ATMOSPHERIC AND SOIL WATER LIMITATIONS ON WATER FLUX COMPONENTS IN A TEMPERATE PINE FOREST

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A Thesis
Submitted to the School of Graduate Studies
In Partial Fulfillment of the Requirements
For the Degree
Master of Science

McMaster University

MASTER OF SCIENCE (2007) McMaster University
(Geography) Hamilton, Ontario

TITLE: Atmospheric and soil water limitations on water flux components in a temperate pine forest

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NUMBER OF PAGES: viii, 52

ABSTRACT

Sap flow measurements scaled to represent canopy transpiration (E_c) and eddy covariance measurements of total forest water vapour flux (E) were compared with soil water, meteorological measurements and modelled interception estimates to quantify the above canopy flux of water to the atmosphere from a temperate White pine ecosystem located on the Norfolk sand plain at Turkey Point, Ontario, for the growing season of 2006. Hydraulic redistribution (HR) was found to have occurred at the site on 26 days during the study (growing season of 2006). During a drought period in June, the nightly increases in stored water (up to 0.50 mm) provided by HR reduced drought intensity in the root zone by maintaining soil water contents (θ) at levels above the water content associated with the approximate wilting point (θ of 0.07). Daily forest water fluxes (E) averaged 2.4 mm d^{-1} and reached maximums of 4 mm d^{-1} regularly. Canopy transpiration (E_c) averaged 1.2 mm d^{-1}. Modelled interception accounted for 18% of gross precipitation over the study period. E_c and interception loss (E_I) contribute the majority (81%) of the water vapour exchanged between the forest and the atmosphere. E_I accounted for 34% of E and E_c accounted for 47%. E_c was controlled linearly by atmospheric demand (VPD) until a variable transition point was reached, after which mid-day E_c rates remained relatively constant. E_c rates were limited to approximately 0.10 mm hh^{-1} through the study period. This limitation was sensitive to early morning VPD and soil water deficit. Increases in early morning VPD caused maximum E_c rates to arrive earlier in the day and to be reduced in magnitude. This shift in the timing and magnitude of E_c rates masked a relationship between E_c and soil water content that caused E_c to be strictly limited once root zone soil water content ($\theta_{0\text{-}25cm}$) reduced to ~0.07. This study illustrates that the water storage capacities of different site characteristics (particularly the canopy and soil) are an important factor to consider when investigating how changing precipitation characteristics might affect the hydrology of an ecosystem, and discusses the inter-relationship between transpiration, soil water supply and atmospheric demand.

ACKNOWLEDGEMENTS

I'd like to thank my supervisor, Dr. Altaf Arain, for giving me the opportunity to work with him and for his untiring devotion to his research. His guidance and knowledge have been instrumental in the writing of this thesis. Myroslava Khomik and Matthias Peichl were also instrumental in my success. I have to thank Matthias for his invaluable help, advice and constructive criticism. Just as valuable, however, was his humour and friendship for the past two years. Thanks. 'Hard workers save the planet.' Myroslava has to be thanked for her help, advice, and willingness to participate in long brainstorming sessions. I'll miss driving around the countryside with you - talking, laughing, and discovering new things and places to eat. It's been so much fun. I have to thank Matthias, Myroslava and Natalia Restrepo-Coupe for the parts of their research that laid the foundation for my project. To Rose Blair, Natalia, Shuhua Yi, Fengming Yuan and Jagdeesh Yeluripati: I learned so much about the world working alongside such a culturally diverse group and have to thank you all for your willingness to help me when I first started out. Mahmoud Pejam needs to be thanked for his friendship and great advice. I also want to thank Gabe Thompson and Wojtek Stepien for their open ears, helpful discussions, and just for being such great friends. I have to thank David Spittlehouse and Steve Williams for their wisdom, advice and technical support.

A lot of thanks have to go my mom and dad for their help, love and never-ending support. I couldn't have achieved anything without you. Also, thanks to my brother Miles for his advice and great help in the field.

And finally, thanks to my beautiful wife Sarah for helping more than anyone else. Your encouragement and support kept me going. Thanks. I'll love you forever.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1: INTRODUCTION

Evaporation is a fundamental process influencing terrestrial ecosystems. It is one of the major components of the surface energy balance and directly affects the behaviour of boundary layer climates, which in turn affect atmospheric circulation patterns and the weather (Kelliher et al. 1993). Terrestrial evaporation is also the main contributor to continental precipitation, with the forest evapotranspiration component returning roughly 60% of precipitation back to the atmosphere (Nosetto et al. 2005; Schafer et al. 2002).

The impact of global climate change on precipitation and temperature regimes in temperate areas threatens to significantly alter forest water budgets (Wullschleger and Hanson 2006). The most recent climate predictions for the Great Lakes region of North America suggest that elevated evapotranspiration due to future warming may cause reductions in runoff, thus decreasing stream flows and exacerbating periodic droughts, even while coupled with predicted precipitation increases (IPCC 1997; IPCC 2001). Some evidence also suggests that the intensity of precipitation events may increase as the precipitable water content of the atmosphere increases under global warming (IPCC 1997; IPCC 2001) affecting the amounts of precipitation being intercepted and returned to the atmosphere by forested landscapes.

Over many landscapes plants exert a strong control on evaporation processes because of their ability to access, transport and evaporate water that would otherwise be detached from terrestrial water cycles (Calder 1998; Nosetto et al. 2005). The effect of concurrent increases in precipitation and evapotranspiration on the water loss of forested ecosystems would likely depend on site specific soil and canopy water holding characteristics and their influence on the evaporation of intercepted water and canopy transpiration, but the topic is poorly understood.

The total evaporation from the forest (E) can be partitioned into four components: canopy transpiration (E_c), understorey transpiration (E_u), evaporation from the soil (E_s) and the evaporation of intercepted water (E_I). With E given as:

$$E = E_c + E_u + E_s + E_I \qquad (1)$$

E_I is difficult to measure and is often modelled based on common stand parameters. Previous partitioning studies have recognised the importance of canopy wetness as the main determiner of the source of the dominant components of above canopy water flux; i.e. when the canopy is wet E_I dominates, and when the canopy is dry E_c dominates (Barbour et al. 2005; Calder 1998; Farley et al. 2005; Grelle et al. 1997; Humphreys et al. 2003; Nosetto et al. 2005; Roberts 1983). The degree to which these two main components dominate the partitioning of forest water flux, on a daily or annual timescale, is largely determined by the openness of the canopy and character of the rainfall. Closed canopy forests often see limited contributions from the other sources of forest water flux (understorey transpiration, E_u and evaporation from the forest floor, E_s) because of the small amounts of advected and radiant energy available below the canopy (Wullschleger et al. 1998a), whereas open canopy forests may see much larger contributions from these components (Barbour et al. 2005; Calder 1998; Unsworth et al. 2004). In closed canopy planted forests with a high Leaf Area Index (*LAI*), and uniform canopy structure it would be expected that evaporation from the soil and understorey (E_s and E_u) would contribute little to the total ecosystem water flux, *E*.

Extensive work has been conducted investigating the control of canopy transpiration, E_c by comparing measurements of sap flow velocity with environmental variables. Transpiration is the process by which water evaporates from a plant, in the presence of light and atmospheric CO_2, through small openings on the surface of leaves called stomata. This evaporation in turn draws water up through the plant (via sap flow within the xylem) from the soil. Transpiration distributes water throughout the plant, used in photosynthesis, to produce carbohydrates. Transpiration also serves to maintain turgidity in cells and tissues, and to bring dissolved minerals in to the plant from the soil (Arnell, 2002). Very little water is used in the photosynthetic process and most of the water drawn into the plant is evaporated (Arnell, 2002). The ascent of xylem sap depends on transpiration and the physical properties of water. Xylem sap flow in the stem can be used to estimate tree transpiration by scaling point measurements of sap flow velocity to represent the whole stem. Sap velocity can be measured using the difference in heat dissipation caused by the flow of sap between heated and unheated thermocouples.

Multiple independent studies have shown that much of the variation in E_c can be explained by variation in vapour pressure deficit (*VPD*). After reviewing relevant literature the prevalence of two recurring findings regarding the control of transpiration by evaporative demand becomes clear; a strong linear relationship is exhibited until a transition point *VPD* is reached and often this relationship is sensitive to soil water supply. Barbour et al. (2005) reported that E_c can be expressed as a strong linear regulation of E_c by *VPD* until a transition point of approximately a *VPD* of 0.60 kPa in a temperate coniferous rainforest. Similarly linear dependencies of E_c to *VPD* were found to exist until a transition point *VPD* of 1.00 kPa in both a temperate hardwood forest in Michigan, U.S.A. (Bovard et al. 2005) and a boreal Trembling aspen stand in Saskatchewan, Canada (Hogg and Hurdle 1997). In each of these cases the lack of a transpiration response to *VPD* above a threshold value was concluded to be a stomatal response to high *VPD*. Other studies have shown that when soil water supply is limited, E_c varies with *VPD* over a much narrower range of *VPD* and the flux of E_c is suppressed or dampened at all but the lowest *VPD* values (Wilson et al. 2001; Wullschleger et al. 1998a).

The pattern of the limitation response of E_c to high *VPD* and low soil water deficit appear similar and are often concurrent, sometimes making interpretation difficult (Kurpius et al. 2003; Oren and Pataki 2001) and it is unclear how E_c responds to the combined effects of *VPD* and soil water content (Kurpius et al. 2003). Soil water supply is important to carbon fluxes within forests, influencing stomatal conductance as well as heterotrophic and autotrophic respiration (Unsworth et al. 2004). The knowledge surrounding the effect of soil water variability on water flux components in temperate conifer ecosystems is relatively limited; soil water is thought to limit transpiration when extreme deficits are present (Roberts 2000) and the sensitivity of the relationship between canopy transpiration and atmospheric demand to soil water supply variations is poorly understood (Bovard et al. 2005). Relatively little is known about how soil water content and atmospheric demand interact to influence canopy transpiration, though it has been suggested that a strong negative feedback between atmospheric demand and canopy conductance, coupled with an insensitivity to typical soil water variations results in similar growing season canopy transpiration rates between forests (Humphreys et al. 2003; Oren and Pataki 2001; Roberts 1983). Relevant studies have shown that stomatal conductance is unaffected by volumetric soil water content until a deficit occurs, at which point transpiration is limited as trees close stomata, conserving water (Bovard et al. 2005; Cinnirella et al. 2002; Irvine et al. 1998; Phillips and Oren 2001; Roberts 1983; Roberts 2000; Wilson et al. 2001; Wullschleger et al. 1998a). The deficit required to induce change in canopy transpiration differs from site to site, most likely due to differences in vegetation type and soil texture as different plants respond differently to given soil water states (Roberts 2000).

In recent years it has been shown that trees can counteract some of the affects of soil water deficit by passively redistributing soil water and facilitating maximum water utility. Hydraulic redistribution is the transfer of water from moist soil to drier soil via the plant root system when the root system spans a gradient in soil water potential, where the root system acts as a conduit taking advantage of the water potential gradient between non-adjacent soil layers. It occurs passively when transpiration reduces and the xylem water potential rises above the soil water potential of the dry soil, at which point the resistance to water loss from the plant roots becomes low enough that water will move from the roots to the dry soils, over time effectively transferring water from moist soil to dry soil, vertically or laterally (Caldwell et al. 1998).

1.2 Hypotheses and objectives

In this study we measure whole ecosystem water flux, E in a temperate white pine forest ecosystem using an eddy-covariance system and compare this estimate with estimates of canopy transpiration, E_c obtained by scaling up measurements of sap-flow from the dominant White pines, and with evaporation of intercepted water, E_I estimates calculated using a well-established interception model developed by Gash (1979).

The objectives of this study are to:

(1) Quantify the above canopy flux of water to the atmosphere from a temperate White pine ecosystem located on the Norfolk sand plain at Turkey Point, Ontario, for the growing season of 2006.

(2) Estimate the magnitude of the primary components of the above canopy water flux.

(3) Assess the possible environmental limitations of canopy transpiration at the site.

We hypothesized that E_c and E_I would account for the majority of the water flux from the forest. We also hypothesized that *VPD* will act as both a control and limitation on E_c and that the sensitivity of E_c to changes in *VPD* will be affected by changes in soil water supply, thus also limiting E_c.

1.3 Significance of study

This work is intended to foster a broader understanding of seasonal water cycling in temperate forests. It also highlights the importance of the coupling between climate and site (forest) characteristics. By comparing water fluxes, measured at the whole ecosystem and whole tree scales, with variations in soil water content and vapour pressure deficit, we seek to gain knowledge of the physical mechanisms limiting forest water use. Improved understanding of these mechanisms would allow better assessments of the effects of future climate changes on water budgets at varying scales. Changes in temperature, precipitation, and vegetation cover can affect the balance between transpiration and interception, and the magnitude of evaporation from a landscape. There is a need for better consideration of ecosystem hydrology when land use decisions are made, particularly in an era pressured by global climate change and an increasing human population.

CHAPTER 2: FOREST WATER USE AND GLOBAL CLIMATE CHANGE

The future consequences of climate change to temperate forested ecosystems are unknown, but the ecological changes could prove to be devastating. Large scale changes in temperature and continental precipitation are expected to change the existing ranges of entire biomes, plant diseases and plant pests. These changes coupled with past and future introductions of invasive plant and insect species would substantially alter the biogeographic distribution of forested ecosystems. Climate and vegetation are in an ever changing balance, held together by their reciprocal influences feeding back on one another (Nosetto et al. 2005). Forests have a significant impact on the hydrologic characteristics of a landscape, dictating the partitioning of the energy, the amount of turbulent transfer and the amount of available water involved in evaporation, runoff and recharge (Arnell 2002). It has been shown that significant changes to cloud cover in the Amazon basin occurred when a value of 20% deforestation in the region was reached due to a significant reduction in evapotranspiration (Nosetto et al. 2005). Likewise, the impact of global climate change on precipitation and temperature regimes in temperate areas threatens to significantly alter forest water budgets (Wullschleger and Hanson 2006), and the rise in global atmospheric CO_2, believed to cause climate change, has the potential to affect forested ecosystems physiologically, modifying mass and energy exchanges; thus further altering forest water budgets and influencing global water cycles (Schafer et al. 2002). The end result of changes to these complex inter-related systems remain to be seen and are the subject of a lot of scientific speculation and investigation.

Though temperate forests cover much of the globe (12.0×10^{12} m^2, or roughly 8%) (Whittaker and Likens 1975) relatively few attempts have been made to study the biome's role in regional and global water cycles. It is now of great interest to understand the role of transpiration from temperate forests in regional and global water cycles and to assess the impacts of possible climate change, land-cover change and the various feedbacks between transpiration and changing environmental factors in these forests. Transpiration is inextricably linked to other forest hydrologic processes, particularly the evaporation of intercepted water and soil moisture availability. Transpiration processes are strongly coupled with plant growth and carbon assimilation, and the processes are in turn affected by atmospheric CO_2 concentrations, temperature and soil moisture availability (Arnell 2002).

The partitioning of ecosystem evaporation becomes an important factor when comparing the water losses of differing vegetation types. In general, it can be said that forests are more closely 'coupled' with the state of the atmosphere than are shorter vegetation types during dry periods (Kelliher et al. 1993). Forests have the ability to evaporate much larger amounts of water on a seasonal or annual basis than areas where forest trees have been removed and replaced with grasses or crops, given equivalent soil water availability, precipitation frequency and precipitation intensity, due to their relatively moderate to high rates of transpiration and much greater rates of interception evaporation (Kelliher et al. 1993; Kelliher et al. 1995). Changes in climate, precipitation, and vegetation cover can greatly affect the balance between transpiration and interception, and thus the magnitude of evaporation from a landscape.

An interesting experiment was established in 1993 to examine the sensitivity of a temperate forest ecosystem to ambient, wet (+33%) and dry (-33%) precipitation regimes, by means of a throughfall displacement (Wullschleger, Hanson 2006). Canopy scale transpiration was measured and it was found that the treatment did illicit a response (Wullschleger, Hanson 2006). As expected transpiration declined (26 – 30%) with a decline in precipitation and increased (9% on average) with an increase in precipitation, as compared to ambient precipitation conditions (Wullschleger and Hanson 2006).

Most ecosystem scale studies have shown that transpiration per unit area doesn't decrease significantly as CO_2 concentrations increase because the increased water use efficiency (WUE: ratio of carbon uptake (i.e. biomass growth) to transpiration) is offset by additional plant growth, thus having little net effect (Arnell 2002; Li et al. 2003; Schafer et al. 2002). Interestingly, overall ecosystem evapotranspiration doesn't decrease with decreasing transpiration rates either, in fact an increase in growth following a rise in CO_2 concentration would offset any decrease in transpiration by increasing leaf area indexes (*LAI*) and provide added evaporation of intercepted water (Schafer et al. 2002). Again the importance of the balance between transpired and intercepted water on maintaining relatively stable evaporation rates in forested ecosystems becomes apparent and suggests that forests have a moderating effect, by dampening changes to the climate and hydrological cycle. Any changes to forest extent or type, due to changes in climate or land-use, would alter these effects. This highlights the importance of characterizing the effects of changes in climate and hydrology on different forest types.

With increasing CO_2 concentrations, all of the models produce an increase in global mean precipitation (IPCC 1997; IPCC 2001). A warming atmosphere leads to a higher atmospheric water vapour content and an enhanced pole-ward movement of water vapour, because increased energy availability at the earth's surface will influence circulation patterns (IPCC 1997; IPCC 2001). This will enhance vapour convergence and precipitation in higher latitudes (IPCC 1997), and in general terms should prove to increase precipitation in the higher latitudes and some tropical regions, and lower precipitation everywhere else (Arnell 2002). For this reason better understanding the relationships between the water loss from temperate forested ecosystems, soil water content dynamics and precipitation characteristics will play a vital role in predicting and adapting to the effects of global climate change.

CHAPTER 3: METHODS

3.1 Site description

The Turkey Point Flux Station is located near Turkey Point, Ontario, Canada (42°71'N, 80°35'W). A 26 m tower was erected in 2002 to monitor mass and energy exchange above the 20 m tall 68 year old forest (Peichl and Arain 2006). The stand is owned and maintained by the Ontario Ministry of Natural Resources (OMNR). The stand was planted, in 1939, on top of a gently undulating (slopes of 0.5 – 3.0° maximum) abandoned wind-blown sand dune system located 3 km north of Lake Erie, but overall the surface of the site can be characterised as flat (Restrepo and Arain 2005). The species composition of the stand is presently dominated by planted White pine (*Pinus strobus* L.) (82%) mixed with Balsam fir (*Abies balsamea* L.) (11%). There is also an emergent population of native Carolinian species mixed through the stand in the intermediate and understorey layers, comprising of oak (*Quercus velutina* L., *Quercus alba* L.) (4%); Red maple (*Acer rubrum* L.) (2%); and Wild black cherry (*Prunus serotina* Ehrh.) (2%) (Peichl and Arain 2006). The understorey is patchy and varies in density through the stand, ranging from sparse in some locations to moderately heavy in areas below gaps in the canopy. The understorey is largely dominated by the deciduous tree species and a variety of forest floor plants. The spacing of the planted White pine varies from 3 × 3 m to 5 × 6 m. A thinning, with a total extracted wood volume of 105 m^3 ha^{-1}, was conducted in 1983. A large patch of oak trees (~ 100 m × 160 m) is located 200 m east of the tower. The stand has an *LAI* of 8.0 (Chen et al. 2006). Important stand characteristics are presented in Table 1.

Table 1. Stand characteristics

Stand parameter	
LAI	8.0
DBH (cm)	34.6 (±5.9)
Base diameter (cm)	39.4 (±7.9)
Tree height (m)	20.2 (±2.1)
Stand basal area (m^2)	37.3
Stem density (stems ha^{-1})	429 (±166)

This landscape is considered to be part of the Norfolk sand plain, a coarse textured glacio-lacustrine deposit (Corporation of Norfolk County et al. 2003). The soil is a brunisolic grey brown luvisol, with a very fine sand to fine sandy loam texture, making it predominantly well drained with low water holding capacities (Restrepo and Arain 2005). The typical soil profile contains a 20 cm Ap horizon, above a 30 cm thick Bm1 horizon and a Bm2 horizon up to 70 cm thick (Arain and Restrepo-Coupe 2005). The average bulk density of the soil in the Ap and Bm1 horizons is 1350 kg m^{-3}. The mineral soil is overlain by a 3-5 cm thick litter layer (Arain and Restrepo-Coupe 2005). Fine root (< 2mm) biomass, important for the uptake of water and nutrients, decreases rapidly with depth from 1.2 mg cm^{-3} in the 0-15 cm depth class to 0.49 mg cm^{-3} in the 15-35 cm depth class, and finally to 0.35 mg cm^{-3} in the 35-55 cm depth class (Peichl 2005). Approximately two thirds of total root biomass is found in the 0-15 cm depth range (Peichl 2005). The water table generally lies 6-9 m below the surface (Corporation of Norfolk County et al. 2003). The estimated water content at the field capacity is 0.16 volumetric soil water content (vol. $vol.^{-1}$) and the estimated water content at the wilting point is 0.07.

The region has a mean annual temperature of 7.8 (±1.3) °C, an annual precipitation of 1010 mm, with 878 mm (87%) precipitating as rain and 133 mm (13%) as snow, and an average of 2021 hours of bright sunshine per year (30 year (1971 – 2000) climate normals established at Delhi located ~ 20km north of the Turkey Point Flux Station (Environment Canada 2005)). Daily precipitation accumulations of $\geq$ 0.2 mm have an approximate exceedance interval of 13 days, accumulations of $\geq$ 5 mm are exceeded approximately every 20 days, accumulations of $\geq$ 10 mm are exceeded approximately every 23 days, and accumulations of $\geq$ 25 mm are exceeded approximately every 51 days. Daily precipitation accumulation exceedance intervals were calculated from Delhi 30 year climate normals (Environment Canada 2004).

The approximate phenology of the coniferous and deciduous species within the stand was noted as observed during the growing season of 2006 with widespread bud break occurring in the 2nd week of April, first leaf date occurring in the 4th week of April, and full leaf development occurring in the 3rd week of May. Senescence began during the 2nd week of October and completed in the 3rd week of November. Therefore, the growing season for this study was defined as May 1st through to September 31st.

3.2 Microclimate

Air temperature and relative humidity were measured at heights of 28, 14 and 2 m using three sets of temperature and humidity probes (HMP45C; Campbell Scientific, Utah, U.S.A.). Wind speed and direction were measured above the canopy using a propeller wind vane and anemometer (05 103; R.M. Young, Michigan, U.S.A.). Incoming and outgoing shortwave and long-wave radiation above the canopy were monitored using a four dome net radiometer (CRN1; Kipp and Zonen, Delft, Netherlands), where net radiation is then derived by summing net shortwave and net long-wave radiation measurements. Photosynthetically active radiation (*PAR*) was monitored above the canopy using a filtered and diffused photodiode sensor (PAR LITE; Kipp and Zonen). Soil temperature was measured in two profile pits with soil temperature probes (107B; Campbell Scientific) buried at depths of 2, 5, 10, 20, 50 and 100 cm below the surface in both pits. Leaf wetness was measured in the canopy at a height of 18 m and near the forest floor at 1 m using electrical impedance grid leaf wetness sensors (237; Campbell Scientific). All meteorological and soil data were recorded as half hourly averages using two data loggers (CR23X; Campbell Scientific). Every day of the growing season was separated into classes based on rainfall amount and leaf wetness duration in order to compare water fluxes under differing canopy wetness states. We adopted a classification scheme similar to the one used by Barbour et al. (2005). Wet days were defined as days where more than 2 mm of rain fell, the below canopy leaf wetness sensor was wet for more than 30% of the day and the within canopy leaf wetness sensor was wet for any length of time. Days were considered dry if less than 2 mm of rain fell, both leaf wetness sensors were completely dry for the entire day and no more than a total of 2 mm of rain had fallen over the previous 3 days. All remaining unclassified day was then deemed as intermediate.

3.3 Soil water content

Half hour variations in the average volumetric soil water content (unitless; vol. vol.$^{-1}$) in the 100 cm soil profile were estimated using 10 water content reflectometers (CS615; Campbell Scientific) in two profile pits at depths of 5, 10, 20, 50 and 100 cm. Each estimate was corrected for temperature, at depth, using the manufacturer's temperature correction based on concurrent soil temperature measurements located in the same pits and at the same depths. The spatial variability of volumetric soil water content of the 0-20 cm soil layer was measured 12 separate times, at 12 points along a 100 m transect during the growing season of 2006 using a hand held water content reflectometer (CS620, Campbell Scientific Inc., Edmonton, AB). From this data the spatial soil water content can be shown to have an average daily coefficient of variation of 20% over the course of the growing season, ranging from 12% to 39%. The key soil water variable used in our analysis was the root zone volumetric soil water content ($\theta_{0\text{-}25cm}$), defined as the depth-weighted average soil water content from the six sensors located in the 0 to 25 cm soil profile.

The appropriateness of using water content reflectometers for estimating short term soil water content variations has been questioned in the past due to concerns about the temperature sensitivity (Seyfried and Murdock 2001). After applying the manufacturer's temperature correction the pattern of variation in soil water content was unaltered. Based upon field and lab comparisons with independent measurements of soil water content, the manufacturer's calibration equations were shown to be accurate (data unpublished). These results were the basis of our conclusion that, not unlike recent conclusions made by Unsworth et al. (2004), the additional uncertainty associated with using water content reflectometers caused by the temperature sensitivity of the associated above ground electronics, the influence of varying soil properties and the influence of moisture content would be accepted and not corrected for in our analysis.

3.4 Precipitation, throughfall and evaporation of intercepted water

Gross precipitation (P_G) was measured using a heated tipping bucket rain gauge (52 202; R.M. Young) placed on a boom three meters from the tower, at a height just below the tree tops (20 m) to avoid under-catch during high wind conditions. These measurements were cross checked with data from Environment Canada's Delhi weather station and a similar tipping bucket rain gauge located ~ 20 km west of the tower site and three standard bucket rain gauges deployed at the Turkey Point site (located near the tipping bucket gauge at the top of the tower and one in a small nearby clearing). All gauges showed consistent data (data not shown).

Net precipitation, otherwise known as throughfall (P_n), was measured using an 8.0 × 0.1 m v-shaped aluminium trough that funnelled collected water into a single tipping bucket rain gauge (CS700; Campbell Scientific) with a bucket resolution of 8 ml per tip, installed below the canopy near the main tower. Frequent clogging of the throughfall apparatus and tipping bucket overflow during intense storms proved problematic and most of the data from the larger storms was unusable. The relationship between rainfall and throughfall for 15 lower-intensity storms free from apparatus clogging and preceded by at least 8 hours of daylight without rain was used in the Gash model parameter derivation. The data was used to estimate the canopy storage capacity (S) and free throughfall coefficient (p) of the canopy, using the 'mean method' as outlined by Klaassen et al. (1998). These stand structure parameters were then used in conjunction with micrometeorological measurements to calculate daily evaporation of intercepted water (E_I) using a modified version of the Gash analytical model of rainfall interception by forests (detailed below), which has been well established for decades (Gash 1979; Klaassen et al. 1998; Link et al. 2004). It was assumed that stem-flow made a negligible contribution to the water balance and was therefore omitted (Link et al. 2004). The Gash model describes E_I based on an analysis of individual storm events. The evaporation from a saturated canopy (E_w) is estimated from the Penman-Monteith equation (Monteith 1965).

The physical process of interception evaporation is very well understood and it has been predicted to acceptable accuracy for many years using less sophisticated methods than the model used here (Roberts 1983). Estimates used for comparison in water flux studies are often simply calculated based on interception fraction found in similar forests (Hogg et al. 1997) or taken as the remainder of a mass balance equation (Barbour et al. 2005). However, it has been shown that assuming static values for p and S in interception modelling can introduce significant errors into modelled estimates (Link et al. 2004); therefore the model was only used to give an estimate of interception loss for comparison with total evapotranspiration and canopy transpiration. The interception model (Gash model) used in this study, was modified slightly to enable it to calculate total intercepted evaporation on an event basis rather than summing over larger periods of time, e.g. a month or entire season, as described by Gash (1979). This was done by calculating the daily interception total for days when the recorded precipitation was enough to saturate the canopy, and for days when the recorded precipitation wasn't large enough to saturate the canopy separately.

The aerodynamic resistance term (r_a) (s m^{-1}) was calculated as follows:

$$r_a = \frac{u}{u*^2} \qquad (2)$$

where u is horizontal wind speed (m s^{-1}) and $u*$ is the friction velocity (m s^{-1}). E_w (kg m^{-2} s^{-1}) is calculated for half hours when the P_G is greater than 2.25 mm using:

$$E_w = \frac{\Delta R_n + \rho C_p \, VPD/r_a}{\lambda(\Delta + \gamma)} \qquad (3)$$

where Δ is the slope of the saturation vapour pressure curve at air temperature (kPa $°C^{-1}$); R_n is net radiation (W m^{-2}); ρ is the density of air (kg m^{-3}); Cp is the specific heat of air at constant pressure (J kg^{-1} $°C^{-1}$); γ is the psychrometric constant (kPa $°C^{-1}$); and λ is the latent heat of vaporization of water (J kg^{-1}). In the model, evaporation after rainfall has ceased, the evaporation from storms too small to fully saturate the canopy and the wetting up of the canopy are all treated as separate terms (Gash 1979). Working under the assumption that those half hours with $P_G \geq 2.25$ mm represented conditions where the canopy was fully saturated. These values were then averaged to estimate the mean evaporation rate from a saturated canopy during rainfall:

$$\overline{E}_w = \frac{\sum_{i=1}^{n} E_{wi}}{m} \qquad (4)$$

where m represents the number of half hour periods (which are denoted as the ith period) when $P_G \geq 2.25$ mm. The mean rainfall rate ($\overline{R}$) during those same half hour periods is given as:

$$\overline{R} = \frac{\sum_{i=1}^{n} P_{Gi}}{m} \qquad (5)$$

The rainfall amount at the point at which the canopy reaches saturation (P'_G) is then given by:

$$P'_G = (-\overline{R}\,S/\overline{E}_w)\ln\{1 - (\overline{E}_w/\overline{R})(1-p)^{-1}\} \qquad (6)$$

Assuming that these mean rates apply, and that stem-flow contributed a negligible amount to evaporation during storm events and need not be included, it follows that the evaporation generated by a storm event large enough to saturate the canopy, E_{Ij} (denoted as the *j*th event) is then given by:

$$E_{Ij} = (1-p)P'_G + (\overline{E}_w/\overline{R})(P_{Gj} - P'_G) \qquad (7)$$

and E_{Ik}, the evaporation generated by a storm event that was not large enough to saturate the canopy (denoted as the *k*th event) is given by:

$$E_{Ik} = (1-p)P_{Gk} \qquad (8)$$

3.5 Sap-flow and canopy transpiration

White pine xylem sap flow was measured using 30 mm long, 1.3 mm diameter, Granier style (Granier 1987) continuously heated thermal dissipation probes (TDP-30; Dynamax, Houston, Texas). Each set of probes consists of two cylindrical thermocouple probes, one heated and one unheated, working on the principle that the thermal conductance of sapwood increases with sap flow velocity. Measurement of the temperature difference (ΔT) between the heated and unheated probe yields a dimensionless flow index (K) which is then used in the calculation of xylem sap flow (J_s) with an empirical relation developed by Granier (1987). The temperature differentials were continuously recorded throughout the year, with half hourly mean values stored using a data logger (CR10X; Campbell Scientific). Probes were installed approximately 1.3 m above the base on the northern side of six mature White pine located within the 20 × 20 m study plot. The study area is within a planted forest where the individual trees are generally of a uniform size and the sample trees were chosen to represent the size distribution of the stand. There is a need for forest hydrologists to estimate transpiration on a ground area basis and due to practical limitations the individual contribution of every single plant to canopy transpiration cannot be measured and thus estimates must be spatially scaled up from a limited number of representative individuals located within a single study plot. Selecting six of the dominant individuals that represent the size distribution of the stand was deemed to be the best way to represent the average sapflow per ground area of the White pine in the stand as accurately as possible with the resources available. All sample tree *DBH*'s are different and were chosen to be within ±2 SD of the mean, in order to represent ~95% of the size distribution within the stand, while only selecting from trees located within the 20 m × 20 m study plot. The biometric characteristics of all six trees are presented in Table 2. All probes were shielded from the effect of direct solar heating using a reflective, foil coated bubble wrap to minimize non-sap flow related temperature fluctuations. The bark at the probe insertion point was removed to a depth just before the boundary with the phloem. Sapwood depth near the insertion point was determined using a wood core to estimate the amount of non-conducting tissue in contact with the probes. The sapwood depth of each tree was quite uniform and between 5 - 7 mm of non-conducting tissue was in contact with each probe. Corrections were made for the proportion of the probes in contact with non-conducting tissue following Clearwater et al. (1999). The Granier style probes integrate the sap flow over the entire radial thickness of the sapwood they are in contact with and in each case our probes were in contact with 100% of the radial sapwood at their insertion points. The xylem sap flow of each sample tree was calculated following Granier (1987) using the following equations:

$$K_i = \frac{\Delta T_{\max i} - \Delta T_{ti}}{\Delta T_{ti}} \tag{9}$$

$$J_{si} = 0.119 \times 10^{-3} K_i^{1.23} \tag{10}$$

where $\Delta T_{\max i}$ is the maximum temperature differential; ΔT_{ti} is the temperature differential at time step t, K_i is the dimensionless sap flow index; and J_{si} is the sap flow velocity (m s^{-1}) for the ith tree.

Two of the main issues in the scaling of sap flow velocity up to stand level canopy transpiration are heterogeneity in sapwood conductance and heterogeneity in stand properties (Kurpius et al. 2003) but the evenly spaced trees within planted forests tend minimize differences in xylem sapwood between trees and differences in stand properties, and thus should be minimized in this planted forest dominated by even-aged, evenly-spaced white pine, located on a flat, texturally homogeneous, and well drained soil (Kostner et al. 1998).

Sap flow velocity was scaled to stand level canopy transpiration (E_c) by calculating the transpiration per unit ground area for each of the sample trees then averaging them. This was accomplished using stand characteristic metrics and allometric equations developed from destructive harvesting and a forest inventory conducted in 2004 (Peichl and Arain 2006). Cross sectional sapwood area of each sample tree was calculated using a previously unpublished stand specific allometric equation developed from the 2004 harvesting experiment (r^2 = 0.92) relating sapwood area (A_s) (m^2) to diameter (m) at 1.3 m (DBH):

$$A_s = 0.815 DBH^{2.2254} \tag{11}$$

Transpiration per unit ground area (E_T) for each tree was calculated each half hour using measured J_s and the tree specific sapwood area to ground area (A_g) ratio. $A_s : A_g$ was calculated for each tree (denoted as the ith tree) using:

$$A_{si} : A_{gi} = B_A (A_{si} : A_{wi}) \tag{12}$$

where $A_s : A_w$ is the ratio of tree sapwood area to total tree wood area (A_w) at 1.3 m above the ground and B_A (m^2 m^{-2}) is the basal area of the stand. Transpiration (kg m^{-2} s^{-1}) for each tree is then calculated as:

$$E_{Ti} = \rho_w J_{si}(A_{si} : A_{gi}) \tag{13}$$

where ρ_w is the density of liquid water (kg m^{-3}). Stand level canopy transpiration per unit ground area, E_c (mm hh^{-2}), was then calculated by averaging the E_T (kg m^{-2} s^{-1}) from the sample trees:

$$E_c = \frac{\sum_{i=1}^{n} E_{Ti}}{n} \tag{14}$$

where n is the number of trees sampled, and then converting to half hourly hydrologic units (mm hh^{-1}) of water flux.

Table 2. Sample tree characteristics

Tree	*DBH* (m)	radius (m)	A_w (m^2)	A_s (m^2)
1	0.443	0.222	0.154	0.038
2	0.355	0.178	0.099	0.023
3	0.400	0.200	0.126	0.030
4	0.430	0.215	0.145	0.035
5	0.261	0.130	0.054	0.012
6	0.463	0.232	0.168	0.041

3.6 Whole ecosystem water flux

Whole ecosystem water flux (E) was measured using the eddy covariance technique according to Fluxnet-Canada protocols (Fluxnet Canada 2003). Reynolds decomposition is used to calculate turbulent statistics and associated eddy fluxes from high frequency (sampled at 20 Hz) measurements of wind speed and direction in three dimensions, and H_2O mixing ratio, where water fluxes are then calculated as the covariance between the fluctuation in vertical wind speed and water vapour concentration. All flux measurements were made using a closed path Eddy Covariance (CPEC) system located 28 m above the forest floor consisting of a sonic anemometer (CSAT3; Campbell Scientific), an infrared gas analyser (IRGA) (LI-7000; LI-COR) and a 12.5 μm diameter (fine-wire) thermocouple. The IRGA was housed in a fully climate controlled box located at the top of the tower. Sample air was drawn through a 4.5 m long Dekaron tube (4 mm i.d.) and into the IRGA sample cell using a diaphragm pump (DOA-V191-AA; Gast Inc., Ohio, U.S.A.). The short tube length precluded the use of frequency-response (lag) corrections. To prevent condensation within the tube it was wrapped in thermal insulation and heated with a heating wire coiled around its length. All raw CPEC flux data was saved on a computer housed in a climate controlled trailer at the base of the tower. A detailed description of all corrections, calibrations and gap-filling procedures applied are provided by Arain and Restrepo-Coupe (2005).

3.7 Data processing and statistical analysis

All data were post-processed using the MatLab 7.1 software package (MathWorks Inc.). Statistical tests were conducted using the SPSS 12.0 statistical software package (SPSS Inc.). The association between *VPD* and E_c was determined by least squares linear regression. A one-factor analysis of variance with a Tamhane's T2 post-hoc multiple comparison of observed means test was conducted to investigate the effect of daily mean *VPD* between 600 and 800 hours (VPD_{in}) on half hourly diurnal E_c. Mean values are presented with associated standard deviations given in parentheses (i.e. μ ($\pm\sigma$)) when applicable.

CHAPTER 4: RESULTS

4.1 Microclimate

Variations of daily total photosynthetic photon flux density or photosynthetically active radiation (*PAR*), mean mid-day air temperature (T_a), mean mid-day saturation vapour pressure deficit (*VPD*) and mean daily root zone soil water content ($\theta_{0\text{-}25cm}$) for the 2006 growing season (May-September) are shown in Figure 1. The growing season would best be characterised as warm and wet, with temperatures regularly exceeding 20 °C, with a maximum of 32.5 °C (July 16th), a minimum of 0.6 °C and an average mid-day temperature of 18.6 °C. 2006 was a particularly wet year and total growing season P_G (697 mm) was 34% greater than the 30-year normal P_G (520 mm) for the region (Fig. 2b). Variations in T_a and *VPD* followed incoming solar radiation closely. On several occasions *VPD* rose above 2.00 kPa as a result of clear hot conditions, reaching a maximum of 2.90 kPa on July 16th, which corresponded with the maximum observed T_a for the year. *PAR* fluctuations indicate frequent cloudy conditions, with highs above 30 mol m^{-2} d^{-1} regularly occurring on clear days. Maximum incoming *PAR* observations occurred in mid June and mid July. These maximums correspond with observed maximums in T_a and *VPD*. All indications point to a strong interdependence between T_a, *PAR* and *VPD*. There was a strong coupling between the canopy and the atmosphere, as indicated by the high daytime aerodynamic conductance ($G_A = {}^{1}\!/_{r_a}$) at the site, which generally ranged from ~100 mm s^{-1} to ~350 mm s^{-1} (data not shown) (Bovard et al. 2005; Hogg et al. 1997).

The spring (May 2006) was cool and wet until a sharp increase in temperature in late May. Precipitation totalled 107 mm in May (Fig. 2b) 29% greater than the 30-year normal of 83 mm. Consequently $\theta_{0\text{-}25cm}$ remained high for most of the month (Fig. 1d). June was seasonably warm but dry with only 62 mm of rain falling, roughly 25% less rain than normal. The site experienced a dry period during late June and early July. During this early summer dry period $\theta_{0\text{-}25cm}$ remained quite low at values below 0.10 for exactly one month (June 10th to July 10th, 2006) despite numerous rain events totalling 50 mm of rain. $\theta_{0\text{-}25cm}$ reached a minimum during this period (on July 2nd) of 0.06; thus dropping below the soil water content associated with the approximate wilting point (0.07) and indicating the presence of drought conditions. The rest of the summer was seasonably hot and uncharacteristically wet. Repeated storms brought 528 mm of rain over the months of July, August and September. For the same period the 30 year normal precipitation is 270 mm (49% less than observed). During one short dry period in early August $\theta_{0\text{-}25cm}$ returned to levels below 0.10, but otherwise $\theta_{0\text{-}25cm}$ steadily rose as temperatures declined and the unseasonably frequent and large precipitation events continued to occur.

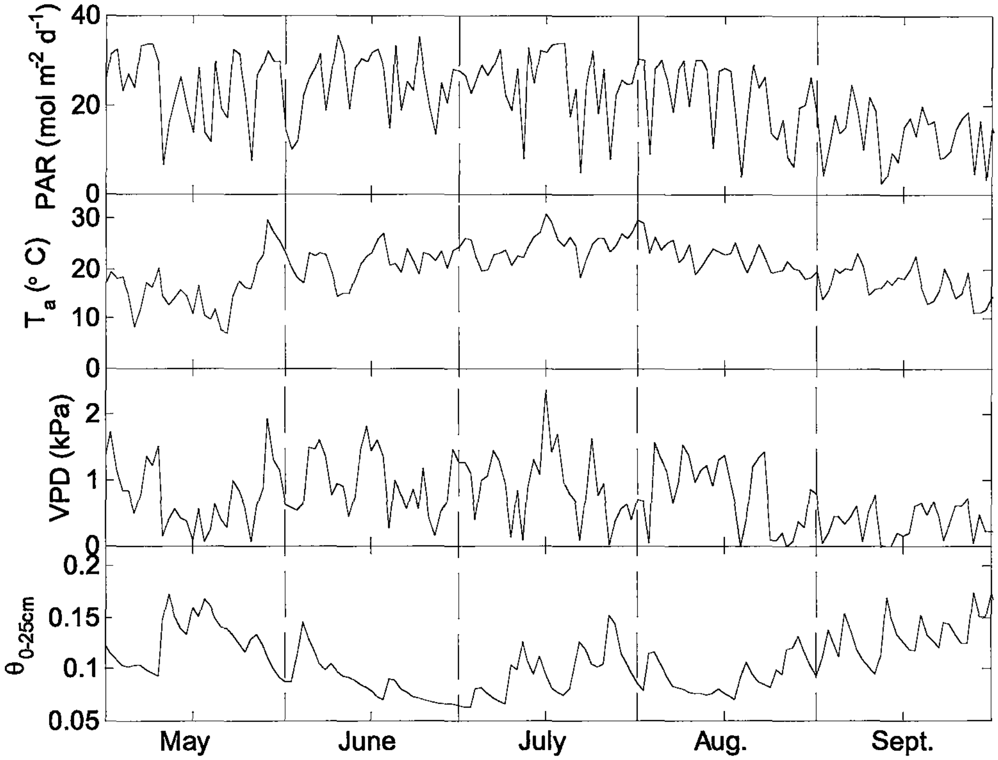

Figure 1. Meteorological measurements. a) mean daily photosynthetically active radiation, b) mean daily air temperature, c) mean daily vapour pressure deficit, and d) mean daily root zone volumetric soil water content.

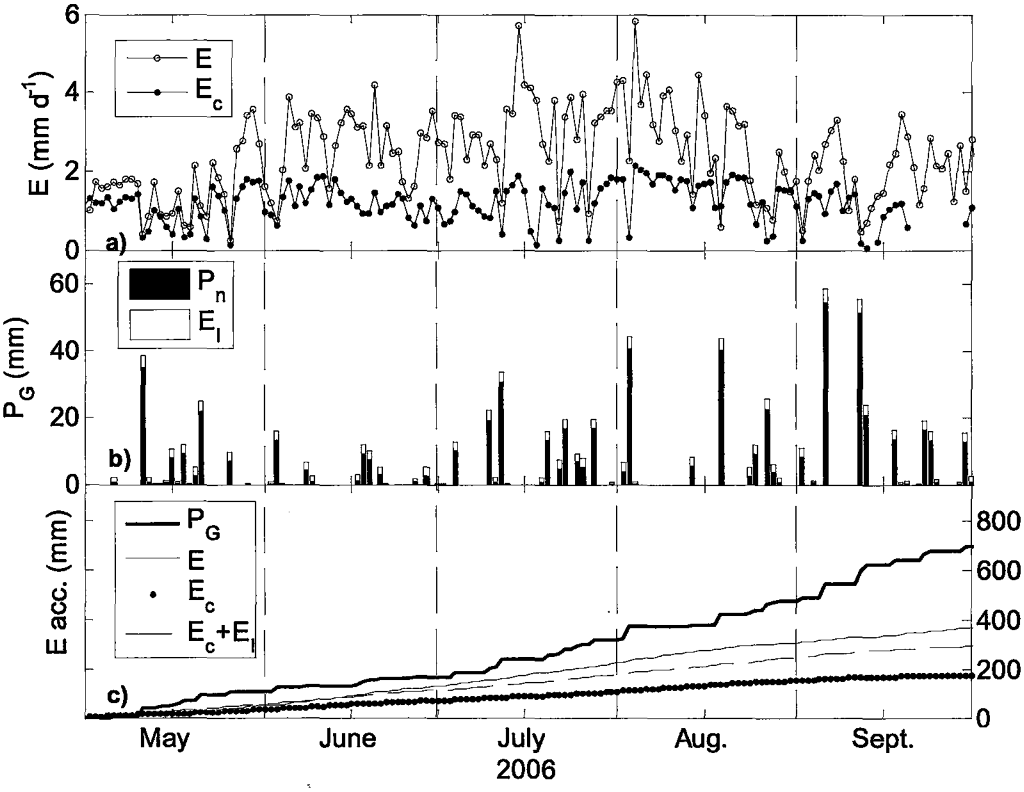

Figure 2. Water fluxes. a) mean daily water flux components: E is total water flux, E_c is canopy transpiration, b) daily sums of gross precipitation P_G, throughfall P_n and interception E_I, c) accumulated precipitation and water flux components.

4.2 Soil water patterns

$\theta_{0\text{-}25cm}$ values at this site were generally quite low, ranging between 0.29 and 0.06, and tended to be higher in the spring and early fall, and lower in the summer despite the large precipitation input. Over the course of the season it broadly followed that as daily air temperatures increased, soil water content decreased as evaporation and transpiration increased. On a half hourly scale $\theta_{0\text{-}25cm}$ increased in correspondence with precipitation inputs and then decreased steadily as excess water drained from the soil until reaching field capacity. After reaching the field capacity $\theta_{0\text{-}25cm}$ would decrease much less rapidly in a 'stair-case' pattern with a draw down from transpiration and evaporation during the daylight hours and a plateau during the night where $\theta_{0\text{-}25cm}$ would remain largely unchanged (Fig. 3a). During the driest periods (and only the driest periods) when $\theta_{0\text{-}25cm}$ would approach the wilting point and the water table depth was presumably at its deepest, the shallow soil layers began to gain more noticeable amounts water at night without any apparent input due to the presumed water potential gradient between non-adjacent soil layers (Fig. 3b). Though small nocturnal increases were visible during other periods the magnitude was not enough to significantly change daily net water use (calculated as the difference between the maximum soil water storage (mm) of a single day and the maximum soil water storage of the following day). We concluded that nightly increases during extremely dry conditions, that were large enough to change net water use, were likely due to hydraulic redistribution (Burgess et al. 1998). This has been shown to occur in a number of different soil types, climates and species (Brooks et al. 2002; Burgess et al. 1998; Caldwell et al. 1998; Dawson 1993; Oliveira et al. 2005; Unsworth et al. 2004), but to our knowledge this is the first reported evidence of the phenomena in a Canadian forest or in White pine. Root zone soil water storage (in mm of water) was calculated by summing the average water content of the 6 sensors located in the 0-20 cm column (i.e. 200 mm × $\theta_{0\text{-}25cm} = \theta_{stor}$). Hydraulic redistribution occurred on 26 days during 2006. A comparison of the observed change in root zone soil water storage during a period when hydraulic redistribution occurred and the predicted change in soil water without the input of nocturnal recharge provided to the soil by hydraulic redistribution is presented in Figure 4. The difference between the number of days required for the predicted θ_{stor} to reach a given storage and the number of days required for the observed θ_{stor} to reach the same storage can be considered an estimate of the additional days of stored water provided by hydraulic redistribution (Brooks et al. 2002). The predicted θ_{stor} was estimated by simply replacing the nocturnal recharge periods with constant water storage values, to mimic the typical 'staircase' pattern mentioned above. During this period the nightly increases in stored water, of up to 0.50 mm, prolonged the reduction of stored soil water from ~14 mm to ~12 mm by an estimated 7 days, preventing the additional reduction of ~4 mm of stored water from the root zone predicted in the absence of hydraulic redistribution implying, that hydraulic redistribution is reducing drought intensity in the root zone by maintaining soil water contents at levels above the water content associated with the wilting point through dry periods at the site.

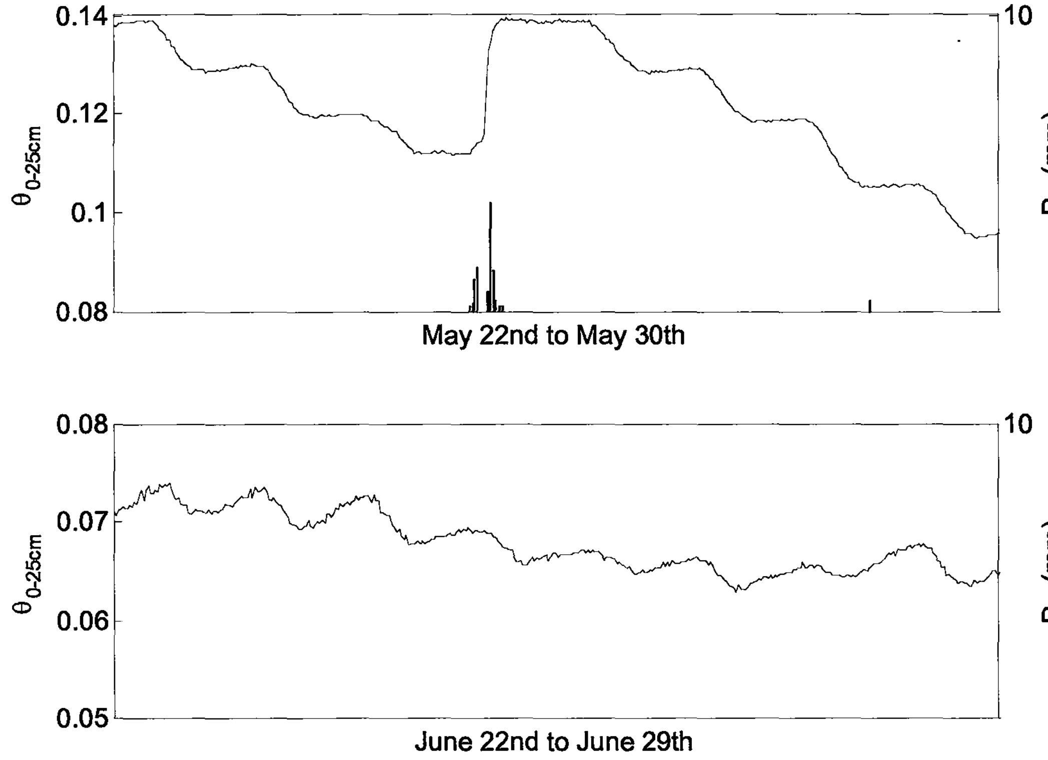

Figure 3. Root zone soil volumetric water content and precipitation input for two selected periods.

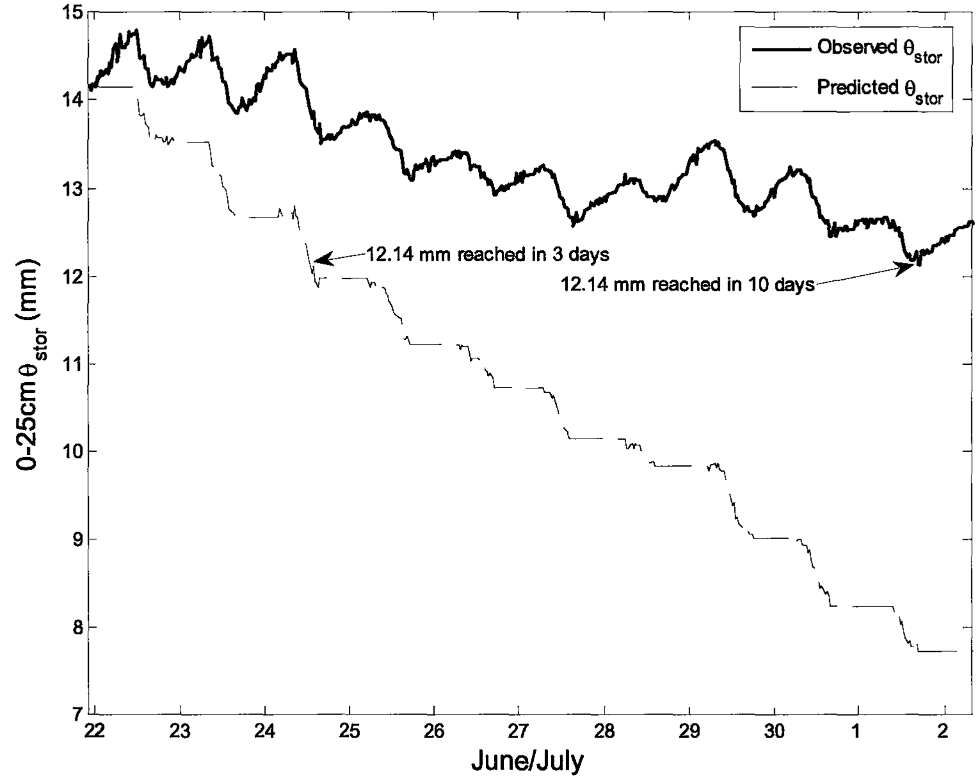

Figure 4. Comparison of time course of measured root zone soil water storage and root zone soil water storage predicted in the absence of hydraulic redistribution.

To investigate the impact of hydraulic redistribution on a daily scale we compared net daily water use from the root zone with total daily water use from the root zone. Total daily water use was calculated as the difference between the minimum and the maximum soil water storage of one single day (Brooks et al. 2002). For the 26 days with hydraulic redistribution the mean total water use was 0.90 mm d^{-1}, ranging from 0.43 to 1.49 mm d^{-1}, while the mean net water use was only 0.43 mm d^{-1} and ranged from 0.03 to 1.00 mm d^{-1}. Net water use, which includes nocturnal recharge contributed by hydraulic redistribution, was always appreciably lower than the total water use by evapotranspiration on these days. The nocturnal increases ranged from 0.92 mm to 0.16 mm of water and averaged 0.46 mm, and there were 4 days where the nocturnal recharge actually increased the amount of soil water stored in the column without precipitation, causing an overall gain in volumetric water content.

4.3 Water flux patterns

Ensemble averaged diurnal water fluxes and key meteorological variables are presented in Figure 5. Both E and E_C tended to peak in the early afternoons, circa 1300 to 1500 hours daily (the peak in E_C is indicated by a diamond in Figure 5a). The response of E_C consistently lags behind E. This lag is likely due to differences in the timing of the water uptake measured by thermal dissipation probes embedded in the stem and actual water loss at the crown. The lag continues at the end of the day and E_C often exceeds E indicating that the tree tissues are replenished after transpiration ceases. This implies that there is a significant water exchange between transpiration and tree tissues, and the water storage capacity of living tissues is important in this forest (Unsworth et al. 2004). Ensemble averaged *VPD* also consistently lagged behind *PAR*. All observed ensembles tended to be, more or less, symmetrical around hours in the early afternoon, except for the E_C ensembles of June and July, which appeared asymmetrical with sharper increases in E_C rates in the morning hours. In May, August, and September the mid-day peaks in E_C tended to arrive later (by approximately 1 to 2 hours on average) in the day than in June and July (Fig. 5a), indicating that maximum rates were occurring earlier in the day during June and July. E tended to increase rapidly in the mornings and decrease rapidly in the afternoons, almost mimicking the response of ensemble averaged *PAR*. *VPD* peaked much later in the day than the other ensembles, usually in the late afternoon or early evening (Fig. 5b). The magnitude of the *VPD* morning inflection point (shown by a star in Figure 5b) generally followed the magnitude of the diurnal peak in *VPD* on a month to month basis. These morning inflection points roughly corresponded with day break each month (between 630 and 700 hours) but tended to be at a higher *VPD* and occur earlier, in relation to day-break, in June than other months.

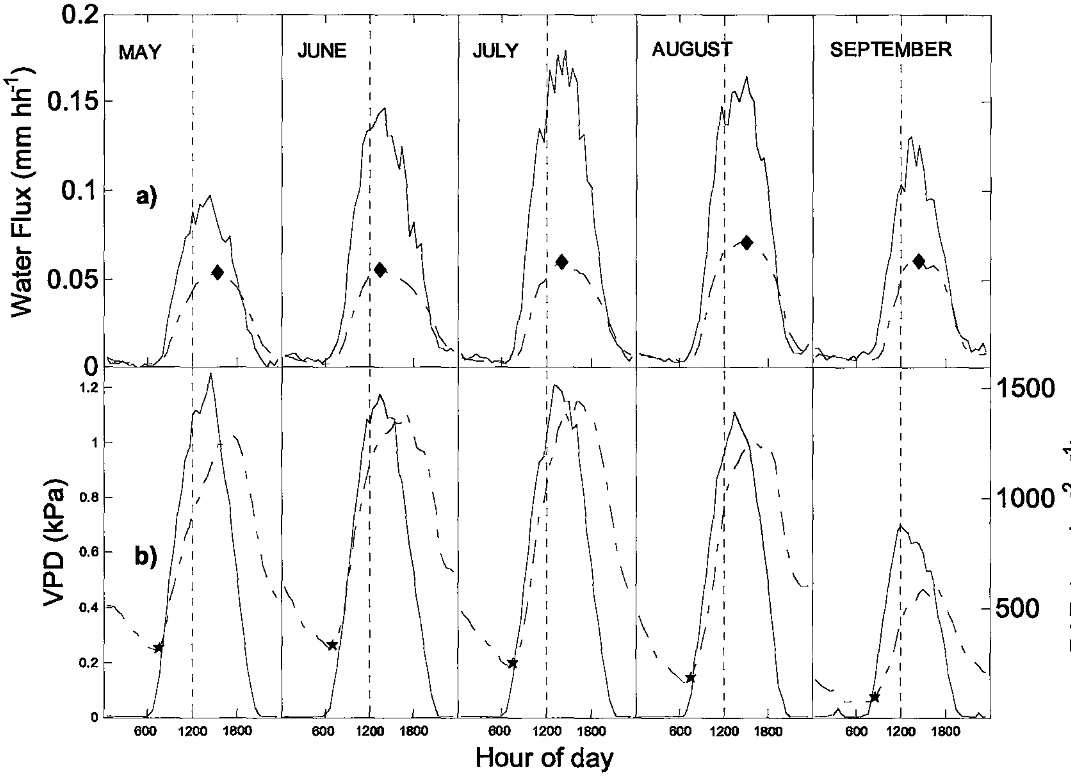

Figure 5. Ensemble averaged diurnal variations in water flux and meteorological variables. a) water flux: total E (solid line), and canopy transpiration E_c (dashed line), and b) photosynthetically active radiation (solid line) and vapour pressure deficit (dashed line).

Daily estimates of E based on eddy-covariance measurements and E_c estimates based on scaled sap-flow measurements are presented in Figure 2a. E varied from 0.3 to 5.8 mm d^{-1}, tending to be higher in the late summer after the dry period. The seasonal daily mean of E was 2.4 (±1.1) mm d^{-1}. The highest E fluxes occurred during late July and early August. The lowest E fluxes were recorded in May. E_c varied from 0.1 to 2.2 mm d^{-1} with a daily mean of 1.2 (±0.5) mm d^{-1}. The highest sustained E_c rates occurred in early August, but the period from May to late July had frequent high daily rates. E and E_c show roughly the same degree of variability, with coefficients of variation of 46% and 41% respectively. The qualitative response of the two variables is similar but their magnitudes differ greatly depending on the time of the season. Daily mean water flux components and monthly totals of water balance components are summarized in Table 2. E_c was 47% of E over the season, but varied between 31-67% on a monthly basis. During the early growing season (May) E_c accounted for a much larger proportion (67%) of E than at any other time. A divergence from this initially high proportion began in late May with the difference between the two variables growing until the early summer dry period, when observed E began to fall slightly relative to E_c. Despite the month long dry spell E and E_c estimates remained relatively high, at levels just below spring values and the difference between the estimates continued to grow. E estimates increased over June and July from a mean daily flux of 2.6 (±0.9) mm d^{-1} to 3.0 (±1.0) mm d^{-1}, while E_c estimates remained unchanged from 1.2 mm d^{-1}. There was a short term drought during this period with little precipitation and high sustained temperatures. After the dry spell ended in mid July the difference between E and E_c rose again and both variables reached their highest seasonal means in July and August respectively; 3.0 (±1.0) mm d^{-1} for E in July and 1.5 (±0.5) mm d^{-1} for E_c in August. Both began to decrease soon thereafter and continued to decrease until the end of the growing season. The free through fall coefficient (p) was determined following the mean method outlined by Klaassen et al. (1998) and was estimated to be 0.34 (see Figure 6.). The canopy storage capacity (S) was estimated to be 2.4 mm also following the mean method (see Figure 6.). The estimated S for the forest is similar to other conifer forests with high *LAI*'s (Link et al. 2004). The S of a Douglas-fir stand with an *LAI* of 8.6 was 2.7 mm (Link et al. 2004) and was 2.4 mm for another Douglas-fir stand with an *LAI* of 9-13 (Klaassen et al. 1998). Modelled net precipitation, or throughfall (P_n), and interception (E_I) components of daily sums of precipitation (P_G) are shown in Figure 2b. Modelled E_I was in good agreement ($r^2 = 0.85$, $p < 0.001$) with measured interception from the 15 selected low-intensity storms (Fig. 7). Modelled E_I increased linearly with the size of the rain fall event, averaging 18% of P_G, but the proportion of an event intercepted decreased as the size of the event increased, as was expected (Gash and Morton 1978; Grelle et al. 1997; Link et al. 2004). E_I was generally between 2 and 3 mm per event; the maximum amount intercepted for a single event was 4 mm during a 55 mm event and the proportion of E_I to P_G ranged from 7% to 65%. Modelled E_I usually exceeded measured E on wet days.

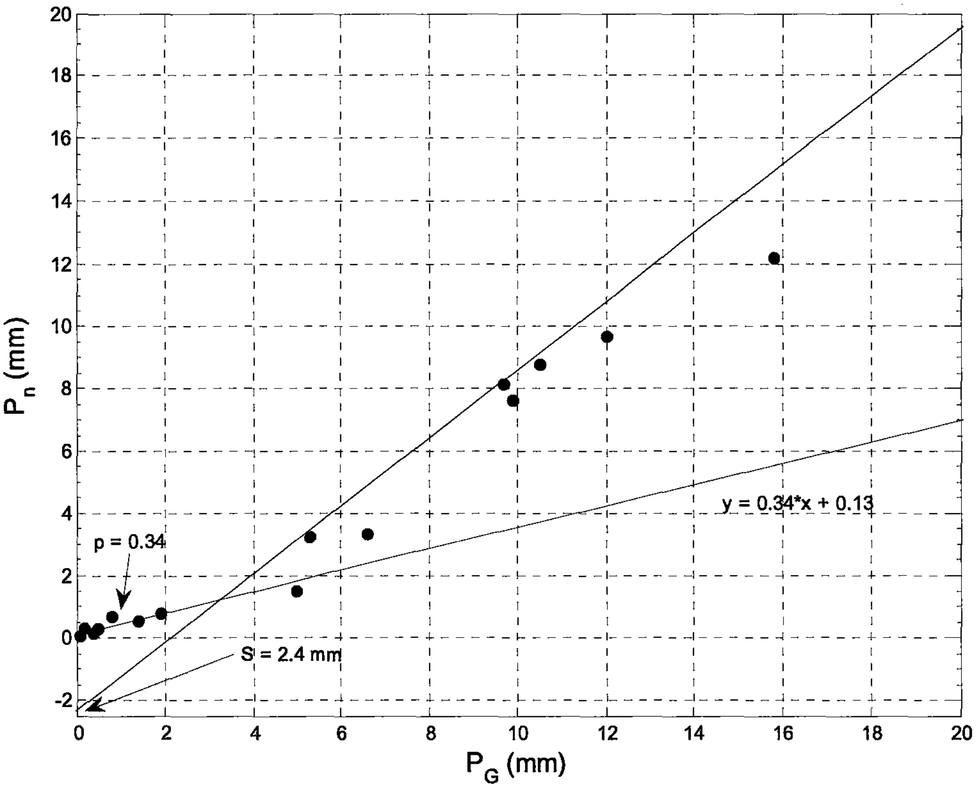

Figure 6. Interception model parameter determination following the 'mean method'. Where P_n is net precipitation, or throughfall and P_G is gross precipitation.

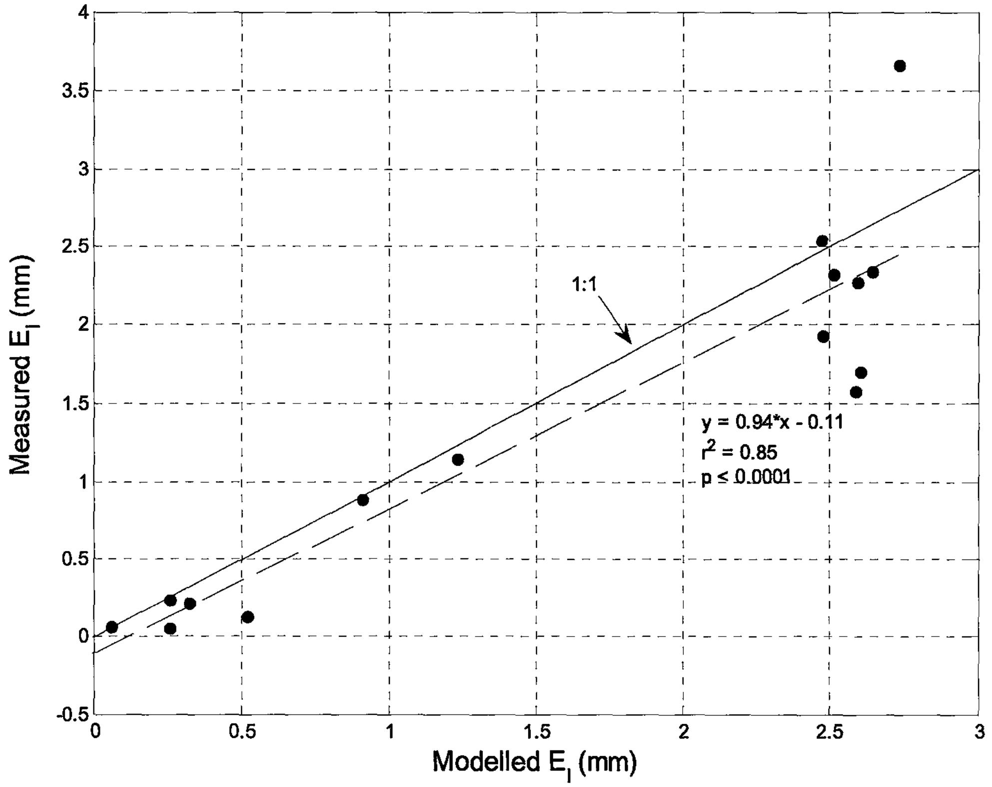

Figure 7. Agreement between modelled and measured interception (*E_I*) for 15 selected low intensity storms. Solid line represents 1:1 relationship. Dashed line is a least squares regression.

Monthly E_I totals varied conservatively from 21 mm to 29 mm throughout the growing season while P_G varied quite a lot (from 62 mm to 220 mm) even though each month had roughly the same number of days with rain (varying from 9 to 11 per month). Consequently, the proportion of E_I to P_G and E varied greatly through the growing season. Table 2 presents the monthly E_I and the proportion of E_I to P_G and E. The maximum amount of rain was intercepted in June, the month with the least amount of rainfall, and the least amount of rain was intercepted in September, the month with the highest amount of rainfall, indicating that a greater proportion is evaporated on days with lesser amounts of precipitation. Interestingly, during the drought of late June and early July, 50 mm of rain fell, but due to the low intensity of the rainfall events (never exceeding 7 mm hh^{-1}) a greater proportion of rain was intercepted by the canopy, thus at least contributing to the development of the drought. This implies that the relatively high water holding capacity of the canopy (2.4 mm) is exacerbating periodic droughts at the site. These extremes were likewise matched by monthly E_I proportions of P_G; 33% in June and ~12% in September. The proportion of E_I to E was the highest in September (~47%) and lowest in June (~26%).

Table 3. Seasonal water flux components, precipitation and canopy wetness

Month	P_G	E	*mean* E	E_c	*mean* E_c	E_I	*% of* P_G	*% of* E		Days	Dry	Inter.	Wet
	(mm)	(mm)	(mm d^{-1})	(mm)	(mm d^{-1})	(mm)	(E_I)	(E_c)	(E_I)				
May	107	49.1	1.6 (0.8)	33.0	1.1 (0.5)	21	19.9	67.3	43.4	31	13	12	6
June	62	79.0	2.6 (0.9)	37.0	1.2 (0.3)	21	33.0	46.8	26.0	30	11	14	5
July	153	93.5	3.0 (1.0)	36.2	1.2 (0.5)	29	18.7	38.7	30.5	31	7	16	8
August	154	86.7	2.8 (1.3)	46.8	1.5 (0.5)	25	16.0	53.9	28.4	31	10	13	8
September	221	58.7	2.0 (0.8)	19.5	1.0 (0.5)	28	12.7	33.2	47.9	30	5	17	8
Season	697	367.0	2.4 (1.1)	172.5	1.2 (0.5)	123	17.7	47.0	33.6	153	46	72	35

A comparison between accumulated precipitation and evaporation components is given in Figure 2c. Accumulated P_G over the growing season amounted to 697 mm, comprised of 574 mm P_n and 123 mm E_I (18% of P_G). The cumulative total E was 367 mm, with 173 mm (47% of E) accounted for by E_c and 123 mm (33% of E) accounted for by E_I, combining ($E_c + E_I$) to total 296 mm or 81% of E.

A comparison of seasonal water flux components on days classified by canopy wetness is presented in Figure 8. The 35 days identified as wet accounted for the least amount of the seasonal water flux (63 mm estimated E) and the lowest seasonal E_c. Understandably, E_I was the highest flux for the wet days and, as mentioned above, modelled E_I exceeded the estimated total flux (as estimated by E from the eddy-covariance system) on days when the canopy was regarded as wet. Due to the frequency of rain events over the season, most days (72 of 153) were classed as intermediate, having either small amounts of precipitation or following days with significant amounts of precipitation. Accordingly, these days accounted for the greatest amount of the total seasonal water flux, with 194 mm total E, 89 mm of E_c and 23 mm of E_I. 46 days were classed as dry. These days accounted for a moderate amount of the total flux from the system (E equalling 113 mm), most of which came from E_c (58 mm) and a surprising 4 mm from E_I, coming from several small isolated rain fall events that were too small to fully saturate the canopy or significantly wet the leaf wetness sensors.

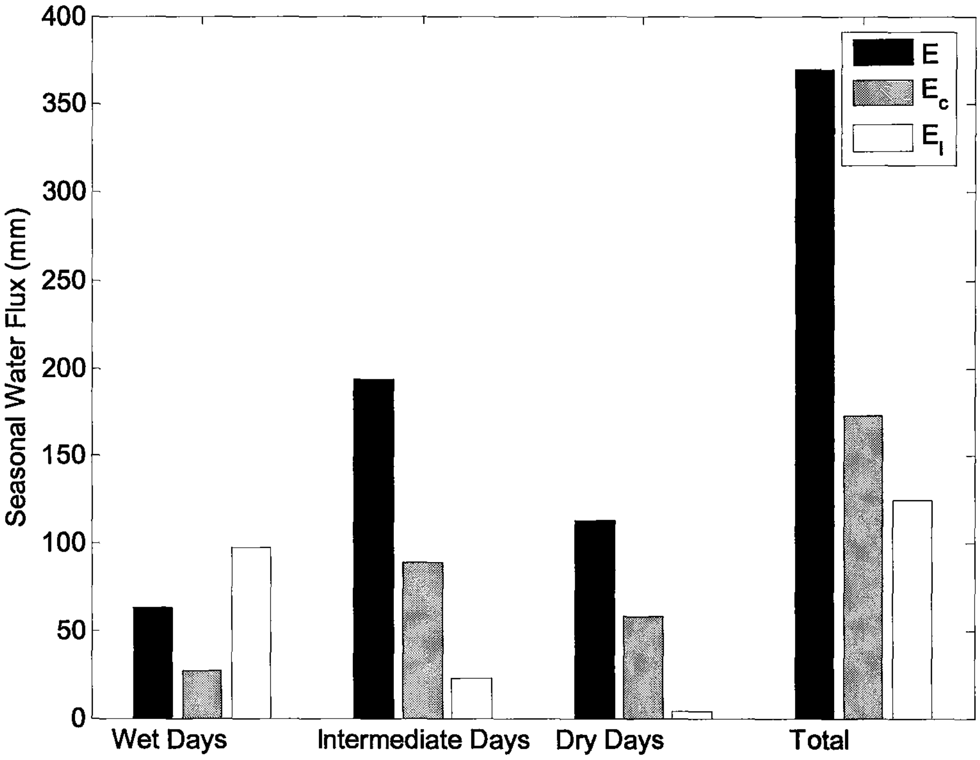

Figure 8. Seasonal water flux components classified by canopy wetness.
Where *E* is total evaporation, E_c is canopy transpiration and E_I is interception evaporation.

4.4 Control and limitation of canopy transpiration

The relationship between daytime half hourly (600 to 1800 hours) E_c and *VPD* for a cloudless eight day period near the beginning of the growing season, when soil moisture and light levels were not likely to severely limit E_c, is shown in Figure 9. As anticipated, a positive linear relationship exists between E_c and *VPD* ($r^2 = 0.7$, $p < 0.001$) below a *VPD* transition point of ~ 1.00 kPa. During this period maximum half hourly E_c rates were limited to 0.07 mm hh^{-1} resulting in a plateau beyond 1.00 kPa where midday E_c remained constant as *VPD* increased. The relationship between *VPD* and E_c during differing soil water availabilities was investigated and initially no significant differences were found. We recognised however, that *VPD* and soil water content are not necessarily independent of one another and that low soil water contents can cause diurnal time shifts in maximum transpiration rates relative to maximum *VPD* (Kurpius et al. 2003) and that a response to soil water deficits might be obscured by changes in E_c rates caused by a change in the daily pattern of *VPD* as soils dry. We investigated the possibility that increases in daily initial *VPD* (or the daily mean *VPD* between 600 and 800 hours (VPD_{in})) were obscuring the influence of soil water content on E_c during dry periods. Figure 10 illustrates the trend of E_c diurnal time courses for three days spanning a drying period (June 11 to 18, where $\theta_{0\text{-}25cm}$ fell from 0.10 to 0.07). As time progressed the daily maximum E_c rate decreased concurrently with an increase in daily maximum *VPD*, steadily drying soil, and an increase VPD_{in}. On the first selected day (June 11th), the slope of the relationship between E_c and *VPD* was maintained until reaching an apex at 1530 hours. On the second selected day (June 14th, three days into the drying period) the relationship began much the same as the first day, but with the slope reducing at around 900 hours due to a reduction in the change of E_c rate relative to the change in *VPD*. The maximum E_c rate of the second day (~ 0.06 mm hh^{-1}) was reduced by roughly 25% from the first selected day (~ 0.08 mm hh^{-1}). The second day also saw roughly a doubling of VPD_{in} relative to the first day. Surprisingly, the total E_c flux was exactly the same for the two days (1.8 mm d^{-1}) despite the reduction in maximum half hourly E_c rate. The final selected day also began much the same as the other days, and again the incline of the relationship decreased at 900 hours, but this time much more dramatically. The E_c rate of the final day (June 18th) then reached a plateau and was maintained at an almost constant level (of approximately 0.04 mm hh^{-1}) as the *VPD* continued to climb throughout the rest of the day. The maximum E_c for the final day (~ 0.04 mm hh^{-1}) was reduced by roughly 25% relative to the second selected day (~ 0.06 mm hh^{-1}), and 50% relative to the first (~ 0.08 mm hh^{-1}). Oddly, on the final day the E_c rate apparently increased between 600 and 800 hours from 0.00 mm hh^{-1} to 0.01 mm hh^{-1}, while *VPD* decreased from 0.73 kPa to 0.52 kPa. One possible cause for this could be a slight decrease in *VPD* due to the evaporation of dew as light and temperature levels rise in the early morning hours and photosynthesis begins. The VPD_{in} of the final day was almost 3 times that of the first day. Despite this increased limitation in maximum rate, the total E_c for the final day was 1.2 mm, a reduction of 0.6 mm from both other days (a 33% decrease). The relationships between E_c and *VPD*, for all three days, have very similar slopes in the mornings, before their respective incline reductions.

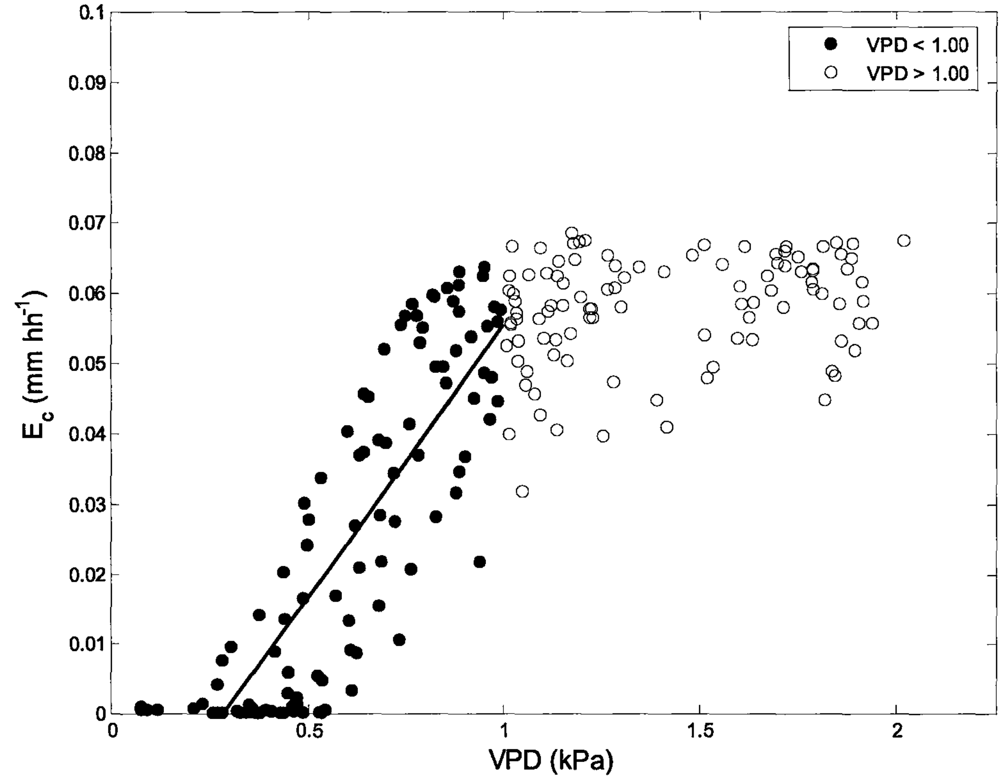

Figure 9. Control of canopy transpiration. Relationship between daytime half-hourly canopy transpiration E_c and vapour pressure deficit *VPD*. Closed circles represent relationship when VPD < 1.00 kPa, and open circles represent relationship when VPD > 1.00 kPa. Line represents least squares regression ($y = 0.077x - 0.022$, $r^2=0.7$, $p<0.001$) between E_c and VPD when VPD < 1.00 kPa.

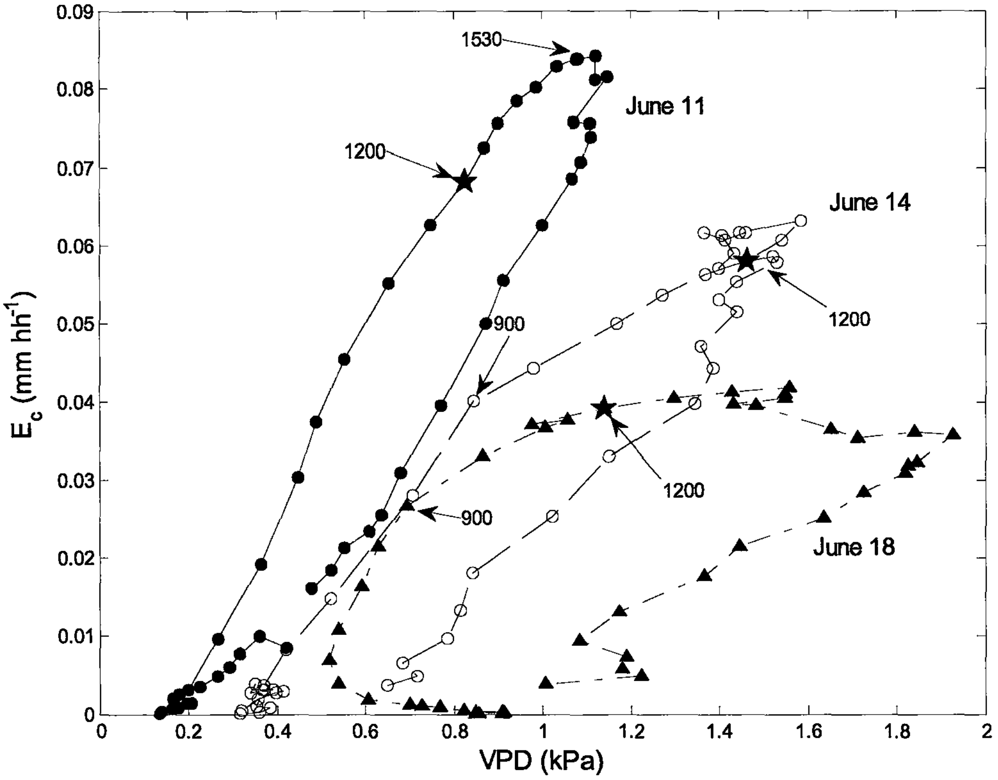

Figure 10. Limitation of transpiration on selected days. Diurnal relationship between half-hourly canopy transpiration E_c and vapour pressure deficit *VPD* for three selected 24 hour periods: June 11th (closed circle), June 14th (open circle), and June 18th (closed triangle). The closed star symbols mark 1200 hours.

To illustrate the effect of VPD_{in} on the relationship between E_c and VPD for the entire growing season, we present diurnal ensemble averages of the relationship, separated by a VPD_{in} classification scheme in Figure 11. VPD_{in} values were classed into three ranges, low; $VPD_{in} < 0.02$ kPa, moderate; $VPD_{in} \geq 0.02$ kPa and $VPD_{in} \leq 0.05$ kPa, and high; $VPD_{in} > 0.05$ kPa. An almost identical generalised pattern is observed in the ensemble averaged data when compared with the set of selected days. The low VPD_{in} class tended to maintain the slope of the E_c – VPD relationship through the morning and have higher mean afternoon E_c rates, with a maximum mean rate of 0.08 mm hh^{-1} at 1500 hours. The middle class reduces the slope slightly at 1000 hours (from 0.11 mm hh^{-1} kPa^{-1} to 0.6 mm hh^{-1} kPa^{-1}), later reaching a maximum mean E_c rate of 0.07 mm hh^{-1} at 1400 hours, but also had higher morning E_c rates than the low class. The high VPD_{in} class tended to have a slightly steeper E_c – VPD slope (0.22 mm hh^{-1} kPa^{-1}, compared to 0.11 mm hh^{-1} kPa^{-1}) in the morning (between 800 and 900 hours) and higher morning E_c rates relative to days with lower VPD_{in}. The high VPD_{in} slope then reduces steadily, reaching a E_c plateau of ~ 0.05 mm hh^{-1} at 1200 hours. E_c – VPD slopes between 1100 and 1200 hours (marked with arrows in Figure 11) progressively decreased with increasing $\mathrm{VPD_{in}}$ class from 0.11 mm hh^{-1} kPa^{-1} (low $\mathrm{VPD_{in}}$) to 0.05 mm hh^{-1} kPa^{-1} and 0.03 mm hh^{-1} kPa^{-1} (mid and high $\mathrm{VPD_{in}}$ respectively). This correspondence of reductions in slope with increases in VPD_{in}, on a day-to-day basis, imply that increases in early morning VPD tend to reduce the sensitivity of E_c to changes in mid-day VPD. Likewise, the correspondence of reductions in maximum mean diurnal E_c rates with increases in VPD_{in}, on a day-to-day basis, indicate that increased early morning VPD maybe causing reductions in maximum daily E_c rates. These observations also indicate that maximum daily $\mathrm{E_c}$ rates arrive earlier in the day as early morning VPD increases on a day-to-day basis. Again, as observed with the limitation of transpiration on selected days, the average E_c rates when VPD_{in} values are high, exhibit an increase in the early morning hours (between 600 and 800 hours) with concurrent decreases in average VPD. Importantly, while the maximum daily E_c rates decrease with increasing VPD_{in} mean daily E_c rates do not, implying that the changes in the diurnal pattern of E_c with rising VPD maybe compensatory and do not significantly affect daily tree water use. The mean daily E_c rate on dry days remains the same at 1.2 mm d^{-1} when progressing from the low VPD_{in} class to the moderate class, and increase slightly to 1.4 mm d^{-1} for the high class.

From these combined observations (Figures 10 and 11) it appears that increases in early morning VPD tend to reduce the sensitivity of E_c to changes in VPD, cause reductions in maximum daily E_c rates, and cause maximum daily E_c rates to arrive earlier in the day.

A one-factor analysis of variance with a Tamhane's T2 Post-Hoc multiple comparison of observed means was conducted to establish that the difference in daytime half hourly E_c means between VPD_{in} classes was significant ($p < 0.001$, $F = 53.36$, c.v. 19.5). The relationship between daytime half hourly E_c and daytime half hourly VPD classed by VPD_{in} is presented in Figure 12, and similar to the patterns observed in the individual selected days and ensemble averaged data, we see that E_c rates tend to decrease and that the general slope of the E_c – VPD relationship tends to become less steep moving from lower to higher VPD_{in} class. A clear seasonal limit to E_c rate of 0.1 at the site is also apparent. The trend of limitation in maximum daily E_c rates as VPD_{in} values increase is presented in Figure 13. As mean early morning *VPDs* rise, the values of the highest observed maximum daily E_c rates decrease linearly and the lowest observed maximum daily E_c rates increase. These two trends tend to focus maximum daily E_c rates into an increasingly narrow band of observed values as mean early morning, or initial *VPD* levels increase. By accounting for the effect of differing initial *VPD* levels we were able to find a relationship between E_c and $\theta_{0\text{-}25cm}$ while observing the change in the relationship between *VPD* and E_c under differing soil water availabilities. No apparent change in the relationship between *VPD* and E_c was seen until the confounding effects of differing VPD_{in} values were removed by considering days in different VPD_{in} classes separately. Figure 14 illustrates the relationship between E_c and *VPD* for all growing season days where the VPD_{in} value was below 0.02 kPa (the low VPD_{in} class), separated between periods when the $\theta_{0\text{-}25cm}$ was above 0.07 and below 0.07. This demarcation of soil water content was not arbitrarily chosen, but rather was found by observing the relationship between E_c and *VPD* under iteratively decreasing soil water content states and then settling upon a low soil water content transition, below which a response in E_c, similar to the response to high *VPD* with a clear plateau, was elicited. Interestingly the soil water content demarcation settled upon roughly corresponds with the aforementioned plateau value observed in $\theta_{0\text{-}25cm}$ during dry periods is also just above the approximate wilting point water content of 0.07 and also corresponds with the observed onset of the apparent nocturnal increases in $\theta_{0\text{-}25cm}$ during dry periods (or periods with hydraulic redistribution). The relationship between E_c and *VPD*, in both form and control, is similar to the one exhibited earlier in Figure 5. Again a positive linear relationship exists between E_c and *VPD* until a threshold *VPD* value is reached, after which a plateau with strictly limited E_c rates forms. This was true for daytime half hour periods when $\theta_{0\text{-}25cm}$ was above 0.07 or below 0.07, but the *VPD* transition point and the E_c rate plateau were both considerably lower when $\theta_{0\text{-}25cm}$ was below 0.07. When $\theta_{0\text{-}25cm}$ was above 0.07 there was a positive relationship ($r^2 = 0.64$, $p < 0.001$) between E_c and *VPD* until a *VPD* of approximately 0.60 kPa, and when $\theta_{0\text{-}25cm}$ was below 0.07 there was a strong positive relationship ($r^2 = 0.97$, $p < 0.001$) between E_c and *VPD* until a *VPD* of approximately 0.40 kPa. While the slopes and intercepts of the two regression equations are similar, the plateau of observed E_c rates for days when soil water content is low (i.e. $\theta_{0\text{-}25cm} > 0.07$) is limited to ~ 0.06 mm hh^{-1}, compared to ~0.10 mm hh^{-1} when the soil water content was higher (see Fig. 13).

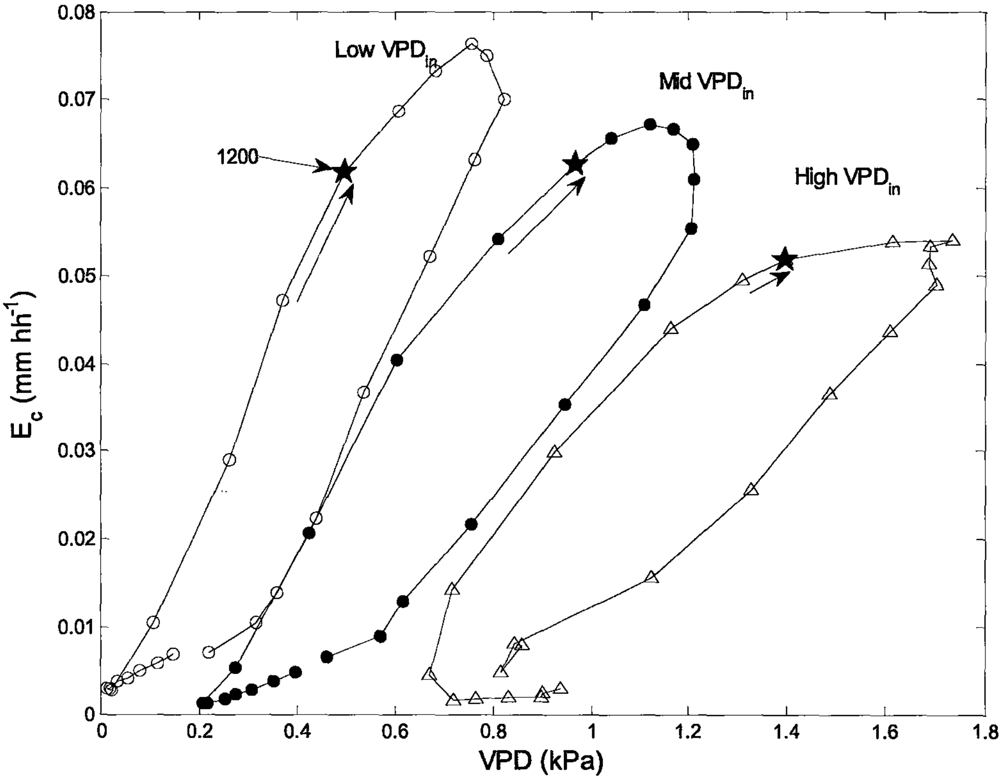

Figure 11. Diurnal ensembles of the limitation of transpiration. Ensemble averaged hourly diurnal relationship between E_c and VPD separated by daily initial *VPD* (or the daily mean *VPD* between 600 and 800 hours (VPD_{in})) class: low; $VPD_{in} < 0.02$ kPa (open circle), moderate; between $VPD_{in} \geq 0.02$ kPa and $VPD_{in} \leq 0.05$ kPa (closed circle), and high; $VPD_{in} > 0.05$ kPa (open triangle). The closed star symbols mark 1200 hours. Arrows mark E_c – *VPD* slopes between 1100 and 1200 hours.

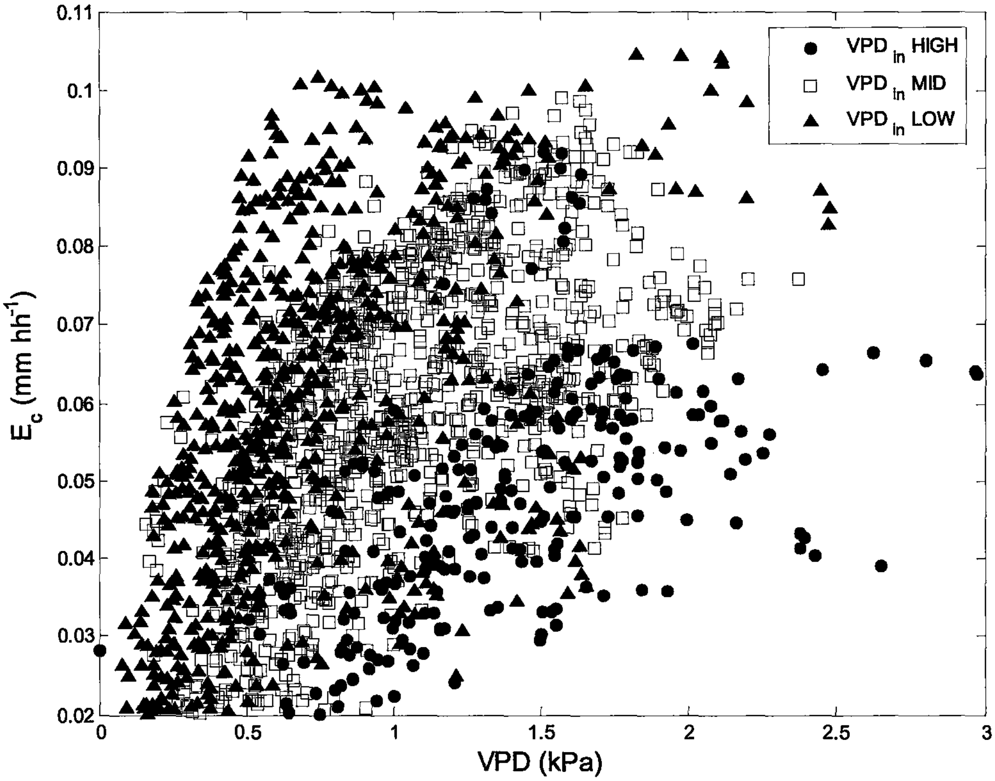

Figure 12. Relationship between daytime E_c and *VPD* separated by daily initial *VPD* (or the daily mean *VPD* between 600 and 800 hours (VPD_{in})) class: low; VPD_{in} < 0.02 kPa (closed triangle), moderate; between $VPD_{in} \geq 0.02$ kPa and $VPD_{in} \leq 0.05$ kPa (open square), and high; VPD_{in} > 0.05 kPa (closed circle).

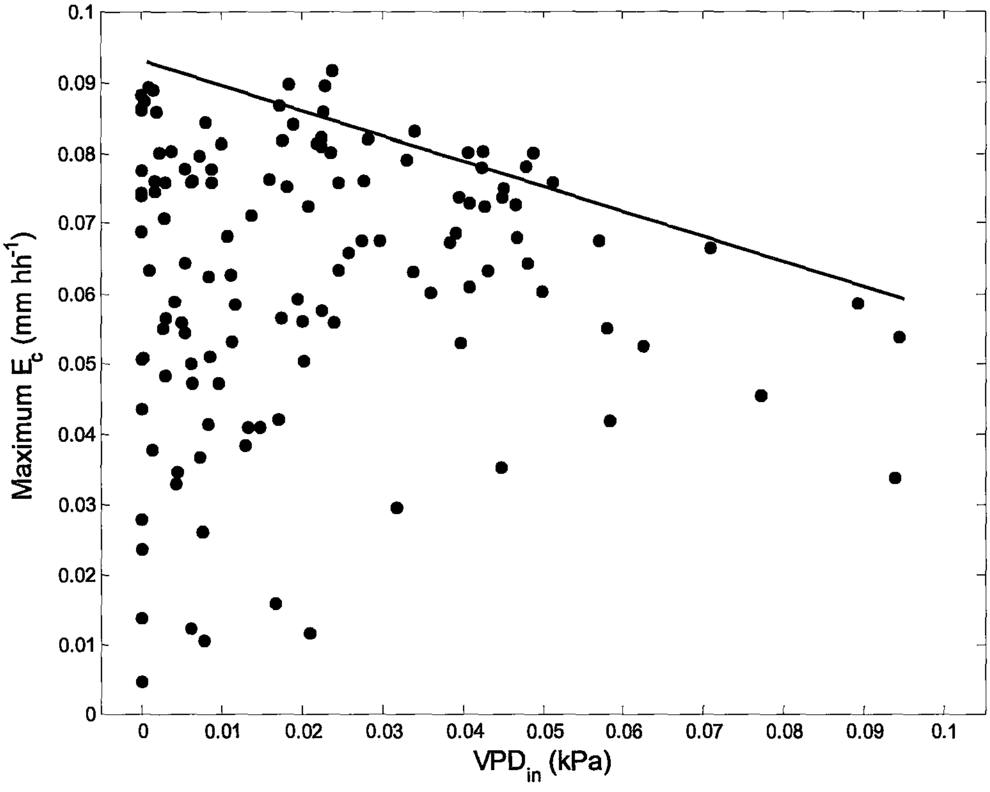

Figure 13. Relationship between daily maximum E_c rate and daily initial vapour pressure deficit (VPD_{in}). Line represents approximate upper limit of maximum daily E_c with increasing VPD_{in}.

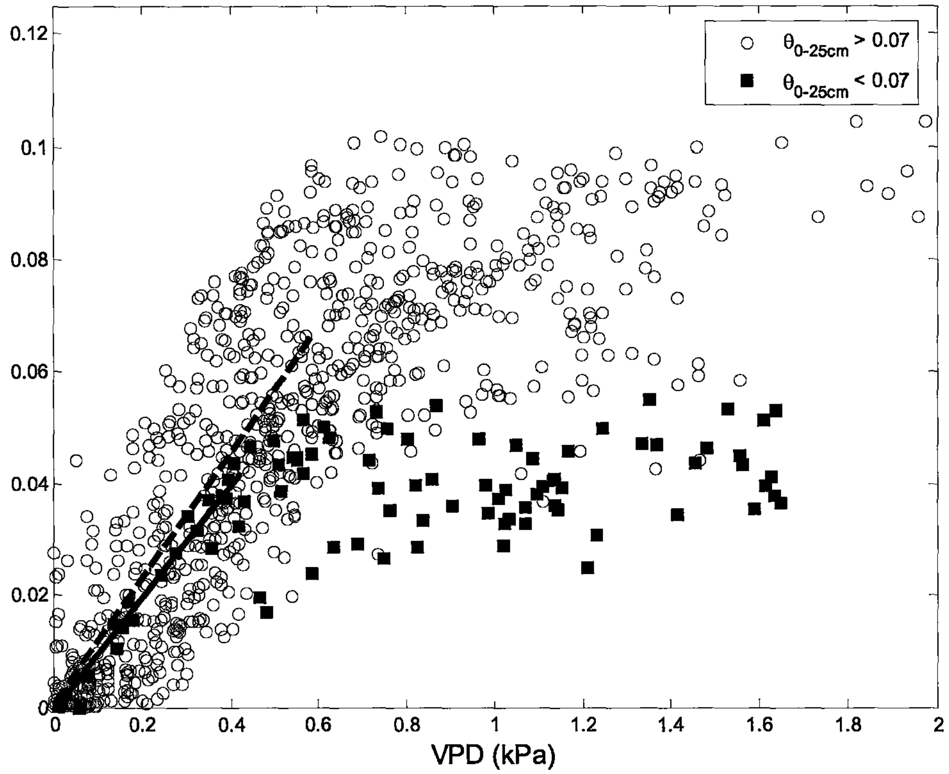

Figure 14. Limitation of transpiration by a reduction in soil water content. Relationship between E_c and *VPD* for all growing season days where the VPD_{in} value was below 0.02 kPa, separated between periods when the $\theta_{0\text{-}25cm}$ was above 0.07 (open circles) and below 0.07 (closed circles). Dashed line represents least squares regression ($y = 0.12x - 0.0013$, $r^2=0.64$, $p<0.001$) when the $\theta_{0\text{-}25cm}$ was above 0.07 and solid line represents least squares regression ($y = 0.1x - 0.0017$, $r^2=0.97$, $p<0.001$) when the $\theta_{0\text{-}25cm}$ was below 0.07.

CHAPTER 5: DISCUSSION

5.1 Water fluxes

Studies of forest water loss can be used to help predict the effects of climate change, successional dynamics or land use change on forest growth, function and carbon budgets. One related point of interest in recent years has been to assess the impact of drought on forested ecosystems (Bernier et al. 2006; Cinnirella et al. 2002; Irvine et al. 1998). This endeavour is particularly relevant in regions where reduced stream flows and periodic droughts are predicted to increase in frequency under future climate change scenarios with increased evapotranspiration, even as precipitation amounts increase concurrently (IPCC 1997; IPCC 2001).

Both daily total water loss (E) and daily canopy transpiration (E_c) responded broadly to changes in meteorology. Observed daily values declined in response to weather events, when PAR and VPD were low, and also showed a gradual decline over the course of the growing season in response to changing day-length and reduced incoming solar radiation. The highest fluxes (both E and E_c) were recorded on hot summer days immediately following precipitation events and the lowest rates were recorded on cool cloudy wet days in the spring. The maximum daily E rate of 5.8 mm d^{-1} at the Turkey Point white pine forest site is somewhat larger than many other mature temperate conifer forests located in wet environments (4.4 mm d^{-1}; Barbour et al., 2005, 4.0 mm d^{-1}; Grelle et al., 1997, 3.7 mm d^{-1}; Humphreys et al., 2003 and 3.6 mm d^{-1}; Unsworth et al., 2004). Two extremely high daily water losses were recorded during the study. Without these two values the maximum observed E rates would be ~ 4 mm d^{-1}. The first extreme (with an E of 5.7 mm) occurred on July 15th, corresponding with the single highest mean daily VPD (2.13 kPa), and occurred two days after a large rain storm and the day after a small storm. The second extreme (with an E of 5.8 mm) occurred on August 4th the day after a large storm when the mean daily VPD was high (1.40 kPa). These two extremes greatly exceed the general range of E values for the season. It is likely that these extreme estimates are the result of an unusually large evaporation contribution from the well wetted soil. This is supported by the extremely low water holding capacity of the sandy soil (conducive to rapid evaporative water loss) and the large reductions in soil water storage observed in the 0-25 cm layer on these two days (~3 mm and ~4 mm respectively), with the remainder likely coming from wet canopy E_I, and E_c derived from deeper soil layers. These magnitudes of water loss would likely only occur on hot summer days following large storms when the canopy and upper soil layers are wet.

We removed turbulent flux outliers following Restrepo and Arain (2005) and gap filled water vapour flux data following Amiro et al. (2006). Several sources of potential systematic error associated with the eddy covariance technique are well known. It is generally accepted that variability in a forested environment (atmospheric and surface) and instrument error restricts the accuracy of half hourly turbulent water vapour flux measurements to between 10 and 20% (Moncrieff et al. 1996). Under non-steady state conditions with little advection, changes in water vapour storage between the surface and the instrument can cause error, but it has been shown that these are generally small during the day and largely only significant during the night when water vapour fluxes are low (Moncrieff et al. 1996).

The modelled growing season evaporation of intercepted water can be shown to account for 34% of the total flux, while measured canopy transpiration accounts for 47%, the two estimates thus combining to account for 81% of evaporative water loss (E). Growing season E_I accounted for 18% of P_G, well within the range of observed net interception losses in temperate conifer forests (Link et al. 2004). Hormann et al. (1996) published values of interception loss from a number of interception studies, and temperate conifer forests were found to have interception losses ranging from 9-48% of gross precipitation. The relatively large contribution of monthly E_I to E (34%) and narrow range of observed monthly E_I (21 mm to 28 mm), despite large fluctuations in monthly P_G (62 mm to 221 mm), illustrate the influence of canopy storage capacity on forest water loss and its affect on proportional interception with varying storm size. As storm size increases, proportional interception loss decreases (Gash, Morton 1978; Link et al. 2004) resulting in E_I accounting for 33% of P_G in June, the month with the least amount of rain, and E_I accounting 13% of P_G in September the month with the most (see Table 2).

The uncertainty of modelled E_I is associated with any inaccuracies in the model itself and any errors propagated through to the modelled estimates from errors in precipitation measurement. Gash (1979) outlined the potential error associated with the variables in the model and it is assumed that we have similar potential errors in this case. There is an error associated with calculating the evaporation from a saturated canopy (E_w) due to the assumption that the evaporation for half hours when P_G is above a certain threshold (in our case 2.25 mm) is equivalent to the evaporation for all hours of rainfall onto the saturated canopy (±15%), the canopy capacity is assumed to have been determined to within ±10%, and the relatively large potential error associated with determining p (assumed to be ±30%) results in a total error from all variables considered to be 8% of the total E_I (Gash 1979). Assuming there were no systematic errors in the rain gauge measurements (i.e. errors associated with levelling or calibration) the stated accuracy of the rain gauges, by the manufacturers, are better than 3% for the gross precipitation (P_G) gauge (model 52202, RM Young) and better than 2% for the net precipitation (P_n) gauge (model CS700, Hydrological Services Ltd).

The water status of a plant is related to both soil water supply and atmospheric demand, and interception is an important control of the amount of available soil water. The high LAI and S (Link et al. 2004) of this forest make the water balance at the site particularly sensitive to reductions in precipitation characteristics, such as frequency, duration or intensity, because the resulting reduction in net precipitation would be amplified by the canopy storage capacity. In fact, during the early summer drought 50 mm of rain fell during 16 low intensity events (never exceeding 7 mm per half hour), but the proportion of E_I to P_G increased (in June) relative to other months and consequently less P_n reached the soil. This undoubtedly exacerbated the drought and likely prolonged its duration.

On a daily basis, the remainder after subtracting E_c from E cannot always be accounted for by modelled E_I due to the different temporal frameworks used to make the estimates. E_I usually exceeds E on wet days but is under-estimated on the days immediately following rainfall events when E usually greatly exceeds E_c. This is because modelled estimates of E_I are given on a per rain event basis rather than on a daily basis, with reported E_I representing the sum of the evaporation of water intercepted during and after the event, but can only be reported as the sum for the day the rain event began. It should be understood that for any significant rain event a large proportion of the reported E_I would have likely evaporated on the day(s) and hours after the cessation of rainfall.

A large portion of the total flux during dry canopy conditions can be attributed to E_c (51%), and likewise approximately 47% of the flux over the whole growing season can be attributed to E_c. Our E_c ranged from 0 – 2.2 mm d^{-1} and had a mean daily rate of 1.2 (±0.5) mm d^{-1}. These rates are similar to reported E_c rates from other studies conducted in mature wet temperate conifer forests. Unsworth et al. (2004) reported mean summer rates of 1.5 mm d^{-1} and 1.4 mm d^{-1} (June and July), which are quite similar to our mean daily rates of 1.2 mm d^{-1} for June, 1.1 mm d^{-1} for July and 1.4 mm d^{-1} for August. Barbour et al. (2005) reported a range of E_c rates of between 0 and 1.8 mm d^{-1} in their study of a temperate conifer rainforest and Irvine et al. (1997; temperate Scots pine) report the same range as found in our forest (0-2.0 mm d^{-1}). There was a distinct lack of seasonality and variability in E_c rates, apart from the responses to storm events, compared to the seasonality and day to day variability exhibited by daily E rates. This is especially true of the daily ensemble E_c averages for each month of the study, which show little change until the beginning of the dormant season. However, small but noticeable declines in late June and early July E_c rates do show a broad response to reductions in soil water content. This relative stability is an indication of the importance of the physiological and climatic limitations on canopy transpiration and lends support to the idea that for a single species the range of variation in transpiration is likely to be dampened by a strong negative feedback between stomatal conductance and *VPD*, and an overall coupling with climate (Roberts 1983).

The E_c proportion on dry days was 51% of E. The proportion attributed to E_c is quite low compared to most other conifer forests studied. Oren et al. (1998) reported that E_c accounted for 69% of E in a temperate Loblolly pine (*Pinus taeda*) plantation, Unsworth et al. (2004) reported 65% in a temperate Douglas fir – Western hemlock (*Pseudotsuga menziesii - Tsuga heterophylla*) old growth forest, and Grelle et al. (1997) reported 75% in a Boreal mixed conifer (*Picea abies – Pinus sylvestris L.*) forest. Two studies, however, did find similar partitioning in conifer forests; one in a Ponderosa pine (*Pinus ponderosa*) plantation in California U.S.A., found that 53% of E came from E_c (Kurpius et al. 2003), the other in a temperate old growth coniferous (*Dacrydium cupressinum*) rainforest, in New Zealand, reporting 39% of E was derived from E_c over the growing season, 51% on dry days (Barbour et al. 2005). Both of these forests have much smaller *LAI*'s than our White pine forest, 2.2 and 2.9 respectively, as compared to 8.0.

The patchy understorey, low E_c proportion and high *LAI* of our forest implies that we are under-estimating stand E_c, because it is unlikely that the unmeasured components of soil evaporation (E_s) and understorey transpiration (E_u) could entirely account for 49% of forest water loss on dry days, though they do contribute a modest amount in some forests (Barbour et al. 2005; Roberts 1983). The most likely reason for this underestimation is the difference between the spatial scales involved in the scaling up of sapflow measurements in the 20 × 20 m study plot to estimate canopy transpiration and the estimates of forest evapotranspiration from tower based eddy covariance fluxes, assuming errors associated with the eddy covariance evaporative flux measurements did not contribute significantly to the underestimation. To compare water fluxes from different sets of measurements it was necessary to make assumptions about the representativeness of the data sets. The eddy covariance technique measures water fluxes over a large variable 'footprint' source area, but due to practical and economic restrictions sapflow had to be measured at a much smaller fixed local scale. Our initial assumption that the sapflow from the dominant White pine would represent the response of all species in the forest adequately, and therefore suffice to represent canopy transpiration was inadequate. The confounding factor is the unmeasured contribution of the young emergent deciduous trees and (which make up at least 8% of the species composition) patches of heavy understorey growth distributed throughout the forest. Further support for this reasoning maybe found in the seasonality of the divergence between E and E_c estimates and its relationship to deciduous phenology. The difference between the two estimates was relatively small during the earliest part of the growing season (E_c was 73% of E from May 1 to May 26), but grew in correspondence with the timing of full deciduous and understorey species leaf out in late May and shrank in correspondence with the onset of senescence in October. Hogg et al. (1997) similarly reported that eddy covariance measurements showed a rapid increase in water flux from a deciduous aspen canopy in late May due to rapid leaf expansion. This reasoning is also supported by the good agreement of our E_c rates with the typical transpiration rates from wet temperate conifer forests dominated by a single species reported above. It is likely that the unmeasured tree and understorey species at our site contribute significantly to the total water flux measured at the tower from June to September, though presently we have no way of estimating their contribution due in part to their uneven spatial distribution. This finding highlights the difficulty in adequately measuring canopy transpiration in a mature planted forest where the natural succession toward a mixed wood forest has begun. The finding also provides strong support for the use of simultaneous sapflow and eddy covariance measurements to monitor forest water fluxes. Because the errors of the two techniques are different and generally independent their simultaneous measurement helped identify possible problems and methodological weaknesses (Hogg et al. 1997). Any future attempt to partition evapotranspiration more precisely in this forest should include an expanded sapflow experiment that takes into account the emergent species and a detailed analysis of flux source areas to account for the possible contribution of the nearby oak stand to the total measured water flux. Despite this we were still able to account for the majority (81%) of the total growing season evapotranspiration from the forest by estimating the two largest components (transpiration from the dominant White pine and interception evaporation) as we predicted. It has been shown in a past study that the main source of error in estimating canopy transpiration was in the estimation of individual tree water use and not in the scaling procedure (Wullschleger et al. 1998b). A main source of error with the estimate of average E_c from sapflow is from heat sources other than the heating probes affecting the artificially established temperature gradients and altering the base zero-flow temperature estimation used in sapflow velocity calculation (Kostner et al. 1998). Natural temperature gradients in trees tend to be more problematic for sapflow measurement in open stands where steep temperature gradients between stems and the soil develop (Kostner et al. 1998) and thus we did not attempt to compensate for this possible source of error.

We found that hydraulic redistribution added enough water (around 2.8 mm in total) to the root zone to hold the soil water storage at, or above, the soil water content corresponding with the approximate wilting point (θ_{stor} of 12 mm or a $\theta_{0\text{-}25cm}$ 0.07) for 7 days during the height of an early summer drought. The phenomenon was also observed during other shorter dry periods. Numerous possible benefits have been proposed as a consequence of hydraulic redistribution, including; providing water to shallow rooted seedlings and understorey plants, enhancing mineral nutrient availability, enhancing microbial processes and heightening the acquisition of nutrients by roots by keeping the fine root zone hydrated (Caldwell et al. 1998).

5.2 Control and limitation of canopy transpiration

Sapflow measurements of water uptake in the dominant trees scaled to represent stand canopy transpiration increased linearly with *VPD* until a threshold value after which mid-day E_c remained relatively constant until a reduction in light levels ended transpiration. It can be shown that when E_c rates were independent of *VPD*, they were limited to ~ 0.10 mm hh^{-1} through the study period and that this limitation was sensitive to the atmospheric demand at the onset of the daily course of transpiration and to soil moisture deficit. The slope of the relationship between E_c and *VPD* is generally maintained until a point at which it reduces. The onset of the reduction in this slope tends to occur earlier as VPD_{in} increases. This reduction in slope often results in a E_c rate plateau and is an expression of the limitation of transpiration in response to environmental changes like drought, or increases in temperature. It is likely that maximum E_c rates tend to arrive earlier in the day and to reduce in magnitude to moderate steady rates through the mid-day, on a day-to-day, basis as leaf water potentials respond to increasing mean early morning *VPD*, thus decreasing maximum daily E_c rates over time. This would imply that changes in daily basal (or baseline) *VPD* over time can cause White pines to respond to the cumulative effects of weather. Shifts in the timing and magnitude of E_c rates caused by increased VPD_{in} also masked an important relationship between E_c rate and $\theta_{0\text{-}25cm}$. Several studies have indicated that the pattern of the limitation response of E_c to high *VPD* and soil water deficit appear similar and are often concurrent, sometimes making interpretation difficult (Kurpius et al. 2003; Oren and Pataki 2001). Increasing VPD_{in} points to a possible reason for these interpretation difficulties and VPD_{in} could be used as an analytical tool to investigate the combined effects of soil water content and atmospheric demand on transpiration.

It has been postulated that E_c rates are linked to *VPD* through the stomata operating to maintain leaf-needle water potential above a critical minimum value thereby limiting maximum E_c rates (Hogg and Hurdle 1997). Our results support this hypothesis, though we did not directly test it. Keeping in mind that our E_c rates reflect water uptake into the stem and not actual transpiration rates at the needles, it is likely that leaf water potentials are reaching critical minimums earlier in the day and at lower water uptake rates when early morning *VPD* is high. This is because when *VPD* is high at the beginning of the diurnal transpiration cycle, the initial rates of water uptake are inherently lower regardless of *VPD* and can be exceeded by lower rates of leaf water loss than usual and thus the critical minimum leaf water potentials that signal a stomatal response (and hence the daily maximum E_c rates) are met earlier in the day.

Though the maximum E_c rates observed were shown to decrease and occur earlier in the day as VPD_{in} increased, mean daily E_c rates remained largely unchanged indicating that the trees were still able to maintain relatively high levels of daily transpiration even when *VPD*'s were quite high. The shifting of the diurnal centre of E_c into the morning hours has been linked to a specific water use strategy in pine trees where transpiration rates are maximized in the morning on warm dry days, rather than throughout the day thus maximizing transpiration during optimal conditions for stomatal opening when light levels (*PAR*) are close to maximal but atmospheric demand (*VPD*) has not yet peaked (Kurpius et al. 2003). Similarly our findings include; a shift in maximum E_c toward the morning on days when the air is warm and dry early in the morning followed by a steady but reduced E_c (relative to days when the early morning atmospheric demand is not as high) and a general correspondence between high morning *VPD*s and early peaks in E_c during the driest period of the study (June). These findings indicate the presence of a similar water use strategy in this forest where during dry periods the dominant White pine moderate the timing of stomatal behaviour to maintain a constant rate of E_c with changes in *VPD*.

These findings have led to the formation of the hypothesis that a feedback between *VPD* and E_c at our site exists, whereby initial daily increases in *VPD* cause increases in E_c, in turn causing decreases in leaf water potential. If *VPD* continues to increase, the decreasing leaf water potentials will eventually meet a critical minimum prompting a stomatal response lowering the maximum E_c rate obtainable, finally resulting in E_c rates levelling off with increasing *VPD*. This negative feedback on E_c in turn increases in magnitude with increasing mean early morning *VPD* or increasing soil water deficit, further reducing maximum daily E_c rates day by day, as decreases in leaf water potential relative to inherently low morning water uptake rates prompt stomatal responses progressively sooner and sooner. Given that light levels are not a limiting factor, an ancillary effect of this feedback is that the higher *VPD*'s tend to also limit the maximum daily E_c rates into a narrower range and as mean morning *VPD*'s increase the variation in daily maximum E_c rate decreases. It is thought that plants respond to the cumulative effects of daily weather over extended periods (Schwartz et al. 2006) and it may also be the case that trees can respond to the cumulative effects of daily weather on short time scales of a few days to a week as well.

Our finding that diurnal E_c rates were significantly ($p < 0.001$, ANOVA) affected by the atmospheric demand at the onset of the daily course of transpiration is also important because the shifts in the timing and magnitude of daily E_c rates caused by increased early morning *VPD* were masking a relationship between transpiration and root zone soil water content. The reason is likely that high mean early morning *VPD*'s and low soil water contents have much the same effect on the relationship between water loss at the leaf surface and water uptake at the root surface, as both would cause a reduction in leaf water potential signalling a similar stomatal response. This suggests that the actual degree of *VPD* is not as critical to stomatal operation as is the balance between the rate of water loss at the crown and the rate of water uptake into the stem, because it is likely that critical minimum leaf water potentials can be met at any *VPD* and could explain the relative insensitivity of E_c to changes in soil water content over short time scales.

CHAPTER 6: CONCLUSIONS

The results of this study show that maximum observed daily forest water fluxes to the atmosphere are generally around 4 mm d^{-1}. Higher rates of forest water flux are possible at this temperate forest site (~ 6 mm d^{-1}) due to the coarse homogeneous soil texture and high canopy water storage capacity allowing for rapid water losses on warm days following rain events. The evaporation of intercepted water accounts for 34% and transpiration from the dominant White pine trees account for 47% of estimated ecosystem evaporation. Together these two fluxes account for the majority of the water flux from the forest. The large contribution of monthly interception to forest water flux and the narrow range of observed monthly interception, despite large differences in gross precipitation month to month, illustrated the importance of canopy water holding capacity on forest water loss. Transpiration on dry days is comparatively low at this site, but unmeasured contributions from young emergent deciduous species and the understorey likely account for the differences between our site and other similar sites. The simultaneous use of eddy-covariance and sapflow sensors to monitor forest water fluxes was instrumental in quantifying the true contribution of the dominant white pine at the site. Hydraulic redistribution added enough water to keep the soil water content above the soil water content associated with the approximate wilting point for 7 additional days during an early summer drought. In total hydraulic redistribution occurred on 26 days during 2006 growing season.

The relatively large water storage capacity of the canopy and poor water holding capacity of the soil illustrate the importance of precipitation characteristics to the hydrology of the ecosystem. The high canopy water storage capacity captured a greater proportion of the frequent, but small low intensity rain events during the drought, likely prolonging its length. Future changes in precipitation frequency, duration or intensity would impact the forest water balance, as illustrated by the importance of the evaporation of intercepted rain during wet conditions, and by the limits placed on transpiration by low soil moisture and high atmospheric demand during the relatively short dry spells experienced during the experiment. Hydraulic redistribution is helping maintain soil water contents and would likely play a larger role if future precipitation characteristics changed. Even in a situation where the annual precipitation amount stayed the same but the region experienced either a shift toward less frequent large storms with short high intensity rainfalls, or a shift toward more frequent small storms with short less intense rainfalls, the soils would still dry due to either the low water storage capacity soils being unable to hold the increase in infiltrated water or the high water storage capacity canopy evaporating away a greater proportion of the water intercepted.

Transpiration from the dominant White pine increased linearly with *VPD* until a variable transition value was reached, after which mid-day transpiration rates remained relatively constant. Transpiration rates, that were independent of *VPD*, were limited to approximately 0.10 mm hh^{-1} through the study period and this limitation was sensitive to early morning atmospheric demand and soil water deficit. Increases in early morning atmospheric demand caused maximum transpiration rates to arrive earlier in the day and to be reduced in magnitude, but did not affect mean daily transpiration rates significantly and transpiration rates were sustained at relatively high levels through periods of high atmospheric demand. This is likely because stomata are operating to maintain leaf-needle water potentials above a critical minimum value and limiting E_c rates in response to the *VPD*. On days when the early morning *VPD* is relatively high these critical minimums are met earlier in the day because, regardless, morning water uptake rates are low and can be easily exceeded by leaf water loss. We believe there could be a specific water use strategy, similar to one already observed in pine trees, active at the site where transpiration rates are maximized earlier on warm dry days which take advantage of the optimal conditions for stomatal opening present in the morning and then are sustained at moderate but strictly limited rates for the rest of the day. Shifts in the timing and magnitude of transpiration rates caused by increased early morning atmospheric demand masked a relationship between transpiration and soil water content that caused transpiration to be strictly limited once a transition point in soil water content of approximately 0.07 was reached. This is likely because when the wilting point was approached, water uptake at the roots reduced, at which point relatively low leaf water losses caused the leaf-needle water potential to meet a critical value, signalling stomatal closure in much the same way as high early morning *VPD,* thus also limiting E_c in a similar manner.

Atmospheric demand and soil water supply often co-vary during warm dry periods and likely interact with one another via their mutual influence over the stomatal response to reductions in leaf water potentials, which directly limits E_c. This better understanding of E_c limitation could help refine land surface scheme models and links E_c to a feedback that now includes a mechanistic connection between declining soil water contents and increasing *VPD* that could explain the difficulty in the interpretation of how E_c responds to the combined effects of *VPD* and soil water content (Kurpius et al. 2003). The evidence that E_c rates are responding to changes in early morning *VPD*, on a day-today basis, indicates that trees respond to the cumulative effects of weather over short time periods through the same feedback between *VPD* and E_c that causes E_c to level off with increasing *VPD*.

REFERENCES

Amiro BD, Barr AG, Black TA, Iwashita H, Kljun N, McCaughey JH, Morgenstern K, Murayama S, Nesic Z, Orchansky AL, Saigusa N (2006) Carbon, energy and water fluxes at mature disturbed forest sites, Saskatchewan, Canada. *Agricultural and Forest Meteorology,* **136,** 237-251.

Arain MA and Restrepo-Coupe N (2005) Net ecosystem production in a temperate pine plantation in south-eastern Canada. *Agricultural and Forest Meteorology,* **128,** 223-241.

Arnell N (2002) *Hydrology and Global Environmental Change.* Pearson Education Ltd., Edinburgh Gate, Harlow, Essex, UK, 346 pp.

Barbour MM, Hunt JE, Walcroft AS, Rogers GND, McSeveny TM, Whitehead D (2005) Components of ecosystem evaporation in a temperate coniferous rainforest, with canopy transpiration scaled using sapwood density. *New Phytologist,* **165,** 549-558.

Bernier PY, Bartlett P, Black TA, Barr A, Kljun N, McCaughey JH (2006) Drought constraints on transpiration and canopy conductance in mature aspen and jack pine stands. *Agricultural and Forest Meteorology,* **140,** 64-78.

Bovard BD, Curtis PS, Vogel CS, Su HB, Schmid HP (2005) Environmental controls on sap flow in a northern hardwood forest. *Tree physiology,* **25,** 31-38.

Brooks JR, Meinzer FC, Coulombe R, Gregg J (2002) Hydraulic redistribution of soil water during summer drought in two contrasting Pacific Northwest coniferous forests. *Tree physiology,* **22,** 1107-1117.

Burgess SSO, Adams MA, Turner NC, Ong CK (1998) The redistribution of soil water by tree root systems. *Oecologia,* **115,** 306-311.

Calder IR (1998) Water use by forests, limits and controls. *Tree physiology,* **18,** 625-631.

Caldwell MM, Dawson TE, Richards JH (1998) Hydraulic lift: Consequences of water efflux from the roots of plants. *Oecologia,* **113,** 151-161.

Chen JM, Govind A, Sonnentag O, Zhang YQ, Barr A, Amiro B (2006) Leaf area index measurements at Fluxnet-Canada forest sites. *Agricultural and Forest Meteorology,* **140,** 257-268.

Cinnirella S, Magnani F, Saracino A, Borghetti M (2002) Response of a mature Pinus laricio plantation to a three-year restriction of water supply: structural and functional acclimation to drought. *Tree physiology,* **22,** 21-30.

Corporation of Norfolk County, Long Point Region Conservation Authority, Haldimand-Norfolk Health Unit (2003) Norfolk Municipal Groundwater Study. Figure 2-49: Depth to Water Table.

Dawson TE (1993) Hydraulic lift and water-use by plants: implications for water-balance, performance and plant-plant interactions. *Oecologia,* **95,** 565-574.

Environment Canada (2004) Canadian Climate Normals. **2007**. http://www.climate.weatheroffice.ec.gc.ca/climate_normals/index_e.html

Environment Canada (2005) Canadian Climate Data. **2007**. http://www.climate.weatheroffice.ec.gc.ca/climateData/canada_e.html

Farley KA, Jobbagy EG, Jackson RB (2005) Effects of afforestation on water yield: a global synthesis with implications for policy. *Global Change Biology,* **11,** 1565-1576.

Fluxnet Canada (2003) *Fluxnet-Canada Measurement Protocols.* Fluxnet-Canada Network Management Office, Faculté de Foresterie et de Géomatique, Université Laval, Québec, PQ, 109 pp.

Gash JHC (1979) Analytical model of rainfall interception by forests. *Quarterly Journal of the Royal Meteorological Society,* **105,** 43-55.

Gash JHC, Morton AJ (1978) Application of Rutter model to estimation of interception loss from Thetford forest. *Journal of Hydrology,* **38,** 49-58.

Granier A (1987) Sap Flow Measurements in Douglas-Fir Tree Trunks by Means of a New Thermal Method. *Annales des Sciences Forestieres,* **44,** 1-14.

Grelle A, Lundberg A, Lindroth A, Moren AS, Cienciala E (1997) Evaporation components of a boreal forest: Variations during the growing season. *Journal of Hydrology,* **197,** 70-87.

Hogg EH, Black TA, den Hartog G, et al (1997) A comparison of sap flow and eddy fluxes of water vapour from a boreal deciduous forest. *Journal of Geophysical Research-Atmospheres,* **102,** 28929-28937.

Hogg EH, Hurdle PA (1997) Sap flow in trembling aspen: implications for stomatal responses to vapour pressure deficit. *Tree physiology,* **17,** 501-509.

Humphreys ER, Black TA, Ethier GJ, Drewitt GB, Spittlehouse DL, Jork EM, Nesic Z, Livingston NJ (2003) Annual and seasonal variability of sensible and latent heat fluxes above a coastal Douglas-fir forest, British Columbia, Canada. *Agricultural and Forest Meteorology,* **115,** 109-125.

IPCC (2001) *Climate Change 2001: Impacts, Adaptation, and Vulnerability: Contribution of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change.* The Press Sydicate of the University of Cambridge, New York, NY, U.S.A., 744, 745, 746, 747 pp.

IPCC (1997) *IPCC Special Report on The Regional Impacts of Climate Change: An Assessment of Vulnerability.* Cambridge University Press, The Edinburgh Building Shaftesbury Road, Cambridge UK, 517 pp.

Irvine J, Perks MP, Magnani F, Grace J (1998) The response of Pinus sylvestris to drought: stomatal control of transpiration and hydraulic conductance. *Tree physiology,* **18,** 393-402.

Kelliher FM, Leuning R, Raupach MR, Schulze ED (1995) Maximum conductances for evaporation from global vegetation types. *Agricultural and Forest Meteorology,* **73,** 1-16.

Kelliher FM, Leuning R, Schulze ED (1993) Evaporation and Canopy Characteristics of Coniferous Forests and Grasslands. *Oecologia,* **95,** 153-163.

Klaassen W, Bosveld F, de Water E (1998) Water storage and evaporation as constituents of rainfall interception. *Journal of Hydrology,* **213,** 36-50.

Kostner B, Granier A, Cermak J (1998) Sapflow measurements in forest stands: methods and uncertainties. *Annales des Sciences Forestieres,* **55,** 13-27.

Kurpius MR, Panek JA, Nikolov NT, McKay M, Goldstein AH (2003) Partitioning of water flux in a Sierra Nevada ponderosa pine plantation. *Agricultural and Forest Meteorology,* **117,** 173-192.

Li JH, Dugas WA, Hymus GJ, Johnson DP, Drake BG, Hungate BA (2003) Direct and indirect effects of elevated CO2 on transpiration from Quercus myrtifolia in a scrub-oak ecosystem. *Global Change Biology,* **9,** 96-105.

Link TE, Unsworth M, Marks D (2004) The dynamics of rainfall interception by a seasonal temperate rainforest. *Agricultural and Forest Meteorology,* **124,** 171-191.

Moncrieff JB, Malhi Y, Leuning E (1996) The propagation of errors in long-term measurements of land-atmosphere fluxes of carbon and water. *Global Change Biology,* **2,** 231-240.

Monteith JL (1965) Evaporation and the environment. *Proceedings of the Symposium of the Society for Experimental Biology,* **19,** 205-234.

Nosetto MD, Jobbagy EG, Paruelo JM (2005) Land-use change and water losses: the case of grassland afforestation across a soil textural gradient in central Argentina. *Global Change Biology,* **11,** 1101-1117.

Oliveira RS, Dawson TE, Burgess SSO, Nepstad DC (2005) Hydraulic redistribution in three Amazonian trees. *Oecologia,* **145,** 354-363.

Oren R, Pataki DE (2001) Transpiration in response to variation in microclimate and soil moisture in south-eastern deciduous forests. *Oecologia,* **127,** 549-559.

Peichl M (2005) Biomass and carbon allocation in a chronosequence of white pine (*Pinus strobus L.*) plantations in Southern Ontario, Canada. MSc. Thesis, McMaster University, Hamilton, 160 pp.

Peichl M, Arain AA (2006) Above- and belowground ecosystem biomass and carbon pools in an age-sequence of temperate pine plantation forests. *Agricultural and Forest Meteorology,* **140,** 51-63.

Phillips N, Oren R (2001) Intra- and inter-annual variation in transpiration of a pine forest. *Ecological Applications,* **11,** 385-396.

Restrepo NC, Arain MA (2005) Energy and water exchanges from a temperate pine plantation forest. *Hydrological Processes,* **19,** 27-49.

Roberts J (2000) The influence of physical and physiological characteristics of vegetation on their hydrological response. *Hydrological Processes,* **14,** 2885-2901.

Roberts J (1983) Forest Transpiration - a Conservative Hydrological Process. *Journal of Hydrology,* **66,** 133-141.

Schafer KVR, Oren R, Lai CT, Katul GG (2002) Hydrologic balance in an intact temperate forest ecosystem under ambient and elevated atmospheric CO2 concentration. *Global Change Biology,* **8,** 895-911.

Schwartz MD, Ahas R, Anto A (2006) Onset of spring starting earlier across the Northern Hemisphere. *Global Change Biology,* **12,** 343-351.

Seyfried MS, Murdock MD (2001) Response of a new soil water sensor to variable soil, water content, and temperature. *Soil Science Society of America Journal,* **65,** 28-34.

Unsworth MH, Phillips N, Link T, et al (2004) Components and controls of water flux in an old-growth Douglas-fir-western hemlock ecosystem. *Ecosystems,* **7,** 468-481.

Whittaker RH, Likens GE (1975) The biosphere and man. In: *Ecological studies: Primary production of the biosphere* (eds Lieth H, Whittaker RH), Springer Verlag, New York, NY.

Wilson KB, Hanson PJ, Mulholland PJ, Baldocchi DD, Wullschleger SD (2001) A comparison of methods for determining forest evapotranspiration and its components: sap-flow, soil water budget, eddy covariance and catchment water balance. *Agricultural and Forest Meteorology,* **106,** 153-168.

Wullschleger SD, Hanson PJ (2006) Sensitivity of canopy transpiration to altered precipitation in an upland oak forest: evidence from a long-term field manipulation study. *Global Change Biology,* **12,** 97-109.

Wullschleger SD, Hanson PJ, Tschaplinski TJ (1998a) Whole-plant water flux in understory red maple exposed to altered precipitation regimes. *Tree physiology,* **18,** 71-79.

Wullschleger SD, Meinzer FC, Vertessy RA (1998b) A review of whole-plant water use studies in trees. *Tree physiology,* **18,** 499-512.