light of the unknowns of current environmental change. Previous work has demonstrated how implementing managed plantations can support increases in regional biodiversity (B. A. Haveri & Carey, 2000; Sullivan et al., 2002; Kanowski et al., 2005; Ares et al., 2010; Verschuyl et al., 2011), reduce stream flow (Sahin & Hall, 1996; Brown et al., 2005; van Dijk & Keenan, 2007) and impact the forestry industry (Duncker et al., 2012). At the Turkey Point, Ontario, Canada, plantations in former agricultural fields or heavily deforested lands with varying species, ages, and management strategies provide a unique opportunity for studying energy, water and carbon dynamics in an age-sequence of pine forests, and how they would be affected by future climate change and management activities.
1.3 Climate interactions and management impacts

1.3.1 Past, present and future climatic change

In the context of all known geologic history, current anthropogenically-caused global climate change continues to proceed at an unprecedented rate. The International Panel on Climate Change (IPCC) assessed 1983 to 2012 to be the warmest 30-year period of the last 800, if not 1400 years (IPCC, 2014). Globally, combined air and ocean temperatures were shown to have warmed by 0.65 to 1.06 °C from 1880 to 2012. The IPCC projects that continuing greenhouse gas emissions will lead to pervasive changes in the climate system; the 2081-2100 period is likely to be 2 °C warmer than the 1850-1900 average, with precise estimates dependent on the scale of international actions to control emissions. In southern Ontario, where this study was conducted, projected changes between the 1971-2000 and 2071-2100 periods include summer warming of at least 3-5 °C, winter warming of 4-5 °C, and reductions of summer and winter precipitation by 10 and 20%, respectively. Although the precision of such projections is subject to debate, it is clear that the region will experience considerable climatic change.

1.3.2 Forest/climate interactions

The critical role of forests in cycling carbon has led to a focus on their role in mitigating the extent of temperature rise. Indeed, Baccini et al. (2012) suggest that 6-17% of anthropogenic CO₂ emissions are due to deforestation. Elucidating the net temperature effect of forest removal or planting is a complex exercise involving changes in albedo, surface turbulence, and moisture supply. While carbon sequestration by planted and natural forests can lead to a less intense greenhouse effect and cooler temperature, Bala et al. (2007) showed deforestation to have a net cooling effect. A focal point of this project is the interaction between forest water use dynamics,
carbon intake for growth, and climatic variables. Knowledge gained from investigating these interfaces, and comparing three plantations of different ages, may contribute to an understanding of how changing temperatures and precipitation patterns might affect similar forests throughout their life cycle.

1.3.3 Forest management implications

When considering planted forests, management strategy is important to factor into studies. Such a strategy may include selective thinning, which can increase the commercial value of future harvested timber by encouraging the growth of the most desirable (i.e. larger) trees (Cameron, 2002). Forest thinning impacts can extend to forest ecosystem health. With moderate reductions in a forest’s stem density, the remaining trees have access to more nutrient and water resources (Bréda et al., 1995). Biodiversity of plant and animal communities may rise, if the increase in light reaching the forest floor and resource availability leads to greater habitat complexity (Ares et al., 2010; Haveri and Carey, 2000; Sullivan et al., 2012). This ‘imitation of nature’ management regime parallels the progression of a naturally generated forest, wherein stem density is controlled through interspecies competition and succession stages (Stanturf & Madsen, 2002).

1.4 Forest water use monitoring and applications

1.4.1 Forest Water Balance

The water balance of a forest stand can be summarized by the following equation from Simonin et al. (2007), considering soil water storage (SWS) as the reservoir in flux:

\[ \Delta SWS = P_T - R - D - E \]  
(Equation 1)
Where $P_T$ is throughfall precipitation, $R$ is surface runoff, $D$ is drainage and $E$ is total ecosystem evapotranspiration. Of these components, $P_T$ and $E$ tend to represent the greatest influx and efflux, respectively (cite). $E$ can be further subdivided as follows:

$$E = E_t + E_s + E_i \quad \text{(Equation 2)}$$

Where $E_t$ is water transpired by the trees, $E_s$ is bare soil evaporation and $E_i$ is the evaporation of intercepted water on the canopy and/or litter (Dingman, 2008). Both $SWS$ and $E$ can be monitored at high frequency, along with their controlling meteorological variables, to conduct detailed investigations of forest response to environmental change and management regimes. Vertically stratified networks of soil content reflectometer provide continuous measurements of soil moisture, with high spatial variability generally necessitating several points of measurement for improved accuracy (Brocca et al., 2007). Of the many methods of measuring $E$, including lysimetry, pan evaporation, and automated chambers, the eddy covariance method has emerged in the past two decades as a popular approach (Baldocchi et al., 2001). Eddy covariance (EC) systems measure forest ecosystem fluxes of carbon, water and energy through high frequency sampling. EC systems are mounted on towers extending above the forest canopy, conveniently hosting other instruments to monitor the micrometeorology of the stand. Fluxes are estimated by multiplying above-canopy quantities of water vapor or carbon by vertical variations in wind speed, combined with a canopy storage quantity determined through measurements at lower points on the tower (Baldocchi et al., 1988).

Monitoring of a forests’ $E_t$ is predominantly conducted through the sapflow sensors in a number of trees throughout the stand. This method, pioneered by Granier (1987), relies on a vertical gradient in the temperature of a tree’s stem as water (i.e. the “sap”) moves upwards through it’s
sapwood. This heat flux method has been implemented throughout different species (Wullschleger et al., 2001; Link et al., 2014) and geographical regions (Lagergren & Lindroth, 2002; Cavaleri et al., 2014), and as such can be summarized as a widely accepted estimate of tree sap velocity. The velocity can be up-scaled to individual tree transpiration using parameters of that tree’s sapwood area and total wood area (i.e. the basal area), and then further scaled to stand level by incorporating the stand parameters of basal area (Granier, 1987; McLaren et al., 2008). With these concurrent measurements of total $E$ and $Et$, and variations in $SWS$, much of a stand’s water balance can be monitored at high frequency, with the capacity to be sustained over long-term monitoring projects such as in Turkey Point.

1.4.2 Water use efficiency

In essence, the water use efficiency of a forest is the ratio of its productivity (carbon assimilation for growth) to water expended (Keenan et al., 2010). Several methods exist to obtain this metric, however the two most encountered approaches are 1) isotopic analysis and 2) ecosystem measurements of $E$ or stomatal conductance ($Gs$) and gross productivity. The isotopic approach uses the carbon isotope composition ($\delta^{13}C$) of cellulose samples to estimate intrinsic water use efficiency, or iWUE. One benefit of this method is that researchers can integrate tree ring dating to infer a time sequence of iWUE (i.e. Gagen et al., 2011; Knapp and Soulé, 2011). However, this method is not as accurate as measured quantities of water and carbon exchange, and caution is taken when interpreting results (Knapp & Soulé, 2011). To employ the direct measurement method, EC-measured $E$ and gross ecosystem productivity ($GEP$) can be used via the equation $WUE = \frac{GEP}{E}$ (Beer et al., 2009). When $Gs$ is employed in lieu of $E$, the product of the equation is iWUE, the same leaf-level metric as by the isotopic method. Alternatively, studies
have used biometric-based growth measurements and sapflow-derived $E_t$ (Forrester et al., 2010; Kunert et al., 2012) to calculate WUE.

In general, forest WUE depends upon stand vegetation composition, tree physiology, and meteorology. To consider the controls on forest WUE, potential impacts on both water use and productivity must be considered. Broadly, a tree’s water use is dependent upon soil moisture supply, atmospheric demand and photosynthetic radiation (Lagergren & Lindroth, 2002; Clausnitzer et al., 2011; Link et al., 2014), and at the stand level species composition and total sapwood area are other important factors (Moore et al., 2011; Cavaleri et al., 2014). Meteorological variables influencing tree productivity, and hence carbon assimilation, include air and soil temperature for energetically favorable growing conditions (Keenan et al., 2014) and incident radiation to drive photosynthesis (Medvigy et al., 2010). Looking to the future, recent studies have shown that iWUE and WUE may increase in response to rising atmospheric CO$_2$; this may be the consequence of a fertilization effect, reduction in stomatal aperture and thus water release due to an increase in atmospheric to leaf [CO$_2$], or a combination thereof (Leakey et al., 2009; Gagen et al., 2011; Keenan et al., 2013).

1.4.3 Practical applications of forest water use monitoring

Forest water use studies have an expansive range of uses across policy, water management, industry, and climate modeling. The capacity of forests to retain water is important in light of flood risk in a changing climate, with precipitation patterns projected to shift towards resulting in fewer, more intense rain events (IPCC, 2014). Piao et al. (2007) proposed that along with climate, land use change, such as tropical deforestation, had increased global runoff by
0.08 mm/year during the 20th century; clearly, understanding forest water dynamics’ response to global change is a complex yet vital topic of study.

In the forest industry, WUE findings may help managers understand how climate change might impact profits, or determine which species to plant in order to maximize productivity: in Australia, Forrester et al. (2010) demonstrated that a planted mixture of *Eucalyptus* and *Acacia* had greater biomass production than monocultures of each of the same two species. Conservation authorities may use species’ water use characteristics to plan restoration of degraded landscapes; for example, native trees were shown to be less water intensive than invasive species (Cavaleri et al., 2014).

A third application of the results of forest water use studies is their implementation in global modeling of climate impacts. Knowledge of ecosystem response to environmental change, and differences in such responses between species, geography, and ecosystem structure, can be integrated into existing datasets to parameterize and validate projections of regional temperature and precipitation, runoff, and atmospheric CO2 (Mango et al., 2011; Samuelsson et al., 2011). These projections can assist policy makers make decisions with respect to drought, climate mitigation, and the many aspects of watershed management.
CHAPTER 2: AGE EFFECTS ON FOREST WATER DYNAMICS

2.1 Contribution to the manuscript

The candidate performed collection and processing of field data from 2013, all statistical analyses, construction of all figures, and wrote the majority of text. The manuscript was accepted with revisions at Hydrological Processes (HYP-14-0862).
Age Effects on the Water Use Efficiency and Water Balance of Temperate Pine Plantation Forests

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 Submitted: October 30th 2014
 Decision received: March 12th 2015

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Key Words: Evapotranspiration; Surface Conductance; Water Use Efficiency; Eddy Covariance; Pinus strobes L.; Coniferous Forest
Abstract

This study analyzed age-related water use dynamics across three temperate conifer forest plantations (aged 11-, 39-, and 74-years old, as of 2013, henceforth referred to as TP02, TP74, and TP39, where the last two digits represent the year of planting) in Southern Ontario, Canada from 2008 to 2013. Eddy covariance-measured mean evapotranspiration over the growing season (April-October) was 438 ± 19, 392 ± 19 and 323 ± 25 mm at TP39, TP74 and TP02 respectively. Daytime bulk surface conductance was highest and most variable at the TP39 site (8.5 ± 4.0 mm s⁻¹), followed by the TP74 (7.0 ± 2.8 mm s⁻¹) and TP02 (5.4 ± 2.5 mm s⁻¹) sites.

Evapotranspiration at all the forests was sensitive to air temperature and also tended to decrease with increasing atmospheric dryness. The youngest forest’s evapotranspiration was most conservative, which led to an increase in water use efficiency throughout the study period, in particular during drought events. The oldest forest was the least restrictive in its water use during drought, which led to lower water use efficiency during such events as compared to the younger forests. The oldest forest was thinned in early 2012, when about 1/3 of trees were commercially harvested. No significant change in evapotranspiration or water use efficiency was observed at this site following thinning, however daytime bulk surface conductance declined. Our results suggested that changes in stand structure with forest ageing, such as reduction in stem density and increase in sapwood area, were responsible for differences in soil water demand during drought and non-drought periods, leading to differences in forest water use. Hence, forest age, due to its structural implications, is an important control on the stand-level water use efficiency and forests’ response to drought events. Our study suggested that younger forests may be best suited to maximize growth and carbon uptake efficiency under rising air temperatures and increasing precipitation variability as predicted by regional climate models for Southern Ontario.
Introduction

Forests are a significant sink for anthropogenic CO$_2$ emissions that otherwise would intensify the greenhouse effect and further warm the Earth (Stephenson et al., 2014). Globally, forests absorb 4.0 Pg C yr$^{-1}$ on average, which accounts for nearly half of the annual CO$_2$ emissions; however, their potential as a sink for atmospheric CO$_2$ may change in the future due to a changing climate (Keenan et al., 2014). Global mean temperatures are projected to rise by at least 2 °C by 2100 (IPCC, 2013), but this warming will not be spatially uniform. Southeastern Canada may warm by 3 to 5 °C (Colombo et al., 2007). In addition to warming, extreme weather events, such as drought, flooding, and intense heat waves are projected to become more frequent and severe (Colombo et al., 2007; IPCC, 2013). Many studies have discussed challenges for forest growth and health due to extreme weather events, in particular droughts (Chaves et al., 2003; Bréda et al., 2006; Allen et al., 2010; Hasselquist et al., 2010; MacKay et al., 2012; Eamus et al., 2013).

The severity of these environmental impacts depend on a number of factors that influence forest productivity and water use such as stand age, tree density, sapwood area, amount of foliage and root network (Coomes & Grubb, 2000; Schenk & Jackson, 2002, 2005; Sperry et al., 2002; Chaves et al., 2003; Bréda et al., 2006); soil characteristics (Bristow et al., 1984; Schenk & Jackson, 2002); water table depth (Soylu et al., 2014) and chemical factors such as aquaporin content and abscisic acid concentration (Jackson et al., 2000; Chaves et al., 2003).

The response of forest ecosystems to climate change and extreme weather events may change over time because of the numerous interacting factors that transform as trees age and forests mature. For example, as forests grow older, more resources are allocated towards growing stems, branches and foliage and developing a larger root system to support rising water demand (Sperry
et al., 2002; Claus & George, 2005; Peichl & Arain, 2006). Older forests’ root networks may be able to sustain access to water during dry periods and be more resilient to droughts as compared to younger stands. It is important to understand age-related differences in forest carbon and water cycles, especially in light of climate change and the associated changes in extreme weather events. Previous work has found differences in water dynamics between older and younger stands. For example, Shwartz et al. (2004), found that the water flux of the oldest of a three-stand ponderosa pine chronosequence near Sisters, Oregon (USA) was least affected by climatic variability, including drought events. Similarly, Jassal et al. (2009) found that the oldest stand of their three different-aged boreal Douglas-fir forests in British Columbia, Canada had the least variability in surface conductance (Gs). Ryan et al. (2000) compared the water fluxes of 40- and 290-year old ponderosa pine stands in Black Butte, Oregon (USA), and found that the younger stand had greater transpiration and surface conductance. However, studies examining water balances and responses of different-age forests to environmental changes are lacking in temperate North American areas. Many forests in the Southern Ontario region are re-establishing because of re-growth on abandoned agricultural lands or plantations. These different-age forests are a large sink of carbon (Goodale et al., 2002; Woodbury et al., 2007). It is important to investigate how the growth patterns and water balances of different-age forests in this region would be affected by future climate change and extreme weather events.

When studying environmental impacts on forest ecosystems, it is important to consider both carbon and water fluxes along with environmental controls, because the two are tightly coupled due to CO₂ and water vapour exchange through plant stomata. Often this coupling is described by water use efficiency (WUE), which refers to the amount of carbon fixed by plant per water
lost through their stomata. Because carbon and water fluxes measured by the eddy covariance (EC) technique provide data for the whole ecosystem, a stand-level WUE can be derived as the ratio of gross ecosystem productivity (GEP) to evapotranspiration ($E$), expressed in units of g C per kg water. This ecosystem or stand-level WUE, hereafter referred to as WUE, can be used to understand how effectively a forest responds to environmental changes such as warming, drought and increased CO$_2$ concentration (Forrester et al., 2010; Mu et al., 2011; Brümmer et al., 2012).

The objectives of this study were (1) to assess the stand age effect on evapotranspiration and water use efficiency in an age-sequence of temperate pine forests in eastern North America, and (2) to examine the sensitivity of their water balance, WUE and bulk surface conductance to environmental changes and extreme weather events.

**Methods**

**Study site description**

This study was conducted at the Turkey Point Flux station (TPFS), near Turkey Point Provincial Park on the northern shore of Lake Erie in Southern Ontario, Canada. The study sites included three different-age eastern White Pine (*Pinus Strobus* L.) forests, which were planted in 1939 (TP39), 1974 (TP74) and 2002 (TP02) to either stabilize sandy soils (TP39 and TP74) or to afforest abandoned agricultural land (TP02). All three sites are located within 20 km of each other. They are situated upon an extensive aeolian sandy plain (Barnett, 1998), whereupon topography is slightly undulating. For all sites, the soil is Brunisolic Gray Brown Luvisol (following the Canadian Soil Classification system) and composed of ~98% sand. The soils are
well drained with a low to moderate water holding capacity. The TP39 site was thinned in early 2012, when about 1/3 of trees were commercially harvested (Kula, 2014). Site characteristics and biometric parameters for each site are given in Table 1 and 2, respectively. In the absence of leaf area measurements at the young TP02 stand, reflected PAR is shown to approximate canopy development throughout the 6-year study period (Figure 1). Over this period, a decline in reflected PAR at this site was apparent as the canopy started to close, particularly in winter, as expanding biomass gradually decreased the proportion of snow- to tree-covered area.

The climate in the Turkey Point region is cool-temperate with a 30-year mean annual temperature of 8.0 °C, and mean annual precipitation of 1036 mm (based on 1980-2010 Environment Canada weather data for Delhi, ON, which is about 25 km northwest of the TPFS sites). Approximately 13% of precipitation falls as snow. This study was conducted for the 2008-2013 period, when continuous closed-path eddy covariance flux data was available at all three sites. The period spanning from April 1 to October 31 was used as the growing season for this study, based on MODIS/Terra Vegetation Indices (16-Day L3 Global 250m SIN Grid) for 2008-2013, which show April and October as the predominant months of acceleration and deceleration of growth, respectively.

**Flux, meteorological and ancillary measurements**

Water, carbon and energy exchange were continuously measured using three closed-path eddy covariance (CPEC) systems. Turbulent flux measurements were made at 20 Hz above the canopies at 28, 20 and 5-6 m heights at TP39, TP74 and TP02, respectively, on top of scaffolding towers (the instrument was moved from a height of 5 to 6 m at TP02 in 2009 to
account for forest growth). Based on methodology outlined by Baldocchi et al. (1988), above canopy fluxes of carbon and water were calculated following the equation:

\[ F = \overline{w'c'} \]

Where \( F \) refers to the flux of carbon or water, \( w' \) to the covariance of vertical wind speed, measured by 3D sonic anemometers (CSAT3, Campbell Scientific Inc. (CSI)), and \( c' \) to \( \text{CO}_2 \) or water vapour concentration, measured by an infrared gas analyzers (IRGA, Li-7000, LI-COR Inc.). To account for \( \text{CO}_2 \) storage in the air column below the eddy covariance (EC) sensors, a storage correction (\( \Delta S \)) was applied at TP39 and TP74 sites by estimating changes in \( \text{CO}_2 \) concentrations every half-hour following Barr et al. (2004). \( \text{CO}_2 \) concentration at the top of tower were measured by EC IRGAs, while \( \text{CO}_2 \) concentrations below the EC sensors were measured 14m and 10 m heights at TP39 and TP74 sites, respectively, using economical IRGAs (model LI-820/Li-800, LI-COR Inc.). Half-hourly NEP (\( \text{NEE}; \text{net ecosystem } \text{CO}_2 \text{ exchange}; \mu\text{mol m}^{-2} \text{s}^{-1} \)) was calculated by adding \( \text{CO}_2 \) flux \( F_c \) and the rate of \( \text{CO}_2 \) storage change in the air column below the EC sensors (i.e. \( \text{NEP} = F_c + \Delta S \)). At night, when there was no photosynthesis, NEP was assumed to represent ecosystem respiration (R). Water vapour flux was calculated as latent heat flux (\( \text{LE}; \text{W m}^{-2} \)), which was also represented in mass units as \( E \) (kg m\(^{-2}\) h-hour\(^{-1}\) or mm h-hour\(^{-1}\)).

Climate variables were also measured at the three sites, including air temperature (\( \text{Ta} \)) and relative humidity (HMP45C, CSI), wind speed and direction (5103L, RM Young Inc.), net radiation (NR-Lite, Kipp and Zonen Inc.), incoming and outgoing components of shortwave and longwave radiation (TP39 site only; CNR1, Kipp and Zonen Inc.) and incident and reflected photosynthetically active radiation (PAR; LI-200S, LI-COR Inc.). Precipitation (\( P \)) was
measured in an open area 2 km northeast of TP39, using a weighed accumulation rain gauge (T200B, Geonor Inc.) and a complimentary tipping bucket rain gauge (TE525, Texas Inst.). Soil water content and soil temperature were measured at depths of 5, 10, 20, 50, and 100 cm, at two different locations at each site using water content reflectometers (model CS615, Campbell Scientific Inc., CSI) and soil temperature probes (model 107B, CSI), respectively.

All flux, meteorological and soil data were averaged and saved at half hourly intervals. Further details of closed-path eddy covariance systems and meteorological and soil measurements are described in Peichl et al. (2010) and Arain and Restrepo-Coupe (2005).

**Soil Water Stress and Bulk Surface Conductance**

The soil moisture measurements were integrated, using depth-weighted averaging, across two depths to estimate soil water content in shallow (0-25 cm, using the 5, 10, and 20 cm probes) and deeper (45-105 cm, using the 50 and 100 cm probes) soil layers. These depth categories were chosen because a previous study showed that most coarse and fine roots at the TPFS sites were in the 0-35 cm soil layer (Peichl & Arain, 2007). To assess site-scale soil water content in a way that was physiologically relevant, we used relative extractable water (REW) as suggested by Black (1979). REW expresses the amount of soil water available for plant use as a proportion of the maximum possible extractable water for the site. This approach helps to evaluate the response of forest ecosystems to water deficit (Granier et al., 1999, 2007; Collet et al., 2002; Pataki & Oren, 2003; Maseyk et al., 2008; MacKay et al., 2012). REW was calculated as:

\[
REW = \frac{\theta - \theta_{wp}}{\theta_{fc} - \theta_{wp}}
\]
Where $\theta$ is the measured soil volumetric water content in $\text{m}^3\text{m}^{-3}$, $\theta_{wp}$ is the soil volumetric water content at plant wilting point (0.01 $\text{m}^3\text{m}^{-3}$), and $\theta_c$ is the volumetric water content at field capacity (0.16 $\text{m}^3\text{m}^{-3}$). These wilting point and field capacity values were estimated from long term soil moisture data for these sites by Peichl et al. (2010). Several past studies have observed responses of forest ecosystems to water stress, such as stomatal closure, when a REW threshold of 0.4 is reached (Bréda et al., 1995; Granier et al., 1999, 2007; Davi et al., 2006; Maseyk et al., 2008). In our study, REW values were used to directly infer the soil water availability or water stress conditions at the site level, confirm drought onset (when REW<0.4) and compare interannual soil moisture trends among the three study sites.

In addition, a Palmer drought severity index (PDSI) was calculated following Palmer (1965) using thirty-six years (1977-2012) of air temperature and precipitation data from the Environment Canada weather station at Delhi, Ontario. The PDSI is an ecosystem-scale meteorological drought index with the advantage of calibration using long-term norms (Alley, 1984; Karl, 1986; Heddinghaus et al., 1991). The PDSI has been widely employed to monitor current and historical drought patterns in North America (Stahle et al., 2000; Cook et al., 2004) and South America (Scian, B., Donnari, 1997), Europe (Briffa et al., 1994; Jones et al., 1996) and Asia (Li et al., 2007). It has been used to study interactions between surface temperature change, soil moisture, and drought (Dai et al., 2004). In our study, PDSI values were used to distinguish monthly water supply relative to historical or normal water stress conditions in the region.
Bulk surface conductance (Gs) is an ecosystem-scale measure used to monitor the physiological responses of forest ecosystems to environmental changes (Anthoni et al., 1999; Wullschleger et al., 2000). We calculated half-hourly values of Gs (mm s\(^{-1}\)) using the inverted Penman-Monteith equation (Blanken et al., 1997):

\[
\frac{1}{G_s} = \frac{\rho c_p}{\gamma} \frac{VPD}{LE} + \left[ \frac{(S)}{\gamma} B_r - 1 \right] \frac{1}{g_a}
\]

Where \(\rho\) is air density (kg m\(^{-3}\)), \(c_p\) is the specific heat of air (J kg K\(^{-1}\)), \(s\) is the change of saturation vapor pressure with temperature (J kg K\(^{-1}\)), \(\gamma\) is the psychrometric constant (kPa K\(^{-1}\)), LE is latent heat flux (W m\(^{-2}\)), Br is the Bowen ratio (sensible heat/latent heat), VPD is vapour pressure deficit (kPa) and \(g_a\) is the aerodynamic conductance (m s\(^{-1}\)) of the air layer between the canopy and the height of flux measurement, calculated using direct measurements of friction velocity (u*) by eddy covariance as: \(g_a = u^{*2}/u\), where u is wind speed (m s\(^{-1}\)). Daytime dry foliage Gs values were calculated by eliminating those half-hourly Gs values when incident PAR was less than 200 µmol m\(^{-2}\)s\(^{-1}\) and when precipitation was recorded.

**Data Analysis, Quality Control and Gap-filling**

Data filtering, cleaning and gap-filling were performed using, following protocols designed by the Fluxnet Canada Research Network and Brodeur (2014). Meteorological and flux data were quality controlled for inaccurate and unrepresentative data, first using set thresholds for data inclusion, then with an interactive tool to visually identify and remove erroneous points. To identify and remove remaining outlying flux data points, a program based on the algorithm outlined by Papale et al. (2006) was employed. For each half-hourly measurement, a ‘flux footprint’ was calculated following Klujn et al. (2003), wherein wind velocity along three dimensions was integrated to yield a one-dimensional estimation of cumulative flux contribution.
(Brodeur, 2014). When a half-hour period of data coincided with a footprint extending outside of pre-defined site boundaries, these fluxes were eliminated. To further remove unrepresentative measurements, a friction velocity (\(u^*\)) threshold of 0.5 was applied, in accordance with previous studies at the TPFS sites (Restrepo & Arain, 2005; Peichl et al., 2010). Gaps in carbon fluxes were filled based on a non-linear regression method introduced by Richardson et al. (2007) and adapted for the Turkey Points sites (Peichl et al., 2010; Brodeur, 2014), wherein R was modelled using established relationships with soil moisture and temperature. GEP was then calculated as modeled R plus NEP. Gaps in LE were filled using a neural network tool, with LE of previous years and meteorological data from the same year used for training. Meteorological data was filled through cross-referencing with the same variables’ measurements at the other sites.

In order to find the most influential environmental controls on half-hourly and daily E, a multivariate regression model was fit to the data using incident PAR, REW (0-25cm), Ta and VPD as explanatory variables. To capture peak daytime variability, the analysis was restricted to those half-hours where incident PAR was greater than 1000 \(\mu\text{mol} \text{ m}^{-2} \text{ s}^{-1}\). Variables included in the resultant models were significant at \(\alpha <0.05\), based on a t-test and a one-way analysis of variance (ANOVA). The fit of the model was assessed using residual analysis and the coefficient of variation \(r^2\). To determine the relative explanatory power of variables in the model, a residual method suggested by Lindeman et al. (1980) was followed, in which a variable’s contribution to model \(r^2\) is determined through finding the difference in fit between the model with all variables, and the model without the given variable, then expressing this residual as a percentage of model \(r^2\). All data processing and statistical analysis was done using Matlab software (The Mathworks Inc.).
Results

*Climate and Hydrologic Trends*

Seasonal and annual cumulative dynamics of P are shown in Figure 2a and Table 3. In general, P events tended to be frequent and large in early spring (March to May) then declined during the summer months, and ascended in late summer (August to September). Two extreme P months of 156 mm and 224 mm occurred in June of 2010 and 2013, respectively. The highest annual P was observed in 2011 and 2013 and the lowest P was recorded in 2010, driven by dry conditions earlier in the year (Table 3). Although annual P in 2012 was similar to the 30-year normal value of 1036 mm for the Turkey Point region, the seasonal cycle of PDSI indicated that 2012 was the most notably dry year, as shown by negative values through the year, reaching a peak value of -2.5 in July (Fig. 2b). Ta generally reached a peak in July-August (Fig. 2a). The winter antecedent to the 2012 growing season was relatively warm when compared to the rest of the years, tending to range from -7.5 to 9.2 °C, versus the 6-year norm of -12.4 ± 3.1 to 7.6 ± 1.3 °C. Vapor pressure deficit (VPD) was similar at TP02 and TP74 throughout the study period, while TP39 was lowest from 2008-2011, yet similar to the other two sites in 2012-2013 (Fig. 2.2c). This relative increase in VPD at the oldest site followed the thinning event of February to March 2012, which resulted in a more open canopy that coincided with decreased RH (not shown). Increases in VPD generally coincided with declines in PDSI; for example, the dry conditions of the 2012 growing season are clearly reflected in its sustained high monthly VPD from June through August
Soil moisture showed similar trends across all three sites in terms of the timing of increases, decreases, and sustained lows. REW in the shallow (0-25 cm) soil layer was fairly consistent between the three sites, approaching the 0.4 drought threshold at least once during each growing season (Fig. 2.2d). For the deeper (45-105 cm) soil layer, REW was more distinct between sites (Fig. 2.2e). TP02 had the highest REW values the majority of the time, likely due to the site’s higher water table (1-2 m versus 6-7m at TP39 and TP74), while TP74 consistently had the lowest REW values for 45-105 cm soil layer.

**Evapotranspiration**

E measured by the eddy covariance system followed a similar annual pattern at all three age-sequence sites during most years. The two oldest sites (TP39 and TP74) were characterized by similar annual E totals, ranging from 447 to 514 mm over the study period (Table 2.4, Figure 2.3a-b). Annual E at the youngest site (TP02) ranged from 350 to 408 mm over the six study years (Table 2.4, Figure 2.3c). The two older sites had the greater mean growing season E totals as well, at 438 ± 19 mm (TP39) and 392 ± 21 mm (TP74) compared to 328 ± 25 mm at TP02 (Table 2.4). Seasonal dynamics of E variations from their 6-year mean values are shown in Figure 2.3 d-f. These variations were more pronounced at two older sites, except in 2010 when total annual E at the youngest site exceeded the mean by 44 mm. No major decline in E was observed at the TP39 site during the post-thinning period in 2012. In all years, E at TP39 was either larger or similar to E at TP74 (Table 2.3). The P-E balance showed pronounced mid-growing season declines only at TP39 and TP74 (Fig. 2.3g-h). 2010 and 2012 had notably less difference between P and E when compared with other years, however, P exceeded E in all years by at least 382 mm (TP39 in 2010). Lows in P-E and PDSI values over the study period
indicated drought recurrences in the middle of the growing season at all three forest sites, except in 2013. However, at the young TP02 site, a P-E balance with the least pronounced mid-growing season lows (Figure 2.2i), as well as relatively high 45-105 cm REW, indicated less severe restrictions on water availability.

**Surface Conductance**

Overall, the TP39 site had the greatest daily mean daytime (PAR > 200 µmol m$^{-2}$ s$^{-1}$) values of \((8.5 \pm 4.0 \text{ mm s}^{-1})\), followed by the TP74 \((7.0 \pm 2.8 \text{ mm s}^{-1})\) and TP02 \((5.4 \pm 2.5 \text{ mm s}^{-1})\) sites. Compared with values from the pre-thinning period (2008-2011), a t-test showed that mean daily daytime Gs in the post-thinning period (2012-2013) was significantly lower at the thinned TP39 site \((p < 0.001)\), higher at the un-thinned TP74 site \((p = 0.01)\), and consistent at the young un-thinned TP02 site \((p = 0.06)\). The daily courses of half-hourly Gs and VPD for two select days - one having wet and the other having dry soil conditions - at all three sites are shown in Figure 2.4. Daily mean incident PAR was comparable, being 658 and 624 µmol m$^{-2}$s$^{-1}$ on the dry and wet days, respectively. Gs during dry conditions was suppressed at all sites, and showed little variability throughout the day. On both days, all sites showed a general increase in VPD throughout the day until declining around 19:00. Gs decreased with increasing afternoon VPD, with the highest Gs occurring on the day with wet soil conditions, at VPD values between roughly 1.0 to 1.5 kPa for all three sites.

**Water Use Efficiency**

The WUE of the oldest forest was most consistent among years, whereas TP02 and TP74 reached particularly low (2008) and high (2013 and 2010, respectively) annual values (Table
2.4). The relationship between all sites’ growing season $E$ and GEP during the study period was moderate yet significant ($r^2 = 0.24$, $\alpha < 0.05$). Mean growing season WUE was similar between the middle-aged TP74 site (3.85±0.40 g C m$^{-2}$ kg H$_2$O$^{-1}$) and the young TP02 site (3.89 ± 0.68 g C m$^{-2}$ kg H$_2$O$^{-1}$), and lowest at TP39 (3.22±0.08 g C m$^{-2}$ kg H$_2$O$^{-1}$). Annual WUE was most consistent at TP39 (coefficient of variation, CV, of 3.6%), while TP74 and TP02 were more variable (CV = 12.4% and 20.7%, respectively). In the last three years of the study, the young TP02 site’s WUE surpassed that of TP74 at both the annual and growing season scale, due to increased GEP and consistent total $E$.

Considering both Gs and WUE values, the oldest site was the least water-conservative, and most consistent on an inter-annual basis. The youngest site was the most dynamic in terms of WUE, and displayed the most dramatic increase in WUE throughout the study period as the forest grew.

**Environmental Controls on Water Dynamics**

We performed statistical analyses on stand-level water fluxes at half-hourly and daily time scales. The contribution of parameters to model $r^2$, estimated following Lindeman et al. (1980) did not fully illustrate relative explanatory power of the parameters. Daily and half-hourly $E$ residuals had approximately normal distribution at all three sites. Overall, model explanatory power was highest at TP02, and for all sites the daily model had higher $r^2$ than the half-hourly model (Table 2.5). Stand-level $E$ showed similar results across all the sites, with Ta explaining most variability at both time-scales. In the daily models, PAR was ranked next in explanatory power at TP39 and TP74, although at TP02 REW at 0-25 cm explained slightly more variability. Notably, TP02 was the only stand in which REW appeared to influence the model at the daily scale, while in the half-hourly models all sites included REW as the second most influential
variable. VPD had a significant negative effect on $E$ at all stands and timescales (Table 2.5), with the exception of the model of daily $E$ at TP74. To further examine the interaction between climate and water use, the relationship of total daily $E$ and GEP with mean daily $Ta$ was examined at each age-sequence site (Figure 2.6). All sites showed a similar increase in $E$ and GEP with rising $Ta$; the linear relationship was strongest at TP39 ($r = 0.56$ and $0.69$, respectively, $\alpha <0.001$), followed by TP74 ($r = 0.45$ and $0.64$, $\alpha <0.001$) and TP02 ($r = 0.40$ and $0.57$, $\alpha <0.001$).

**Discussion**

*Age Effects on Surface Conductance and Water Use Efficiency*

The $Gs$ of our plantation forests tended to exceed that measured in other forests in the literature, which could have been due to a combination of climatic and species differences. For example, Jassal *et al.* (2009) found mean daytime dry-foliage canopy conductance values of 5.3, 2.8 to 4.1, and 0.5 to 4.1 mm s$^{-1}$ in an age-sequence of Douglas Fir forests planted in 1949, 1988, and 2000, respectively, in Vancouver Island, British Columbia, Canada. Wullschleger *et al.* (2000) found daily mean $Gs$ values ranging from 1.4 to 6.7 mm s$^{-1}$ in an Oak forest in Eastern Tennessee, United States. Leaf area at the two oldest Douglas fir forests (5.0-7.3 m$^2$m$^{-2}$), and at the Oak forest, (6.2 m$^2$m$^{-2}$) was similar to our mature stands (5.3-8.5 m$^2$m$^{-2}$), however climatic differences such as lower growing season rainfall at the Douglas fir sites (< 50 mm from July to September, versus 367 ± 36mm at our sites) and lower summer temperatures ($Ta$ of 15-18 °C from June to July versus 17-21 °C at our sites) may have contributed to their relatively lower $Gs$ values. Contrary to our findings, Ryan *et al.* (2000) and Ewers *et al.* (2005) found that shorter trees or younger forests have the highest stomatal conductance when compared with taller trees.
or older stands. Ryan et al. further suggested that hydraulic limitations of taller trees may lead to lower leaf-level conductance. Although leaf-level conductance was not directly tested in the present study, our finding of increasing Gs with forest age and tree height suggested hydraulic limitation did not affect Gs at our sites. This may be due to differential species composition among the stands. Our oldest TP39 stand had the greatest abundance of emerging understory deciduous species (Table 1; White, 2009). Higher Gs values associated with deciduous species as reported by Ewers et al. (2005) and Wullschleger et al. (2000) may have contributed to the high Gs value of this site. Furthermore, our oldest forest showed the strongest correlation between GEP and Ta (Figure 2.6). Understory deciduous trees species’ ability to take greater advantage of increased Ta for productivity compared to the coniferous pine species may have contributed to this relationship.

A notable trend in WUE was that of the youngest forest’s continual increase with age over the course of the study, overtaking the mid-aged TP74 stand in 2011. Although LAI was not measured at this site, decreasing reflected PAR (Figure 2.1) and increases in measured basal area, and thus sapwood area, of the stand (Table 3; Kula, 2014) suggested that canopy cover and water-conducting xylem volume consistently rose over the study period, which allowed an increase in photosynthetic capacity. Water use in this stand did not increase at the same rate as GEP, which explained the gradual increase in observed WUE. This may have been due to a combination of two factors. Firstly, as a consequence of the TP02 site’s open canopy, which would accommodate soil evaporation to complement transpiration. Although total annual $E$ was consistent among years, partitioning between soil evaporation and transpiration shifted over time, with transpiration increasing along with canopy cover and sapwood area. Secondly, a
younger forest’s root system is composed of smaller diameter and shallow roots than older sites, making it more prone to water stress during dry conditions (Sperry & Ikeda, 1997).

Overall, the youngest forest’s tendency towards low water use served to maximize WUE across all moisture regimes. Consistent year-to-year WUE (Table 4) also showed that the older forests were able to tolerate drought conditions.

**Thinning Impact on Water Use Efficiency**

The two older stands had almost-closed canopies, with very little change in LAI over the study period, except at TP39 where LAI was reduced from 8.5 to 5.3 m$^3$m$^{-3}$ in early 2012 due to selective thinning. Despite this large decrease in LAI, the basal area of TP39 was only reduced to 36.0 from 40.9 m$^2$ha$^{-1}$ (Table 1 and Kula 2014). This disproportionality was likely a result of the foresters’ preferential selection of smaller trees for removal, so that the good-quality legacy trees remained (Kula, 2014). No significant change in monthly WUE was observed at this site during the post-thinning year of 2012 (t-test, p = 0.53), although total growing season $E$ increased from 436 to 447 mm from 2011 to 2012, while total GEP increased slightly, from 1357 to 1456 g C. This lack of change in WUE with thinning may have been due to the rapid growth of ground and understory species following greater canopy openness, which would provide another source of transpiration and carbon uptake. Previous studies have shown the importance of climate in determining forest response to thinning (e.g. Saunders *et al.*, 2012). At our sites, the growing season drought in 2012 may have contributed to the TP39 stand’s subdued WUE response to thinning. Similar to our study, Simonin *et al.* (2007) monitored forest response to a thinning treatment that coincided with severe drought by comparing a thinned plot with an un-thinned
control plot. While there was no thinning effect upon their WUE, the authors found that there was a decline in total evapotranspiration. Understory evaporation had increased, partially compensating for the decline in tree transpiration resulting from basal area reduction. At our TP39 site, the drought conditions of 2012 and greater canopy openness due to tree removal may have facilitated understory E, thus leading to a similar stand E when compared to TP74 despite decreased tree transpiration at the oldest stand. With respect to productivity, Saunders et al. (2012) found no significant changes in net primary productivity (NPP) or GEP following thinning, which was attributed to a compensatory photosynthesis response by the remaining trees facilitated by increase in temperature and incident PAR relative to the pre-thinning years. Further explaining such stasis in net productivity, Campbell et al. (2009) also showed that rapid understory growth countered an expected decrease in ecosystem NPP due to thinning. At our TP39 site, a proportional change in White Pine transpiration and photosynthesis due to a decrease in LAI, and an increase in understory species’ transpiration and productivity, likely contributed to the lack of observed change in WUE with thinning.

**Implications of Soil Water Access for Carbon and Water Exchanges**

Our youngest TP02 site had the lowest E during drought, which may be attributed to its shallow roots, lower sapwood area and canopy extent, and thus lesser potential for E. This low ecosystem water use during dry periods resulted in pronounced peaks in WUE, such as during the 2012 drought. Conservative water consumption at TP02 appeared to benefit the site throughout the study period, enabling a continual increase in growth and hence WUE over successive growing seasons. For example, between 2008 and 2013, growing season GEP increased by 456 g C, while E varied by 77 mm over this period (Table 4). The mid-aged TP74 stand showed similar monthly
peaks in WUE, coincident with declines in E, particularly during the late growing season. The consistently lower REW at this stand, likely tied to its high stem density (Table 3), may have contributed to a stronger water conservation response, and thus the lower E and Gs, relative to the oldest stand. In a similar study that examined the impacts of stand structure on E and GEP (hence WUE) of a Douglas fir age-sequence, Jassal et al. (2009) followed changes in Gs in response to environmental variables. Similar to our study, Jassal et al. observed that WUE had the greatest variability at their younger site, which was attributed to it having the most prevalent understory. Hasselquist et al. (2010) looked at both developing and mature evergreen and deciduous trees, and found that younger trees, which used more of the shallow soil water than the older trees, had a greater leaf-level WUE. Hasselquist et al. suggested that younger trees had a high density of roots in the surface soil layer, which accordingly dried more rapidly than the deeper soil, causing a subsequent decline in water use and increase in WUE. Similar phenomena may have contributed to the peaks in WUE at our TP02 and TP74 sites.

A synthesis study by Cairns et al. (1997) demonstrated that across temperate, tropical, and boreal forests, root biomass density tends to increase with forest age. Supporting these findings, a previous destructive harvesting experiment found the older TP39 site was to have a significantly greater per-tree mass of large (> 5 mm diameter) and medium (2-5 mm diameter) roots, and total belowground biomass compared to the mid-aged TP74 site (Peichl & Arain, 2007). The more developed root network of the older site may have resulted in greater soil water access during drought, facilitating the higher E observed at such times. The higher proportion of large roots found at TP39 may further explain the differences in the rate of water supply between the two sites; the greater a root’s size and diameter, the larger its capacity to supply water (Jackson et al.,
2000). These structural differences suggested that WUE would be higher at the TP74 site during a drought period compared to TP39, which could maintain a higher rate of transpiration due to its steady groundwater access. Indeed, compared with TP39, the TP74 site had higher WUE during the drought in the June–August period of 2012 ($\alpha < 0.001$), although $E$ and GEP were not significantly different ($p = 0.5$). This suggested that marginal age related differences in WUE response to drought at our forests contributed to a divergence in water conservation between the two well-developed older stands. Future research may shed light on whether tree aging leads to intrinsic physiological changes affecting sensitivity to drought, at the level of both leaves (i.e. stomatal sensitivity to D) and internal water pathways (i.e. root sensitivity to soil moisture change). Different trends in water use and REW among our sites suggested that in plantation forests, selective thinning to prevent soil moisture decline through overuse may be an effective management strategy to sustain stand WUE over time and to decrease potential for water stress.

**Sensitivity of Carbon and Water Exchanges to Environmental Controls**

We observed a mid-afternoon decline in Gs in response to heightened afternoon D, beginning around 1.0 to 1.5 kPa, at our age-sequence sites, which suggested stomatal conservation of water use by the forests (Figure 2.4). Noormets et al. (2010) monitored the carbon and water dynamics of a coastal plain Loblolly pine plantation in North Carolina, USA and found comparable thresholds for Gs. A similar relationship between water use and dryness arose when the six years of daily and half-hourly peak daytime $E$ values were modeled, with VPD having a consistent negative relationship with $E$ in most scenarios (Table 5).
The results of our statistical analyses suggested that high VPD and lower $\theta$ associated with seasonal drought could reduce ecosystem water use, and thus increase WUE relative to moist conditions. Although our oldest stand appeared least conservative in water use, through its highest $E$ and Gs, the lack of a negative trend in WUE or GEP suggested no adverse impacts at this site. Increasing Ta was strongly associated with $E$ and GEP at all of our sites (Table 2.5, Figure 2.6), likely due to warm conditions being ideal for Eastern White Pine growth and transpiration. This relationship also indicated that cool continental climate of the Turkey Point region had not imposed severe water stress at our sites.

The IPCC (2013) has predicted rising Ta and increased P variability in Eastern North America. Similarly, regional climate models for Southern Ontario have projected annual Ta increases of greater than 2°C, increased winter and spring precipitation, and decreased summer rainfall over the 21st century (Eum et al., 2014; Jeong et al., 2014). In this region, longer periods of dryness between intense P events, along with a reduced spring melt due to winter warming, could lead to more frequent dry spells (Knapp et al., 2008; Adam et al., 2009). This could have consequences for water resources in Southern Ontario due to changes in runoff and stream flow as suggested by past studies (Running & Nemani, 1991; Adam et al., 2009). Moore et al. (2011) found that smaller-stemmed forests with a lower basal area had the least effect on runoff relative to stands with a greater basal area. In our study, TP02’s highest P-E corresponded with its lowest basal area. TP74 had marginally higher $E$ than TP39; therefore, the difference in P-E balance with age appeared to diminish, as basal area was quite similar. In a separate study, Huntington (2003) showed that higher annual Ta in Eastern North America caused a decrease in runoff. This was attributed to enhanced $E$, which decreased runoff and infiltration (P-E). Our study found a
similar effect, with rising Ta associated with increased E. Differences in water use and conservation among our forest sites emphasized the importance of considering the structural implications of forest age, as well as tree density, given their relationship with water demand and access. Our study may help to further increase understanding of water dynamics in age-sequence forests to future climatic changes.

**Conclusions**

This study explored whether forest age and commercial thinning affected water use efficiency and the sensitivity of water dynamics to environmental change and extreme weather events in an age-sequence (11-, 39-, and 74-years old) of temperate conifer forests. The evapotranspiration of all three forests was sensitive to air temperature and decreased with increasing atmospheric dryness. Evapotranspiration was most conservative in the youngest forest, which led to an increase in water use efficiency throughout the study, eventually overtaking the mature stands. The oldest forest was the least restrictive in its water use, which led to lower water use efficiency as compared to both younger forests, particularly during the 2012 growing season drought. No significant change in evapotranspiration or water use efficiency was observed at the mature forest site during the post-thinning period in 2012 and 2013, although daytime bulk surface conductance declined. Our study suggests that increasing precipitation variability and rising air temperature in Southern Ontario, as predicted by regional climate models, will likely affect forest water dynamics. Furthermore, younger forests may be best suited to maximize growth and carbon uptake during such environmental variability.
Acknowledgements

This study was funded by Natural Sciences and Engineering Research Council (NSERC) Discovery and Strategic grants and the Ontario Ministry of Environment and Climate Change (MOECC). Funding from the Canadian Foundation of Innovation (CFI) through New Opportunity and Leaders Opportunity Fund and Ontario Research Fund of the Ministry of Research and Innovation is also acknowledged. In-kind support from the Ontario Ministry of Natural Resources (OMNR), Natural Resources Canada, Environment Canada, the Long Point Region Conservation Authority (LPRCA), Long Point Waterfowl Research and Education Centre, Normandale Fish Culture Station, and the St. Williams Conservation Reserve Community Council is also acknowledged. We thank the members of the McMaster Hydrometeorology and Climatology research group, especially Janelle Trant and Michelle Kula for their contributions to biometric and flux data, as well as Jing Chen’s research group at the University of Toronto for their measurements of leaf area index. We acknowledge support from Zoran Nesic at the University of British Columbia (Dr. T.A Black’s group) in flux measurements at our sites. We also thank Steve Williams and Ken Elliott from OMNR, Dave Holmes and Paul Gagnon from LPRCA for their help and Bruce Whitside for providing access to his private forest (TP02 site).
CHAPTER 3: SELECTIVE THINNING IMPACTS ON HYDRAULIC FUNCTIONALITY OF A NATIVE-SPECIES FOREST PLANTATION

3.1 Candidate’s contributions to the manuscript

The candidate performed all statistical analysis, constructed all figures and tables, contributed to field data collection and subsequent processing, conducted all literature review, and wrote the majority of the text (i.e. the entire first draft and most revisions). The manuscript is in review at Ecohydrology (ECO-15-0031).
Short-term selective thinning effects on hydraulic functionality of a temperate pine forest in eastern Canada

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Dated: 27 February 2015

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Keywords: Thinning, sapflow, evapotranspiration, hydraulic redistribution, Eastern White Pine, temperate forest, eddy covariance technique
Abstract

Forest plantations have become increasingly common for restoring the ecological and hydrological functionality of landscapes. They also serve as carbon sinks and a source of timber. Plantation forests are actively managed for their sustained growth and health. One of the most commonly used management techniques is thinning, wherein a portion of a stand is harvested so that the remaining trees have better access to light and water. The impact of thinning on a forest’s hydraulic functionality has been a topic of discussion in the literature. In this study, we investigated the hydrologic response of a 75-year old pine plantation forest in southern Ontario, Canada to thinning. The stand was selectively thinned (30% of trees harvested) in 1983 and 2012. Tree-level and ecosystem-level water fluxes were monitored from 2011 to 2013 using sapflow and eddy-covariance techniques, and were compared with an adjacent 40-year old pine plantation forest that was not thinned. In the 75-year old forest, transpiration declined after thinning in the 2012 growing season, while tree-level water transport increased despite a severe drought. Time lag between sapflow and ecosystem evapotranspiration showed that the older stand had a significantly shorter time lag when compared to younger stand, particularly in the thinning year. Linear regression modeling indicated this was likely due to higher soil moisture status in the older stand versus the younger forest. Hydraulic redistribution of soil water was apparent during drought periods in both forests, and did not appear to be negatively affected by the thinning treatment in the older forest. We conclude that selective low density thinning did not negatively impact the forest’s response to seasonal drought, and that the availability of more soil moisture as a result of thinning may improve the resilience of the forest to future climate extreme events such as drought.
Introduction

Reforestation and afforestation have become increasingly common in North America. Lands cleared for timber or agricultural use, then repurposed for forest plantations, have been recognized as integral carbon sinks and local weather and soil erosion moderators (Restrepo & Arain, 2005; Nilsen & Strand, 2008; M Saunders et al., 2012). Once the planted trees reach an economically desirable stage, and/or the canopy has become closed, silvicultural thinning practices are often employed to harvest some of the trees and also to stimulate growth in remaining individuals. In conifer stands, this generally occurs at about 30-40 and then at 60-80 years of age, depending on the density of the plantation and soil conditions (Yemshanov et al., 2005). Thinning disturbances can have variable effects on the forest and its recovery, both positive and negative. We have summarized some of the water-related dynamics impacts in Figure 3.1.

In this study, we focus on the water dynamics of a recently thinned 75-year old temperate pine plantation forest in southern Ontario, Canada and compared it with an adjacent 40-year old un-thinned stand. We incorporated three years of tree and canopy-level water fluxes as well as biometric and soil moisture measurements to explore the following questions:

1. How does thinning affect soil moisture?

Soil moisture response to thinning is largely dependent upon interactions between thinning intensity and climate. Tree removal impacts a forest’s water balance by reducing canopy interception, which increases the proportion of precipitation reaching the forest floor for soil recharge (Slodicak et al., 2011; Qiu et al., 2012). Inter-tree competition for water is decreased, as
more water for transpiration \((Et)\) is available per tree (Reid \textit{et al.}, 2006). Conversely, as thinning intensity (i.e. proportion of basal area removed) increases, the associated reduction in canopy cover exposes the soil to higher temperature fluctuations, wind and radiation (Son \textit{et al.}, 2004), thus increasing soil water evaporation. Furthermore, the remaining trees are exposed to greater radiation and wind loading, which can lead to water stress (Reid \textit{et al.}, 2006). Ma \textit{et al.} (2010) found that the net effect of thinning upon soil moisture was positive across six thinning treatments of mixed-conifer stands, when basal area was reduced by 12.4 - 66.0%. However, Simonin \textit{et al.} (2007) observed a relative decrease in soil moisture in an 82%-thinned Ponderosa Pine stand when compared to an un-thinned control stand.

2. How does thinning affect root density and hydraulic redistribution?

Roots play an important role in forest water balance, both through direct transport of water for \(Et\) and through hydraulic redistribution. Following thinning, fine root production may increase (López \textit{et al.}, 2003; Campbell \textit{et al.}, 2009; Olesinski \textit{et al.}, 2012), partially offsetting an overall decline in the extent of below ground root architecture of the forest. This production may be tied to either canopy expansion, as the remaining trees have more space to maximize foliage and thus photosynthesis (Claus & George, 2005; Hendricks \textit{et al.}, 2006), or understory growth, as more sunlight reaches the forest floor.

Hydraulic redistribution (HR) is the passive movement of water along tree roots resulting from a gradient in soil water potential (Brooks \textit{et al.}, 2002), and plays a role in restoring soil water deficit during drought (Burgess \textit{et al.}, 1998; Warren \textit{et al.}, 2007). Severe forest disturbances, when dominant trees are removed, kill active roots and prevent water from deeper, more moist soil horizons from being redistributed to shallower layers by HR (Bradford \textit{et al.}, 2014). Studies
in the literature have not explicitly evaluated the effect of thinning on HR, so it is unclear whether thinning would result in an increase or decrease in HR. Given the observed increase in soil moisture in the root zone following thinning (Bréda et al., 1995; Covington & Fule, 1997), as well as the increase in fine root production, we hypothesize that compared to pre-thinned conditions the HR capacity of the forest will not be reduced after thinning.

3. How will time-lag between sapflow and evapotranspiration be affected by thinning?

Investigating how efficiently trees are supplied with water, before and after thinning, can illustrate changes in forest hydraulic functionality. As tree height increases, greater tensional force is needed to transport water through xylem to leaves for photosynthesis, and potential for conduit damage during drought (cavitation) increases (Koch et al., 2004). Water transpired at tree crown-level is a combination of water drawn from the soil, and water that has been stored in plant tissues. The primary reservoir is the stem, although roots, shoots and branches also hold small amounts of water (Waring & Running, 1978; Köcher et al., 2013). There is a lag between sapflow measured in the stem (at about 1.3m height) and the actual transpiration of water by stomata at the leaf-level. The proportion of stored water versus soil water used, and the lag between sap-flow and stomatal transpiration, can vary based primarily on weather conditions and soil moisture availability, as well as tree species and their characteristics. For example, Phillips et al. (1997) found that as soil moisture decreased, departure from a mean time lag (from sapflow to evapotranspiration) increased in Loblolly Pines.

As trees grow, their transpiration lag may remain constant despite ageing. Phillips et al. (1997) found that different-sized Loblolly pines had a similar lag, which was ascertained as a result of
physiological adjustment with growth to maintain tree water transport velocity. In a study of five temperate broad-leaved species, Köcher et al. (2013) observed a positive relationship between stem water storage and the lag between sapflow and crown transpiration. In this instance, wood density, which was species-specific, was more influential than sapwood area in explaining stem water storage potential, and thus transpiration lag.

**Methods**

**Study Sites**

The two forest sites are located at Turkey Point, near lake Erie in Southern Ontario, Canada. These adjacent Eastern White Pine (*Pinus Strobes L.*) stands were planted in 1939 and 1974 (henceforth referred to as TP39 and TP74). Tree density at TP39 prior to the 2012 thinning was 413 ± 181 trees ha$^{-1}$, and at TP74 it is 1583 ± 118 trees ha$^{-1}$ (Kula, 2014). Further stand characteristics are given in Table 3.1. Understory species at TP39 include secondary growth white pines, black cherry, hemlock, white birch, and black and white oak, and the forest floor vegetation features bracken fern, poison ivy, Canada mayflower, Allegheny blackberry, and mosses (Restrepo & Arain, 2005). TP74 has almost no understory.

The TP39 stand was managed by the Ontario Ministry of Natural Resources (OMNR) as a shelterwood silvicultural system, and received two partial cuts: one pre-commercial thinning in 1983 and a selective thinning in February-March 2012 (Elliott et al., 2011). In 1983, about 103 tonnes ha$^{-1}$ of wood was removed and in 2012, approximately 60 tonnes ha$^{-1}$ of wood was removed. The 2012 operation reduced the stand basal area by 13% to 321 ± 111 trees ha$^{-1}$. Leaf area index (LAI) measured prior to thinning was 8.6 (Chen et al. (2006) and it reduced to 5.3 (35% reduction) after the thinning (Table 1).
**Water flux and meteorological measurements**

Ecosystem-wide water, carbon and energy fluxes are continuously measured using closed-path eddy covariance (CPEC) systems at each site. Meteorological variables such as net radiation, incident and reflected photosynthetically active radiation (PAR), air temperature ($T_a$) and relative humidity, wind speed and direction and precipitation (P) are also being measured (see Peichl et al., 2010; Brodeur, 2014 for details).

Sapflow probes were installed at a height of 1.3 m above the tree base, on the north-facing side, in twenty-three trees at TP39 and fourteen trees at TP74. Some sensors were particularly inconsistent and/or had long periods with missing data, and were excluded from the study. This left a total of 15 sensors at TP39 and 9 sensors at TP74. Sapflow tree characteristics are given in Table 1. Prior to installing the sensors, bark was scraped-off to reveal the sapwood surface, the interface between bark and phloem. Sapwood depth was sampled using a wood core, and the amount of non-conducting sapwood in contact with the sensor was measured; corrections were made for any non-conducting tissue, following Clearwater et al. (1999) and McLaren et al. (2008). The sampled trees included above average, near average, and average diameter trees, to capture within-stand variability (Kostner et al., 1992; Mackay et al. 2012). The sensors were re-installed each spring to avoid signal loss due to sap-accumulation and tree growth, and were protected by a reflective foil-coated bubble wrap.

Each sensor consisted of two individual thermocouple probes (1.3-mm in diameter and 30-mm long), with the upper consistently heated and the lower unheated probe. The temperature difference ($\Delta T$) measured between the upper and lower probes produces a dimensionless flow
index, \( K \) was used to calculate sapflow velocity \( (J_s) \) following Granier et al. (1987). Continuous measurements of \( J_s \) (m s\(^{-1}\)) were averaged over half-hourly intervals from January 1, 2011 to December 31, 2013, following Granier (1987).

Transpiration \( (E_t) \) for each tree was calculated as:

\[
E_{ti} = \rho_w \times J_{si} \times \left[ \frac{A_{si}}{A_{wi}} \right] \quad \text{(Equation 3.1)}
\]

Where \( i \) denotes the sample tree, \( \rho_w \) is the density of water (1000 kg m\(^{-3}\)) and \( A_{si}/A_{wi} \) is the ratio of sapwood area to total wood area. Next, \( E_{ti} \) was scaled to stand level transpiration per unit ground area \( (E_t) \) by averaging all trees’ \( E_{ti} \), then multiplying this value by stand basal area (BA, m\(^2\)):

\[
E_t = \frac{\sum_{i=1}^{n} E_{ti}}{n} \times BA \quad \text{(Equation 3.2)}
\]

To find the time it took for water to flow from the tree stem to the canopy, we calculated the lag between \( J_s \) and ecosystem evapotranspiration \( (E) \) measured by the eddy covariance system. Following Lundblad and Lindroth (2002), the diurnal time series of \( J_s \) (mean of all sensors) was progressively shifted by one half-hour and regressed against the diurnal \( E \) time series, and the best fit (defined by \( r^2 \)) was taken as the lag time for that day. Lag was defined in the June-August period for days which were preceded by at least two days with \( P \) of less than 0.5 mm, reducing interference from tree and soil evaporation rainfall response (i.e., a reduction or halt of sapflow as found by Silva et al., 2001). This left 48, 37, and 36 days in 2011, 2012 and 2013 (respectively).

**Fine root measurements**

At both TP39 and TP74, soil cores were taken at six points along a 30 m transect in September 2014. First, a 20 x 20 cm segment of the litter layer was removed down to the top of the mineral
soil. Then a 5.4 cm diameter auger was used to extract soil cores from 0-15 and 15-35 cm depths. The samples were then oven-dried at 65°C. For each soil sample, fine (<2mm) and small (2-5mm) roots were isolated and weighed. Live and dead roots were not discriminated during analysis. We compared root analyses results with a previous study at our sites by Peichl et al. (2006).

**Soil moisture and hydraulic redistribution**

Soil volumetric water content (θ) was continuously measured by CS615 probes (Campbell Scientific Inc.) at 5, 10, 20, 50, and 100 cm depth at two points within each site, except for the 100 cm depth at TP74 which had only one point of measurement. The average of the two probes was taken for each depth. Root zone θ (0-25 cm) was obtained by a depth-weighted integration of the 5, 10, and 20 cm probes, and the 50 and 100 cm probes were integrated to obtain θ across the deeper soil layer from 45-105 cm.

Following Meinzer et al. (2004) and Brooks et al. (2002), hydraulic redistribution (HR) at our sites was quantified as the difference between the minimum θ of one day and the maximum of the next day. To isolate HR rather than capillary rise, calculations were restricted to the 30 days of lowest θ in each growing season. As with Js-E lag, values were only kept for days when no P over 0.5 mm day⁻¹ was recorded for the previous two days.

**Data quality control, gap filling and statistical analysis**

Meteorological, flux and sapflow data were quality controlled for spikes and missing periods following Brodeur (2014). For missing half-hourly sapflow values, a neural-network training
tool in Matlab (The Mathworks, Inc.) was used to estimate $J_s$ values, using the same year’s meteorological data for training. To predict $J_s$ for the missing time periods, incident PAR, vapour pressure deficit (VPD), soil temperature, $T_s$ (5 cm depth) and $\theta$ in the root zone (0-25 cm) were used for each sensor. Statistical analysis was performed using cleaned, non-gap filled data.

To explore the nature of the $J_s$-$E$ lag, we constructed multivariate linear models of the daily lag for each year, using daily mean 0-25 cm, VPD and PAR. Model evaluation for all analyses was performed using the second-order Aikaike information criterion (AICc), a metric that considers a model’s parsimony in addition to its fit by incorporating the number of free parameters, thus evaluating a model’s performance removed from a complexity bias (Bozdogan, 2000). In each distinct analysis scenario, the models’ AICc were re-expressed as Aikaike weights ($w_i$) to compare their relative probabilities of accurately representing the measured data (Wagenmakers & Farrell, 2004). All statistical analyses were performed using Matlab.

**Results**

*Meteorological trends*

In 2012, growing season (April to October) mean $T_a$ was 9% higher, while total $P$ was 3 % higher than the 30-year norm values in the region. 2013 was notably well-watered: rainfall exceeded the 30-year norm by 24% (Table 3.2, Figure 3.2a). $\theta$ was consistently higher at TP39 compared to TP74 during all three study years as shown by Figure 2 c-d. In 2011, VPD was greater at TP74, however in 2012 and 2013 TP39 experienced slightly higher atmospheric dryness (Figure 3.2b).
Changes in canopy openness

LAI at TP39 declined significantly after thinning in early 2012 (p<0.001), while TP74 had a slight, non-significant decline. LAI remained similar between 2012 and 2014 at both sites. The ratio of half-hourly VPD between the two sites (TP39/TP74) increased significantly from 0.77 in 2011 to 1.05 in 2012 (p<0.001), which suggested an increase in canopy-atmosphere coupling and atmospheric demand at TP39 after thinning due to the increase in canopy openness.

Tree- and stand-level water fluxes

Sapflow velocity (Js) and transpiration (Et) had different interannual trends at TP39. Following thinning at TP39, 2012 cumulative growing season Et declined and did not return to previous levels during the study (Table 3.3, Figure 3.3), while 2012 Js increased compared to 2011 (Table 3.3, Figure 3.4). At TP74, however, both Js and Et declined from 2011 to 2012. At both sites, Js was highest in 2013, and for TP74 the 2013 growing season had the greatest cumulative Et. Et declined in 2012 following thinning at TP39 and did not return to previous levels during the study. Ecosystem-level E was very similar between the two sites, with growing season totals increasing from year to year (Table 3.3).

Interestingly, 2011 and 2013 were comparable in their growing season climate (Table 3.2), yet the differences in Et and E between TP39 and TP74 were quite different (Table 3.3), reflecting the thinning disturbance. In 2011, TP39 transpired about 54% more and its ecosystem evapotranspiration was 13% higher compared to TP74, yet by 2013 TP39 transpired about 9% less than TP74, while its total annual evapotranspiration was higher by 12% compared to that of TP74.
At both sites in 2011 and 2012, $E_t$ followed a biannual peak pattern, with the first, highest peak around June, a dip during seasonal drought through July and August, and a second, lower peak in early fall then a decline as the growing season drew to a close in October (Figure 3.3). The seasonal patterns in $E_t$ and $J_s$ were reflective of the precipitation patterns at the site (cf. Figure 3.2 and Figures 3.3 and 3.4). In both 2011 and 2012, there was less precipitation in the early growing season compared to 2013, which resulted in the mid-season drought around July, causing $E_t$ and $J_s$ to decline. In contrast, in 2013 May was unusually wet, and this extra early season supply of water kept the trees watered enough to ameliorate any effect of mid-season drought on $J_s$ and $E_t$. Overall, $E_t$ declines during seasonal drought were relatively more severe at TP74 compared to TP39.

**Sapflow-evapotranspiration lag**

Sapflow at both sites generally trailed evapotranspiration measured by the eddy covariance system by 0-2 hours (Figure 3.5). The daily lag time between two sites was significantly different in all years (paired t-test, $\alpha<0.001$), with TP39 having consistently shorter lag. Lag time was approximately normally distributed at TP39, yet positively skewed at TP74. At TP39, multivariate linear modeling indicated that soil moisture ($\theta_{0-25cm}$) was the primary predictor in 2012, in contrast to the pre-thinning year in which PAR was the dominant predictor (Table 3.4). Soil moisture was consistently the most likely predictor of lag time at the younger, un-thinned TP74 site, however the model including PAR was proportional in its probability for 2011.
Impact of thinning on root density

Fine and small root biomass from soil coring showed high spatial variability. Compared with results from Peichl et al. (2006), the only significant change was an increase in fine root biomass at TP39 (t-test, \( p < 0.01 \)), with no detectable change in root distribution at TP74 (not shown).

Hydraulic redistribution

Our estimations of hydraulic redistribution (HR) tended to be of higher magnitude at TP74 than TP39 throughout the study period, which corresponded with the site’s lower soil moisture accommodating greater differential in soil water potential for passive transport (Figure 3.6). The majority of HR at both sites occurred in the 0-25 cm layer, although uplift in the lower 45-105 cm layer was relatively more common at TP74. Notably, HR from 45-105 cm did not occur at TP39 in August 2011 (not shown), but was apparent during this time in 2012 and 2013, while at TP74 HR was detected during all of these periods. At both sites, there was no significant change in 0-25cm HR from 2011 to 2012 (\( \alpha < 0.05 \)).

Discussion

Tree level water dynamics

Sapflow dynamics

Low soil moisture and rainfall, and high vapor pressure deficit compared to 2011 and 2013, indicated that a relatively severe seasonal drought occurred during the 2012 growing season that followed the thinning treatment conducted earlier in the year. The summer of 2012 was also warmer compared to the other two years and 30-year norm. The rise in \( Js \) at TP39 following
thinning was in contrast to the expected drought response of $J_s$, which generally decreases during drought periods, as seen at TP74. In the following 2013 year, which was well watered throughout the summer, both sites’ $J_s$ rose as expected. The higher soil moisture and lower VPD during 2013 would have accommodated stomatal openness rather than closure from frequent summer drought stress as observed in other years (McLaren et al., 2008; MacKay et al., 2012).

Previous studies in forests of Oak (Bréda et al., 1995) and Lodgepole pine (Reid et al., 2006) have found that forest thinning results in greater soil moisture availability and can lead to a higher rate of transpiration among the remaining trees. Without a paired study of a thinned and un-thinned plot at our forest, it was not possible to directly conclude that thinning allowed greater soil moisture. However, it is logical to conclude that the decrease in stem density allowed more soil water per tree, and this was likely a key component of the $J_s$ increase at TP39.

Additionally, if we compare 2011 and 2013 fluxes (Table 3.3), one can see that in 2013 the difference between $E$ and $E_t$, which represents soil evaporation and understory transpiration, more than tripled (i.e. 47 mm ha$^{-1}$ vs 155 mm ha$^{-1}$) at TP39, as expected when the canopy opens up due to thinning, versus declining at TP74 (from 128 mm ha$^{-1}$ to 79 mm ha$^{-1}$). In a study monitoring the effects of a gradient of thinning intensities (14-66\% of basal area removed) in a mixed conifer forest, Ma et al. (2010) found soil moisture and VPD to increase in all treatment plots, which aligned with our results. In contrast, when Simonin et al. (2007) investigated forest response to a more intensive thinning (82\% of basal area removed), the authors found a resultant decrease in soil moisture. The thinning at our site was of a low enough intensity (i.e. 13\% of basal area) to result in a soil moisture increase, which could support a rise in sapflow velocity in the remaining trees.
Tree sapflow - site evapotranspiration lag

In our study, stem flow to evapotranspiration (Js –E) lag showed that tree size and age did not restrict timing of water transport from the roots to the leaves, as previously demonstrated by Philips et al. (1997). Our estimates of time lag were within the range of previous studies such as Kocher et al. (2013), Saugier et al. (1997), Granier et al. (1996), and Perämäki et al. (2001). The consistently lower lag at TP39 versus TP74 during summer might reflect a height-compensation response that serves to reduce hydraulic limitation, as well as suggesting an absence of significant xylem cavitation that would reduce tree capacity for water transport. Accordingly, the influence of soil moisture on Js –E lag may have been greater than that of tree height when comparing lag between the sites, with seasonal drought amplifying such differences. The increase in soil moisture’s predictive power at TP39 in 2012 suggested that greater per-tree soil water availability was important for hydraulic functionality, as measured by lag time. The relatively high probability of soil moisture in predicting lag at TP74 was interesting as it indicated supply of canopy water at the site may be limited by soil moisture availability more so than atmospheric demand or energy available for photosynthesis. Kocher et al. (2013) found that stem storage was nearly depleted past a soil water dryness threshold. In our study, TP74 had consistently lower soil moisture than TP39, so the younger site likely reduced water uptake earlier at the onset of dry conditions.

Ecosystem scale water dynamics

Evapotranspiration

In spite of the increase in tree Js, a decrease in Et at TP39 was observed with stand thinning, as the water-conducting sapwood area declined from 31.5 to 23.7 m² ha⁻¹. At TP74, the decline was
likely tied to the 2012 growing season drought. The consistency of $E$ between sites and years showed a rising importance of soil evaporation in the forest water balance during drought and following thinning. As discussed in previous studies of thinned and un-thinned stands (Simonin et al., 2007; Raz-Yaseef et al., 2010), greater canopy openness allows more solar radiation to reach the forest floor, and thus more evaporation of shallow soil water. This effect may be more pronounced during such hot and dry periods as experienced during 2012 growing season, when transpiration was suppressed due to stomatal closure and more energy was available for soil water evaporation.

Changes in root density

Contrary to results from Peichl et al. (2006), we did not find TP74 to have a higher fine root density than TP39. Both the 2012 and 1983 thinning treatments may have allowed an expansion of understory vegetation and native Carolinian species, which are both sources of fine root production. Future work on hydrological impacts of thinning may benefit from species surveys before and after treatment to investigate the role of understory expansion. Previous studies report that peak fine root abundance corresponds with timing of a forest’s canopy closure (Vogt et al., 1983; Helmisaari et al., 2002; Claus & George, 2005), as fine roots are important in supplying water and nutrients for foliage growth. However, in 2014 peak LAI was 4.8 m$^2$m$^{-2}$ at TP39, and thus did not show an increase from the 5.9 m$^2$m$^{-2}$ peak LAI of 2012 after thinning. This led us to surmise that understory rather than canopy expansion was likely the source of new fine roots. However, the contribution of White Pine fine root expansion to the increase could be decisively ruled out, as there may be a lag between root production and tree foliage expansion.
Soil moisture and hydraulic redistribution

Hydraulic redistribution (HR) appeared to restore soil moisture in the 0-25 cm root zone during dry spells at both TP39 and TP74, which was likely a valuable input for understory and forest floor plants with shallow root systems. During the lowest soil moisture periods in 2011 and 2012, HR was commonly lower than 0.5 mm per day at TP39 and TP74, similar to studies by Brooks et al. (2002), Meinzer et al. (2004), and Warren et al. (2005). However, values that fluctuated as high as 1.6 (TP39) and 1.8 (TP74) mm day$^{-1}$ were more dubious, and may have reflected capillary rise rather than the root-associated HR. The 2013 case in particular was suspect, as even the driest period was interspersed with high-rainfall events (i.e. up to 40 mm day$^{-1}$). It is possible than HR may be most reliably present at our forests when soil moisture is below a dryness threshold consistent with seasonal drought for a prolonged period of time, as was observed in 2011 and 2012. A previous study at our site identified a $\theta_{0-25cm}$ value of 0.07 as the site’s drought threshold, based on $Et$ decline (McLaren et al., 2008). Our results show that soil moisture remained around this threshold value during the 2011 and 2012 seasonal drought periods, possibly due to HR. Future studies, using soil water potential probes (Warren et al., 2005, 2007) or root sapflow sensors (Burgess et al., 1998; David et al., 2013) to support soil moisture measurements are recommended for a more in-depth assessment. Without a paired study it was difficult to conclude whether the removal of roots with thinning impacted passive soil water movement, although the apparent presence of HR during the summer drought of 2012 did suggest that sufficient root structure remained following thinning. It thus appears that the gradient in soil water potential was the limiting factor of HR at the thinned site, rather than the available capacity of water transport conduits.
Conclusion

This study demonstrated the response of a temperate white pine plantation forest in eastern Canada to a selective thinning treatment that reduced basal area by 13%. Transpiration in the thinned stand declined following the treatment, however tree-level water transport increased. In contrast, tree-level water transport decreased at a nearby un-thinned white pine stand, due to drought in the growing season of the thinning year. This suggested increased availability of water supply to individual trees following the thinning, despite a decline in water input. Ecosystem evapotranspiration did not appear to be impacted by the thinning, likely due to a more open canopy accommodating increased soil evaporation and understory transpiration. These divergent trends in transpiration and sapflow velocity following tree harvesting suggested the presence of a physiological response tied to structural change, independent from environmental variability, which drove the increase in sapflow velocity at the treated stand. We conclude that the thinning treatment did not compromise the hydraulic functionality of our mature white pine stand and potentially allowed the stand to become more effective in withstanding seasonal drought stresses.
Acknowledgements

Funding was provided by the Natural Sciences and Engineering Research Council (NSREC), Ontario Ministry of Environment (MOE), Canadian Foundation of Innovation (CFI) and Ontario Research Fund. Support from the Ontario Ministry of Natural Resources (OMNR), Natural Resources Canada (NRCan), Environment Canada (EC), Long Point Region Conservation Authority (LPRCA) and St. Williams Conservation Reserve Community Council is also acknowledged. We are also thankful to Janelle Trant, Michelle Kula, Jing Chen’s (University of Toronto for LAI measurements), Zoran Nesic (T.A Black’s group at UBC) and Steve Williams and Ken Elliott (OMNR).
CHAPTER 4: CONCLUSIONS AND FUTURE RESEARCH

To decipher the impact of climate variability on forests’ water dynamics, many factors must be taken into consideration. Three dominant parameters that emerged during this project were age, stem density and stand basal area. Seasonal drought experienced by our forests shed light on how stands’ water conservation changes with age, and also how water use efficiency might be affected by an increase in rainfall variability, as projected by the IPCC (2014).

Differences among the white pine chronosequence in both scale of water use efficiency and controls on it’s components showed the importance of incorporating biometric and/or age parameters into regional or global projections of water use efficiency and it’s drivers. For example, a young forest might show an increase in WUE during drought, while a mature forest’s WUE may remain stable or decrease. Furthermore, inter-site differences in soil moisture, which were likely related to stem density, resulted in differences in the water supply and subsequent resource limitation during drought. This showed that regional generalizations of drought initiation should incorporate site-specific soil moisture variability in addition to precipitation indices.

Observing a 75-year-old forest’s hydraulic response to selective thinning showed that a reduction in stem density of the dominant tree affected the partitioning of the water balance, but not the total ecosystem balance in terms of evapotranspiration. Although transpiration of the forest decreased, soil evaporation, and likely understory transpiration, increased in the more open canopy. When compared with the interannual dynamics of a nearby unthinned stand, total ecosystem $E$ was not impacted. Furthermore, thinning did not impact WUE, likely also due to the
growth of understory species, which could compensate for the lower production capacity of the mature white pines.

The mid-aged forest consistently had the lowest relative extractable water of all three sites, and compared to the older, thinned forest displayed lower tree water use, particularly during drought. Considering the relatively high stem density of this mid-aged stand, these findings emphasize that thinning of White pine plantations may be necessary as they age, to prevent declines in soil moisture availability that may lead to tree damage such as xylem cavitation, and in more severe cases, mortality.

In future research, a paired study of water balance response to thinning might yield more concrete conclusions about the management impact on drought response throughout the forest ecosystem. Monitoring species compositions post-thinning, and comparing this with the water and carbon flux measurements, might show how the change in understory was involved with the water balance and root structure.

The extent and role of hydraulic redistribution at the research sites is another potential area of investigation. Recurrent dry spells led to water-supply limitation of $E$, which was furthermore not circumvented by sufficient HR to remain above the drought threshold for the sites (particularly TP74), although once the threshold was passed, SWC remained fairly stable. Future research at this site could incorporate soil water potential measurements for hydraulic redistribution monitoring, and regular measurements of fine and small root distribution, to
investigate the quantity and nature of HR at the sites as well as the role of HR in limiting drought conditions.

Incorporating sapflow and ecosystem evapotranspiration measurements to determine lag time between water transport at the stem and canopy level provided another dimension to the detection of hydrologic change post-thinning. The apparent aberration of the hydraulic hypothesis, which states that water supply becomes slower with tree height (Koch et al., 2004), begs further investigation. These results were likely due to the selective timing of analysis, which was aimed to capture as many non-rainfall days as possible, and also to the lower soil moisture status at the younger stand. However, these suppositions could be investigated further, to detect the respective roles of tree height and stand micrometeorology in the water supply dynamics within different aged trees.

Collectively, the results presented in this thesis emphasize the importance of monitoring site-level hydrological trends such as available soil moisture and rate of tree water use, when managing a forest plantation. When evaluating when to perform a selective thinning treatment, forest managers could monitor these trends in addition to basal area and tree volume, and choose to thin a stand should soil moisture or tree water use show a sustained decline over several growing seasons. Such a strategy would increase per-tree water availability at an accordingly identified stand, reducing water stress and tree mortality risk during seasonal drought. In addition, the relatively low water use of the youngest White Pine study site compared with the older forests suggested that forest plantations could be designed and managed towards an uneven-age structure to maximize stand water use efficiency.
References


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Kula, M. V. 2014. Biometric-based carbon estimates and environmental controls within an age-sequence of temperate forests. McMaster University.


### TABLES

**Table 2.1. Stand characteristics for all three study sites.**

<table>
<thead>
<tr>
<th></th>
<th>TP39</th>
<th>TP74</th>
<th>TP02</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stand age (yeas, as of 2013)</td>
<td>74</td>
<td>39</td>
<td>11</td>
</tr>
<tr>
<td>Location coordinates</td>
<td>42.42’, 35.20” N, 80.21’, 26.64” W</td>
<td>42.42’, 24.52” N, 80.20’, 53.93” W</td>
<td>42.39’, 39.37” N, 80.33’, 34.27” W</td>
</tr>
<tr>
<td>Previous land use and management practices</td>
<td>Afforested on Oak savanna cleared for afforestation; thinned in 1983 and 2012</td>
<td>Afforested on Oak savanna cleared for afforestation</td>
<td>Afforested on former agricultural land, fallow for 10 years prior to planting</td>
</tr>
<tr>
<td>Dominant species</td>
<td><em>Pinus strobus</em> L. (Eastern White Pine)</td>
<td><em>Pinus strobus</em> L.</td>
<td><em>Pinus strobus</em> L.</td>
</tr>
<tr>
<td>Understory</td>
<td><em>Quercus vultina</em>, <em>Abies balsamifera</em>, <em>Prunus serotina</em></td>
<td><em>Quercus vultina</em></td>
<td>None</td>
</tr>
<tr>
<td>Ground Vegetation</td>
<td><em>Rhus radicans</em>, <em>Rubus spp.</em>, ferns, mosses</td>
<td>Scattered patches of mosses</td>
<td>Herbs, grasses (<em>Digitaria sanguinalis</em>, <em>Trifolium repens</em>)</td>
</tr>
<tr>
<td>Mean canopy height (m)</td>
<td>23.4 ± 5.9 (22.9 ± 6.15)</td>
<td>16.2 ± 0.50</td>
<td>5.8 ± 0.67</td>
</tr>
<tr>
<td>Basal area (m² ha⁻¹)</td>
<td>36.0 (40.9)</td>
<td>40.0</td>
<td>17.2</td>
</tr>
<tr>
<td>Stem density (trees ha⁻¹)</td>
<td>321 ± 111 (413 ± 181)</td>
<td>1583 ± 118</td>
<td>1567 ± 29</td>
</tr>
<tr>
<td>Leaf Area Index, LAI (m² m⁻²)</td>
<td>5.3 (8.5)</td>
<td>6.6</td>
<td>-</td>
</tr>
<tr>
<td>Water table depth (m below surface)</td>
<td>6-7</td>
<td>6-7</td>
<td>2-3.5</td>
</tr>
</tbody>
</table>

*a* As of 2012, following Kula (2013); brackets show pre-thinning (2011) values for TP39; stem density include trees ≥ 9cm DBH

*b* As of 2012, measured by Dr. Jing Chen, University of Toronto (unpublished data)
Table 2.2: Tree characteristics at all three study sites (biomass is in kg tree$^{-1}$ unless otherwise stated).

<table>
<thead>
<tr>
<th></th>
<th>TP39</th>
<th>TP74</th>
<th>TP02</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean tree diameter at DBH (cm)$^a$</td>
<td>38.99 ± 10.23</td>
<td>17.90 ± 4.9</td>
<td>11.62 ± 3.42</td>
</tr>
<tr>
<td></td>
<td>(37.15 ± 10.33)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean sapwood area at DBH (cm$^2$) $^b$</td>
<td>228.6</td>
<td>139.4</td>
<td>---</td>
</tr>
<tr>
<td>Stem wood biomass $^b$</td>
<td>392.3 ± 147.5</td>
<td>55.6 ± 38.0</td>
<td>---</td>
</tr>
<tr>
<td>Foliage biomass $^b$</td>
<td>10 ± 5.8</td>
<td>7.0 ± 8.5</td>
<td>---</td>
</tr>
<tr>
<td>Stump and root biomass (&gt;10 cm)$^b$</td>
<td>38.9 ± 14</td>
<td>6.8 ± 5.3</td>
<td>---</td>
</tr>
<tr>
<td>Large root biomass (2-10 cm)$^b$</td>
<td>51.1 ± 23.5</td>
<td>7.0 ± 7.7</td>
<td>---</td>
</tr>
<tr>
<td>Medium root biomass (0.5-2 cm)$^b$</td>
<td>7.6 ± 0.9</td>
<td>2.0 ± 1.4</td>
<td>---</td>
</tr>
<tr>
<td>Small root biomass (2-5 mm)$^b$</td>
<td>0.9 ± 0.2</td>
<td>0.5 ± 0.5</td>
<td>---</td>
</tr>
<tr>
<td>Fine root biomass (&lt;2mm)(t ha$^{-1}$)$^c$</td>
<td>3.5 ± 1.5</td>
<td>6.2 ± 1.7</td>
<td>---</td>
</tr>
<tr>
<td>Root to shoot biomass (ratio)$^b$</td>
<td>0.22</td>
<td>0.16</td>
<td>---</td>
</tr>
</tbody>
</table>

$^a$ As of 2012, following Kula (2013); brackets show pre-thinning 2011 values for TP39; DBH and stem density include trees ≥ 9cm DBH

$^b$ Measured in a destructive harvesting study by Peichl and Arain (2007) using 5 trees at TP74 and 4 trees at TP39. TP39 was 65 years old and TP74 was 30 years old. Shoot biomass includes woody twigs and foliage. TP02 was 2 years old at the time of harvesting, thus results were not representative for the current study.

$^bc$ Measured by Peichl and Arain (2006) from seven soil core samples per site: four at 0-15 cm, two at 15-35 cm, and one at 35-55 cm.
Table 2.3: Mean air temperature (Ta) and cumulative precipitation (P) over the growing season. Annual values are given in parenthesis.

<table>
<thead>
<tr>
<th>Year</th>
<th>Ta (°C)</th>
<th>P (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2008</td>
<td>14.6 (7.9)</td>
<td>563 (1133)</td>
</tr>
<tr>
<td>2009</td>
<td>14.1 (7.7)</td>
<td>608 (995)</td>
</tr>
<tr>
<td>2010</td>
<td>15.9 (8.8)</td>
<td>608 (896)</td>
</tr>
<tr>
<td>2011</td>
<td>15.4 (8.7)</td>
<td>715 (1293)</td>
</tr>
<tr>
<td>2012</td>
<td>16.2 (10.4)</td>
<td>571 (1001)</td>
</tr>
<tr>
<td>2013</td>
<td>15.3 (8.5)</td>
<td>741 (1265)</td>
</tr>
</tbody>
</table>
Table 2.4 Cumulative evapotranspiration ($E$) and gross ecosystem productivity (GEP), and mean monthly water use efficiency (WUE) over the growing season. Annual values are given in parenthesis.

<table>
<thead>
<tr>
<th>Year</th>
<th>$E$ (mm)</th>
<th>GEP (g C m$^{-2}$)</th>
<th>WUE (g C m$^{-2}$ kg H$_2$O$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>TP39</td>
<td>TP74</td>
<td>TP02</td>
</tr>
<tr>
<td>2008</td>
<td>454</td>
<td>428</td>
<td>324</td>
</tr>
<tr>
<td></td>
<td>(507)</td>
<td>(481)</td>
<td>(362)</td>
</tr>
<tr>
<td>2009</td>
<td>422</td>
<td>389</td>
<td>310</td>
</tr>
<tr>
<td></td>
<td>(469)</td>
<td>(441)</td>
<td>(350)</td>
</tr>
<tr>
<td>2010</td>
<td>460</td>
<td>387</td>
<td>368</td>
</tr>
<tr>
<td></td>
<td>(514)</td>
<td>(433)</td>
<td>(408)</td>
</tr>
<tr>
<td>2011</td>
<td>411</td>
<td>364</td>
<td>318</td>
</tr>
<tr>
<td></td>
<td>(467)</td>
<td>(419)</td>
<td>(355)</td>
</tr>
<tr>
<td>2012</td>
<td>436</td>
<td>386</td>
<td>291</td>
</tr>
<tr>
<td></td>
<td>(497)</td>
<td>(458)</td>
<td>(344)</td>
</tr>
<tr>
<td>2013</td>
<td>447</td>
<td>400</td>
<td>326</td>
</tr>
<tr>
<td></td>
<td>(486)</td>
<td>(450)</td>
<td>(365)</td>
</tr>
</tbody>
</table>
Table 2.5. Relative contribution of explanatory variables to the multivariate models of peak daytime $E$ (PAR > 1000 µmol m$^{-2}$s$^{-1}$) at TP39, TP74 and TP02, and model performance. Variables included in the model were incident photosynthetically active radiation (PAR), vapour pressure deficit (VPD), air temperature (Ta), and relative extractable water at 0-25 cm depth (REW 0-25cm). Analysis was performed at both half-hourly and daily averaged scales. NS signifies that the variable was not significant in the model.

<table>
<thead>
<tr>
<th></th>
<th>Daily</th>
<th></th>
<th>Half-hourly</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>TP39</td>
<td>TP74</td>
<td>TP02</td>
<td>TP39</td>
</tr>
<tr>
<td>PAR (% $r^2$)</td>
<td>14.3</td>
<td>7.9</td>
<td>15.8</td>
<td>NS</td>
</tr>
<tr>
<td>VPD (% $r^2$)</td>
<td>1.3</td>
<td>NS</td>
<td>9.2</td>
<td>3.6</td>
</tr>
<tr>
<td>Ta (% $r^2$)</td>
<td>23.2</td>
<td>12.2</td>
<td>19.6</td>
<td>64.2</td>
</tr>
<tr>
<td>REW 0-25cm (% $r^2$)</td>
<td>NS</td>
<td>-0.8</td>
<td>16.6</td>
<td>8.7</td>
</tr>
<tr>
<td>Model $r^2$</td>
<td>0.60</td>
<td>0.54</td>
<td>0.63</td>
<td>0.37</td>
</tr>
<tr>
<td>Model F-statistic ($\alpha &lt; 0.001$)</td>
<td>454</td>
<td>331</td>
<td>433</td>
<td>1.67E03</td>
</tr>
</tbody>
</table>
Table 3.1: Stand and sapflow tree characteristics. Pre-thinning values are given in parentheses.

<table>
<thead>
<tr>
<th></th>
<th>TP39</th>
<th>TP74</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age (years) as of 2013</td>
<td>74</td>
<td>39</td>
</tr>
<tr>
<td>Basal area* (m² ha⁻¹)</td>
<td>36.0 (40.9)</td>
<td>40.0</td>
</tr>
<tr>
<td>Sapwood area* (m² ha⁻¹)</td>
<td>23.7 (31.5)</td>
<td>26.3</td>
</tr>
<tr>
<td>Stem density* (m² ha⁻¹)</td>
<td>321 ± 111 (413 ± 181)</td>
<td>1583±118</td>
</tr>
<tr>
<td>Maximum Leaf Area Index, LAI^b (m² m⁻²)</td>
<td>5.3 (8.6)</td>
<td>6.7</td>
</tr>
<tr>
<td>Number of trees for sapflow measurements</td>
<td>11</td>
<td>10</td>
</tr>
<tr>
<td>Mean height of sapflow trees^c (m)</td>
<td>20.9 ± 2.0</td>
<td>10.7 ± 0.6</td>
</tr>
<tr>
<td>Mean basal area of sapflow tree^c (cm)</td>
<td>40.2 ± 5.7 (41.5 ± 6.9)</td>
<td>19.3 ± 3.6</td>
</tr>
</tbody>
</table>

* Measured at 1.3 m height from the tree base
^a Data from 2012 and 2011 (pre-thinning), respectively, as reported by Kula (2013)
^b Maximum annual LAI measured in 2011 (pre-thinning) and 2014, respectively, by Dr. Jing Chen’s group at the University of Toronto (unpublished, personal communication)
^c Measured in 2011 (pre-thinning), and 2014
Table 3.2: Growing season (April-October) climate.

<table>
<thead>
<tr>
<th>Year</th>
<th>Ta (°C)</th>
<th>P (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2011</td>
<td>15.3</td>
<td>715</td>
</tr>
<tr>
<td>2012</td>
<td>16.2</td>
<td>571</td>
</tr>
<tr>
<td>2013</td>
<td>15.3</td>
<td>741</td>
</tr>
<tr>
<td>30-year-norm*</td>
<td>14.9</td>
<td>632</td>
</tr>
</tbody>
</table>

*Based on a nearby Delhi CDA weather station data from 1981-2010
Table 3.3: Growing season ecosystem-level evapotranspiration ($E$), transpiration ($Et$) and mean sapflow velocity ($Js$) at the TP39 and TP74 sites.

<table>
<thead>
<tr>
<th>Year</th>
<th>$E$ (mm)</th>
<th>$Et$ (mm)</th>
<th>$Js$ (mm s$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>TP39</td>
<td>TP74</td>
<td>TP39</td>
</tr>
<tr>
<td>2011</td>
<td>411</td>
<td>364</td>
<td>364</td>
</tr>
<tr>
<td>2012</td>
<td>436</td>
<td>386</td>
<td>216</td>
</tr>
<tr>
<td>2013</td>
<td>447</td>
<td>400</td>
<td>292</td>
</tr>
</tbody>
</table>
Table 3.4: Aikake weights ($w_i$) from stepwise modeling of daily evapotranspiration ($E$)-sapflow velocity ($J_s$) lag values with $\theta_{0-25cm}$, vapor pressure deficit (VPD), and photosynthetically active radiation (PAR), The $w_i$ signifies models’ relative probabilities of representing the measured data.

<table>
<thead>
<tr>
<th></th>
<th>$\theta_{0-25cm}$</th>
<th>$\theta_{0-25cm} + VPD$</th>
<th>$\theta_{0-25cm} + VPD + PAR$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>TP39</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2011</td>
<td>0.00</td>
<td>0.00</td>
<td>1.00</td>
</tr>
<tr>
<td>2012</td>
<td>0.68</td>
<td>0.23</td>
<td>0.09</td>
</tr>
<tr>
<td>2013</td>
<td>0.12</td>
<td>0.26</td>
<td>0.62</td>
</tr>
<tr>
<td><strong>TP74</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2011</td>
<td>0.36</td>
<td>0.29</td>
<td>0.36</td>
</tr>
<tr>
<td>2012</td>
<td>0.58</td>
<td>0.32</td>
<td>0.10</td>
</tr>
<tr>
<td>2013</td>
<td>1.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
</tbody>
</table>
FIGURES

**Figure 1.1**: From Meyfroidt et al. (2011), depicting timing of transitions from deforestation to forest regeneration.

Figure 2.1. Daily reflected photosynthetically active radiation (PAR) at the 11-year old (TP02), 39-year-old (TP74) and 74-year-old (TP39) forest sites, as a proxy for leaf area index (LAI) to show change in canopy cover at TP02. Triangles indicate mean reflected PAR at TP02 for January to March, illustrating contrast between snow cover and canopy cover.
Figure 2.2. (a) Monthly total precipitation (P) and monthly mean air temperature (Ta), (b) monthly Palmer Drought Severity Index (PDSI) to evaluate moisture availability relative to 1976-2013 means, where horizontal bands separated by dotted lines are defined as follows: if a value falls within the band delimited by y-axis values of 2 to 3 it is defined as = ‘moderately wet’; 1 to 2 = ‘slightly wet’; 0.5 to 1 = ‘incipient wet spell’; 0.5 to -0.5 = ‘near normal’; -0.5 to -1 = ‘incipient drought’; -1 to -2 = ‘mild drought’; -2 to -3 = ‘moderate drought’, (c) vapor pressure deficit (VPD), and daily relative extractable water (REW) to express soil moisture relative to field capacity and wilting point at 0-25 cm depth and (d) 45-105 cm depth (e). The shaded area indicates the 2012 growing season drought.
Figure 2.3. Cumulative values of evapotranspiration ($E$, top row), $E$ deviation from the 6-year mean ($\overline{E}$, middle row) and $P-E$ (bottom row) at TP39, TP74, and TP02 sites from 2008 to 2013.
Figure 2.4. Diurnal time series of bulk surface conductance ($G_s$) and vapor pressure deficit ($VPD$) on June 31$^{st}$, 2012, under drought conditions (PDSI $<-2$, REW 0-25cm = 0.36, 0.35 and 0.38 at TP39, TP74 and TP02) and July 1$^{st}$, 2013, under moist conditions (PDSI $>1$, REW 0-25cm = 0.73, 0.72 and 0.62 at TP39, TP74 and TP02).
Figure 2.5. Monthly values of water use efficiency (WUE), evapotranspiration ($E$) and gross ecosystem production (GEP) for the growing season at TP39, TP74, and TP02 sites from 2008 to 2013.
Figure 2.6. The relationship of daily air temperature (Ta) with evapotranspiration (E) and gross ecosystem productivity (GEP) at the 74-year-old (TP39), 39-year-old (TP74), and 11-year-old (TP02) sites, for the growing seasons from 2008-2013. Gap filled values of E and GEP were excluded.
Figure 3.1: Concept map of how thinning treatment might affect transpiration of a forest ecosystem under various climatic stress factors. Arrows illustrate the hypothesized modes of impact through hydraulic, structural, energetic, atmospheric and nutrient limitation.
Figure 3.2: (a) Monthly precipitation ($P$) and air temperature ($T_a$) at TP39 with 1981-2010 30-year-norms from the nearby Delhi weather station included for comparison, (b) vapor pressure deficit (VPD), and (c-d) soil moisture at 0-25 and 45-105 cm depths from 2011-2013 at both TP39 and TP74.
Figure 3.3: Daily total values of sapflow-derived canopy transpiration ($E_t$) and eddy-covariance measured ecosystem evapotranspiration ($E$).
Figure 3.4: Daily averaged sapflow velocity ($J_s$) across all sensors at each of TP39 and TP74, presented as a 7-day moving average.
Figure 3.5: The frequency of daily lag time between sapflow and ecosystem evapotranspiration in the June-August period for 2011 to 2013.
Figure 3.6: Hydraulic redistribution (HR) and soil water content (SWC) at 0-25 cm depth, and precipitation (P) during seasonal drought. HR values for are given for days in which the two previous day’s P did not exceed 0.5 mm.
APPENDIX A: IMPACT OF THINNING ON SOIL NUTRIENTS AND ROOT DISTRIBUTION

Photosynthesis, and therefore growth and transpiration, of a forest are dependent in part upon soil nutrient supply (Beer et al. 2009). It follows that increased nutrient availability has been related to an increase in forest growth (Janssens et al. 2010; Moore et al. 2011). A literature search revealed that forest thinning has had a negative relationship with soil nutrient abundance: Vesterdal et al. (1995) found that as thinning intensity of Norway Spruce stands increased, carbon, nitrogen and phosphorous in the soil decreased relative to a control stand; thirty-three years after stand thinning, Nilsen and Strand (2008) found carbon and nitrogen to still be reduced in a thinned stand relative to the control. The impact of soil nutrient abundance upon growth and transpiration depends upon whether the forest in question is limited by nutrient availability. If nutrient supply exceeds demand both before and after the thinning, then no transpiration response would be expected.

At both TP39 and TP74, soil cores and litter samples were taken along a six-point transect in September 2014. A 20 x 20 cm segment of the litter layer was removed down to the initiation of the mineral soil. For each litter and soil sample, fine (<2mm) and small (2-5mm) were isolated and weighed. Processed soil samples were sent for nutrient analysis (A & L Canada Laboratories, Inc., London, Ontario). The samples were analyzed for total carbon, nitrogen, phosphorus, potassium, and magnesium among other things. Soil and root analyses were compared with results of previous studies at the Turkey Point sites by Peichl et al. (2006) and Khomik et al. (2010).
Both root biomass and soil nutrient profiles showed high spatial variability. Small and fine root biomass was similar between TP39 and TP74 (Figure A1a). The mean fine root abundance at TP39 was higher in 2014 by 2.7 t/ha, but this result was not significant. Both stands’ fine root abundance was greater in the 0-15 than the 15-25 cm layer (Figure A1b), however this was only significant at TP39 (p<0.05). Litter fine root abundance was highest at TP39, however fine root abundance in the litter layer was not significantly related to fine root abundance in the soil.

Compared with results from Peichl et al. (2006), there was significantly greater fine root biomass at TP39 (p<0.01), and no detectable change in root distribution at TP74.

Figure A1. Results of the present study compared with those from Peichl et al. (2006), showing (a) small and fine roots biomass across 0-35 cm, and (b) total root biomass at 0-15 and 15-35 cm depth classes.

Litter and soil characteristics were similar to those from a past study at TP39 and TP74 (Table 1). The two sites generally had corresponding gradients in nutrients abundance from litter horizon to 15-35 cm depth. At both sites, there was a significant increase in soil Mg from 15-35 cm.
Table 1: Selected nutrients and CN ratio of the litter fall horizon (LFH) and soil at depths of 0-15 cm and 15-35 cm. Values in brackets are from a past study (Khomik 2004)

<table>
<thead>
<tr>
<th></th>
<th>P (ppm)</th>
<th>K (ppm)</th>
<th>Mg (ppm)</th>
<th>CN ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>TP39</td>
<td>Litter</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0-15 cm</td>
<td>86.5 ±20.0</td>
<td>91.5±25.6</td>
<td>96.7 ±31.1</td>
<td>18.6 ±5.3</td>
</tr>
<tr>
<td></td>
<td>(123.8 ±31.1)</td>
<td>6.6 ±3.5</td>
<td>17 ±5.7</td>
<td>10.2 ±3.2</td>
</tr>
<tr>
<td></td>
<td>(139±18)</td>
<td>(12±5)</td>
<td>(10±3)</td>
<td></td>
</tr>
<tr>
<td>15-35 cm</td>
<td>137.2 ±35.4</td>
<td>3.3 ±2.3</td>
<td>20 ±3.2</td>
<td>6.7 ±1.7</td>
</tr>
<tr>
<td></td>
<td>(127±35)</td>
<td>(7±4)</td>
<td>(8±4)</td>
<td></td>
</tr>
<tr>
<td>TP74</td>
<td>Litter</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0-15 cm</td>
<td>62.5 ±18.2</td>
<td>89.5 ±32.8</td>
<td>97.7 ±25.6</td>
<td>22.6 ±6.5</td>
</tr>
<tr>
<td></td>
<td>(110.3 ±14.2)</td>
<td>6.83 ±2.6</td>
<td>19.2 ±5.9</td>
<td>14.1 ±1.9</td>
</tr>
<tr>
<td></td>
<td>(117±21)</td>
<td>(10±3)</td>
<td>(13±6)</td>
<td></td>
</tr>
<tr>
<td>15-35 cm</td>
<td>87.7 ±20.4</td>
<td>4.7 ±3.4</td>
<td>18.3 ±2.6</td>
<td>9.45 ±2.5</td>
</tr>
<tr>
<td></td>
<td>(106±23)</td>
<td>(6±2)</td>
<td>(6±2)</td>
<td></td>
</tr>
</tbody>
</table>

Soil nutrient and mineral content in 2014 being equivalent to 2010 measurements indicated that the TP39 site was in a state of equilibrium. This may be attributed to the sandy and well-drained soils, which do not have great capacity to retain nutrients (Silver et al., 2000). Another possibility for the lack of change is that there was a change in nutrients immediately following the thinning – either an influx due to felled trees and organic matter remaining on the ground, or an efflux due to the removal of large trees and forest floor disturbance – and our sampling was not timed properly to capture this change before equilibrium was restored, via drainage or further input. Furthermore, the woody debris may not have decomposed sufficiently to release all nutrients to the soil. The exception to this apparent stasis is Magnesium (Mg) in the 15-35 cm layer, which increased at both sites. Mg, which plays an important role in photosynthesis (Sun and Payn, 1999), has been found to rise in soils in response to litter decomposition over similar timescales by Burghouts et al., 1998 and Ostertag et al., 2003, This input may have similarly supported the increase observed at our Turkey Point sites.
References


APPENDIX B: GROUNDWATER TRENDS AND RELATIONSHIPS

From 2010 onwards, water table depth (WTD) was continuously measured at half hourly intervals using a pressure transducer installed in a well (OTT PLS pressure probe, CSI) at the TP39 site. WTD measurements are applicable to the TP74 site as well, because TP39 and TP74 are adjacent sites and the topography at both sites is relatively flat. The proximity of Lake Erie to the TP39 and TP74 sites (~2 km southeast) suggested that WTD fluctuations might be influenced by lake level. Daily lake level measurements from Port Dover (~15 km east of the TP39 and TP74 sites), attained through the Canadian Department of Fisheries and Oceans website, were used to investigate this relationship.

Water table depth measured at TP39 generally increased with spring recharge, then gradually declined over the growing season (Figure B1). The dry conditions of 2010 are clearly reflected in WTD, as well as the warm winter of 2012 through earlier recharge than either 2011 or 2013 (i.e. beginning in December-January versus February-March).

![Figure B1](image.png)

**Figure B1.** Daily water table depth measured at the TP39 site, and water level of Lake Erie measured at Port Dover, expressed in meters above the International Great Lakes Datum (IGLD), which is approximately equal to sea level.
At both TP39 and TP74 sites, the relationship between daily $G_s$ and WTD was strongest in the growing season of 2012 ($r^2 = 0.24$ and $0.12$, $\alpha < 0.001$, respectively), as expected with 2012 having the lowest PDSI values for the study period (Figure B1). With the exception of 2010 at TP39 ($r^2 = 0.12$, $\alpha < 0.001$), other years showed negative or non-significant relationships, illustrating that if taproot access of groundwater or capillary fringe resources does occur at these sites, groundwater levels themselves are likely controlled moreso by supply and demand factors external to the forest. For example, WTD measured at the TP39 site was significantly related to fluctuations in water level of the nearby Lake Erie, with the greatest correlation detected when water table depth was lagged by 44 days ($r^2 = 0.37$, $\alpha < 0.001$). This possible linkage casts doubt on the validity of inferring forest groundwater access in this scenario, despite apparent relationships with carbon-water exchange, due to potential external interference in WTD dynamics. However, the possible influence of Lake Erie water level on WTD at the TP39 and TP74 sites illustrated the importance of considering lake level, and controls thereupon, when monitoring and evaluating the forests’ water dynamics.