THE IMPACT OF INDUCED DROUGHT ON TRANSPIRATION AND GROWTH IN A TEMPERATE PINE PLANTATION 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 (2010) McMaster University
(Environmental Science) Hamilton, ON

TITLE: The Impact of an induced drought on transpiration and growth in a temperate pine plantation forest

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NUMBER OF PAGES: viii, 61

ABSTRACT

A study evaluating the response of canopy transpiration (E_c) and growth rates to reduced water input, was conducted in a managed 70-year old planted temperate white pine (Pinus strobus L.) forest, in Southern Ontario, Canada from January to December 2009. In order to induce the drought, a 20m × 20m throughfall exclusion setup was established using interlocking aluminum troughs at a 3-inch slope. Throughfall was excluded from April 1st until July 3rd. During this period, 270mm of rainfall occurred (27% of annual precipitation) of which 90% was excluded. Sap flow velocity, soil moisture and soil temperature (at multiple depths) were measured continuously in both reference and drought plots. Dendrometer bands were also installed on all instrumented trees. Prior to enforced drought, adjacent plots showed slight variability in soil moisture while tree diameter and soil temperature did not show significant variability. Daily values of E_c from each plot ranged from 0 to 1.6 mm d^{-1} over the growing season (March-November) for the drought and reference plot respectively. The impact of the rainfall exclusion did not affect Ec until early June, 60 days after the drought was in place. Normalized values of Ec showed a 20% decrease from the drought trees compared to the reference. Cumulative growth rates between the two plots showed a net decrease in the drought trees of 42% from the reference and earlier termination of growth. However, the growing season E_c values were 174 mm y^{-1} and 171 mm y^{-1} for the drought and reference plot respectively. Currently, the effects of extreme drought events on carbon and water balances in conifer forests are poorly understood, due to their sporadic occurrence in natural ecosystems. The findings of this study help to establish the impacts drought may have on these ecosystems and evaluate their potential responses under predicted future climate regimes.

ACKNOWLEDGEMENTS

I would like to thank all the people that have helped me through the completion of my MSc. Without their constant support, guidance, advise and constant supply of coffee, this would not have been possible.

First, I would like to thank my supervisor, Dr. Altaf Arain, for giving me this opportunity, and for helping me get through the many hurdles encountered along the way. Most importantly, I want to thank him for his patience, both in the field-work and in the writing process. His guidance and support was a critical building block in both the design of the project and completion of this document. Next, I would like to thank everyone in the climate lab, that have been there through this process. In particular, I would like to extend thanks to Jason Brodeur, for his constant assistance with technical stuff and ongoing support. You really helped me think out of the box when I needed to, and gave me the desire to try new things when I was hesitant. You have been an inspiration. Also, to Emily Nicholas, for her support in both the lab and the field. We had many interesting adventures at the site!

I would like to extend a HUGE thanks to Matthias Peichl, Myroslava Khomik, Jason Brodeur, Suo Huang, Bin Chen and Altaf Arain, for their help in the construction of the drought plot, especially when in a time-crunch. The long hours in the field, without complaint, was fundamental in the design of this project, and without everyone's participation it never would have happened. I would like to thank Josh McLaren, for being my inspiration and guide, as well as laying the foundation for this project. His willingness to respond to e-mails and give advice was very much appreciated.

A lot of thanks to my mom and dad, and grandma and grandpa, for their on-going support as I continue along the educational path. I also want to thank my Great Aunt Irene and family friend Sandy Coulter, for being the inspiration that brought me to environmental science in the first place. Without you two, I really wouldn't be here!

Finally, I would like to thank my boyfriend, Mike Napper, for his on-going support, help in the field when needed (even on weekends!), ongoing supply of coffee and unconditional love, even when I was loosing my mind. Your encouragement and support was the voice of reason I needed. Without you, I would never have finished this.

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Chapter 1: Introduction

Forest ecosystems have been well established in the literature as an important component of the terrestrial carbon cycle, since they act as net sinks of carbon dioxide (CO_2)(Houghton et al., 2001; Ogaya et al., 2003; Schwarz et al., 2004). Studies have shown that changes in precipitation patterns have a significant control (even considered a dominant control) on carbon and water vapour fluxes in forests (Schwarz et al., 2004; Bovard et al., 2005; Wullschleger and Hanson, 2006; Fisher et al., 2008; McLaren et al., 2008; Limousin et al., 2009). Soil moisture depletion in the root zone may significantly reduce forest ecosystem productivity and growth (Kirschbaum, 2000; Nepstad et al., 2007). Currently, the effects of severe drought events on forest water loss and growth are limited in the literature (Innes et al., 1998; Fisher et al., 2007; Granier et al., 2007). However, the likelihood of severe drought events occurring in the future is increasing, as suggested by the IPCC (2007). In recent years, significant variability in the frequency and distribution of regional precipitation has been observed in many parts of the world, with enhanced periods of drought between relatively larger precipitation events recorded in Eastern North America (IPCC, 2007) and other parts of the Northern Hemisphere (Breda et al., 2006). These changes could have important implications for the water cycles of forested ecosystems in this region, through alterations in the carbon balance, evapotranspiration and soil water content in root zone (Wullschleger and Hanson, 2006).

In the deciduous forests of eastern North America, studies (such as Hanson and Weltzin, 2000; Wullschleger et al., 2001 and Wullschleger and Hanson, 2006) have shown that late-summer and autumn droughts are common to this region, and the forests in the region are well adapted to these events. However, when the drought event occurs in spring and early summer (April-June), it may have a severe impact on forest growth and net ecosystem productivity (Wullschleger and Hanson, 2006). Investigations on the impact of spring droughts on conifer forests of the eastern North American region, however, are limited. Thus, it is critical that we design experiments that will allow us to further investigate these impacts on the growth of eastern conifer forests.

Component analysis of ecosystem water fluxes have shown that transpiration generally accounts for the majority of the total water flux to the atmosphere in forested ecosystems (Oren et al., 1998). In a variety of forest ecosystems, transpiration has accounted for 22-69% of total ecosystem evapotranspiration (Oren et al., 1998; Barbour et al., 2005; McLaren et al., 2008), depending on canopy wetness conditions and time of year. In addition, during periods of drought, tree water use impacts soil water variability and depletion (Schume et al., 2003). Since it is difficult to measure transpiration directly at the canopy level, tree stem xylem sap flow techniques are often implemented as a way to quantify total tree water use (Granier, 1987; Granier et al., 1996; Gartner et al., 2009), and is scaled up to obtain stand level transpiration.

There is a strong coupling between transpiration and carbon uptake. Stomatal conductance is the regulator of both water vapour and CO_2 exchange processes at the leaf level, and soil and atmospheric conditions, along with rooting depth, impact stomatal response. Many studies have focused on the environmental conditions controlling transpiration through empirical relationships between sap flow velocity and environmental constraints (Wullschleger et al., 2001; O'Brien et al., 2004; Bernier et al., 2006). In some studies, radiation and atmospheric demand, coupled with a soil moisture constraint, tend to explain most of the variability seen in transpiration (Wullschleger et al., 2001; Barbour et al., 2005; Bernier et al., 2006; Fisher et al., 2008). In general, daily sap flow linearly responds to photosynthetically active radiation (PAR), and vapour pressure deficit (VPD) until a threshold point ranging from 0.6 to 1.5 kPa is reached, where increases in VPD are associated with non-increasing sap flow (O'Brien et al., 2004; Bovard et al., 2005). Declines in transpiration rates in response to soil water limitations have also been reported in many other studies, depending on soil type and forest species composition (Irvine et al., 1998; Cinnirella et al., 2002; Schwarz et al., 2004; Bovard et al. 2005; Wullschleger and Hanson, 2006; Gartner et al., 2009).

In order to study the effects of a severe drought event, during the spring and early summer period, we established a throughfall displacement experiment in a White Pine Plantation forest, located at Turkey Point, in southern Ontario, Canada. The focus of this study was to quantify the effects of a 90% throughfall exclusion, during a three-month period, on transpiration and growth rates. This is among the first studies to investigate the impact of spring and early summer drought on a conifer forest ecosystem growing in the temperate region of eastern North America. White Pine is a native species and is very well adapted to the environment in the region, as it can grow in dry, nutrient poor soils with little difficulty (Parker et al., 2001). Therefore, White Pine forests are considered a preferred choice for plantations or afforestation in North America (Arain and Restrepo-Coupe, 2005). As such, understanding how these forest ecosystems will respond to severe drought events will not only provide us with more insight to their physiology, but will also help in establishing viable forest management practices by finding the environmental threshold limits of these species and their adaptive/recovery properties.

Thus, the main objectives of this study are: (i) To evaluate and quantify the impact of an induced spring and early summer drought on forest transpiration and growth rates; (ii) To determine the response and recovery time of the forest to the drought events; and (iii) To establish key environmental controls and thresholds, which result in changes in forest carbon and water cycles.

1.2. Significance of Study

Forest productivity and sustainability is strongly influenced by water availability to the ecosystem. Changes in the amount of available water has significant influence on the carbon and water fluxes of various ecosystems (Granier et al., 2007). With predictions suggesting that drought frequency and intensity is expected to rise in many parts of the world (Wullschleger and Hanson, 2006; Piao et al., 2008), it is important that we foster a better understanding of how different regions will respond under drought events, in order to manage our ecosystems accordingly.

Throughfall displacement experiments are becoming a common approach for studying the effects of drought on vegetation response. They have been used extensively in the Eastern Temperate Region of the United States, and in various locations in Europe and Austrailia. However, the temperate region of Canada is poorly documented, and this study may be the first to use a throughfall displacement experiment in the Canadian Temperate region. While some studies have looked at the effects of a throughfall displacement experiment on conifer forests (i.e. Irvine et al., 1998; Cinnirella et al., 2002), a study focusing on the Temperate White Pine species (*Pinus strobus* L.) specifically, has not been done. Thus, our study helps to contextualize the effects of a severe drought on a White Pine forest located within the Temperate Region of South Eastern Canada, in order to broaden our understanding of how ecosystems in this region will change under future climate predictions.

Chapter 2: Methodology

2.1. Site description

The study took place at the Turkey Point Flux station (42° 42' 55" N, 80° 22' 20" W), approximately 20 km southwest of Port Dover, and 3 km North of Lake Erie in Southern Ontario, Canada. The station consists of an age-chronosequence (70-, 35- and 7-year old as of 2009) of white pine plantation stands, located within 20 km of each other. It has been making CO_2 and water vapour flux measurements since 2003 at all three sites. This study was conducted at the oldest site (70-yr old), referred here as TP39.

The site was established in 1939 on cleared oak-savanna lands to stabilize soils. The dominant tree species is 82% white pine (*Pinus strobus* L.), 11% balsam fir (*Abies balsamea* L. Mill) and native Carolinian species including 4% Oak (*Quercus velutina* L., *Q. alba* L.) and 2 % Red maple (*Acer rubrum* L.). The average tree height is 21.8 ± 1.7m, stand density is about 421 ± 166 stems ha^{-1} (Peichl et al., 2010) and the leaf area index (LAI) is 8.0 m^2 m^{-2} (Chen et al., 2006) (Table 1). Understory consists of young white pines, black cherry, hemlock, white birch and black and white oak, in addition to ground cover vegetation, which includes Bracken fern, poison ivy, Canada mayflower, Allegheny raspberry and mosses (Arain and Restrepo-Coupe, 2005; Peichl and Arain, 2006).

The climate in the region is classified as cool temperate, with 30-year (1971-2000) mean annual temperature of 7.8 °C and mean annual precipitation of about 1010 mm, of which 133 mm falls as snow (Meteorological Services of Canada climate records at Delhi, ON, located ~20 km from the Turkey Point Flux station in the west). Precipitation is equally distributed throughout the year. Soil at the site is classified as very fine brunisolic grey-brown luvisol, with a sandy texture, composed of ~98% sand, 1% silt and <1% clay. The soil is well-drained with a low moisture holding capacity (Arain and Restrepo-Coupe, 2005).

2.2. Throughfall Displacement Experiment

To evaluate the impacts of the soil moisture deficit on forest water and carbon dynamics, a 20m × 20m drought plot was established in order to re-route throughfall using aluminum troughs, which were mounted on wooden stands. Three neighbouring 20m × 20m plots in the east, south and west were equipped the same way as the drought plot and here after referred as reference plot. According to a previous study conducted at this site (Peichl and Arain, 2007), maximum lateral root length ranges from 7-10m from the base of the tree. In order to ensure the study trees were not accessing water from around the throughfall exclusion perimeter, we selected trees that were situated in the centre of the plot. When selecting the location of the drought plot, topographic conditions and elevation of the surrounding area was considered to reduce the possibility of water moving laterally into the exclusion.

The wooden stands supporting the troughs were constructed from pressure treated pine wood, erected to a height of 1.37m, decreasing at a slope of 0.0762m to a final height of 0.838m. The 0.61m × 3.05m aluminum troughs were placed on top of these wooden stands to cover more than 90% of the plot area. Stem flow was neither excluded nor accounted for, but was assumed to be small (McLaren et al., 2008). To verify that stemflow input was not a significant component, soil moisture measurements were taken around the base of the trees during and directly following rainfall events using a manual probe (CS620, HydroSense Water Content Reflectometer, Campbell Scientific, Inc. (CSI)) and were compared to areas covered with the troughs. The area around the base of the trees showed no significant deviation ($p > 0.05$; Two-tailed student t-test) from spatial measurements taken directly under the troughs and away from the trees. In order to relocate the excluded water away from the drought area, a 30m long trough was installed at the end of the 20m × 20m area to capture all the through-fall running off the troughs. Measurements were not taken to quantify the amount of through-fall removed from the area, as the mechanics to do so were beyond the scope of this study.

In order to determine spatial variability of soil moisture between the drought and reference plots, soil moisture transects ($n = 54$) were established in each plot and manual soil moisture measurements (CS620, CSI) were taken over the top 20cm root-zone at two-week intervals. This sampling strategy ensured that these measurements were taken during all prevailing soil water conditions. Soil moisture (at 5, 20, 50 and 100cm depths) and soil temperature (at 5, 20 and 50cm depth) were continuously measured in the drought and reference plots using CS615 (CSI) and CS107B (CSI) probes, respectively. In addition, continuous measurements of soil moisture and soil temperature at several depths were available for two additional locations (100-200 m away from drought/reference plots), that are part of the long-term eddy covariance flux tower setup at this site. See Arain and Restrepo-Coupe (2005) for further details.

To assess the change in soil moisture content over the growing season, and determine when the ecosystem was under stress, soil moisture was re-expressed as Relative Extractable Water (REW), as introduced by Black (1979). Many studies have used REW as a way to assess soil water deficit (Breda et al., 1995; Fernandez et al., 1997; Granier et al., 1987; 2000; Cias et al., 2005; Gartner et al., 2009), and thus expressing soil moisture as REW allows us to compare our threshold with other ecosystems. REW was calculated for the root zone (0-20 cm) as:

$$REW = \frac{\theta - \theta_{wp}}{\theta_{fc} - \theta_{wp}} \qquad (1)$$

where θ is the actual soil water content (m^3 m^{-3}), θ_{fc} is the soil volumetric water content at field capacity (m^3 m^{-3}) and θ_{wp} is the soil volumetric water content at the observed wilting point (m^3 m^{-3}). In this study, field capacity and wilting point values were estimated from long-term soil moisture data (CS615, CSI) from 2003-2009, when soil water content was at its maximum 24 hours after freely drained water was removed, and minimum during a natural drought occurrence in 2005. In a similar analysis, Peichl et al. (2010) reported the soil volumetric water content at field capacity and wilting point to be 0.16 m^3 m^{-3} and between 0.01 to 0.04 m^3 m^{-3}, respectively at this site. For the purpose of our analysis, we used the lower end of the range for wilting point (0.01 m^3 m^{-3}) to calculate REW. In well-drained sandy soils (as seen at our site) wilting point can reach soil hydrophobic values. Thus, using a lower wilting point would have no impact on REW values in this study. The values of these variables used in this study are summarized in Table 1. Total extractable water ($\theta_{fc} - \theta_{wp}$) for this site is 150mm.

2.3. Sap flow, Transpiration and Biometric Measurements

Xylem sap flow was continuously measured using the 30 mm long, continuously heated, Thermal Dissipation Probes (TDP-30; Dynamax, Houston, Texas; Granier, 1987). The sap flow probes were installed on the north side of the trees at about 1.3 m above ground level (agl) in 7-trees within the drought plot and 15-trees in the reference plot. Each probe has two cylindrical thermocouple probes (1.3 mm diameter), of which the upper one is heated and bottom one is unheated. Thermal conductance of sapwood increases with sap flow velocity, and thus, measurement of the temperature difference (ΔT) between the heated and unheated probe yields a dimensionless flow index (K). This index is used to calculate xylem sap flow (J_s) with an empirical relation developed by Granier (1987). In our study, ΔT was continuously recorded throughout the year for each individual sensor, and half hourly mean values (the average of measurement every 10 minutes) was calculated and stored using a data logger (CR10X; CSI) and a Multiplexer (AM16/32; CSI). In order to avoid any impact of direct solar heating, the sensors were insulated with Styrofoam eggs and were shielded with aluminum foil to minimize variations in temperature flux.

The trees selected for study varied in diameter at breast (1.3 m) height, DBH. In order to capture the variability within both drought and reference plots, selected tree DBH's ranged to include one large tree, three intermediate (near-average) trees, and one smaller tree (Kostner et al., 1992). The biometric conditions of each tree, at the end of the growing season, are summarized in Table 2.

In order to install the sap flow sensors, the bark of the tree was carefully scrapped to reveal the surface of the sapwood (the boundary before coming in contact with the phloem). A study conducted by McLaren et al., (2008) took wood core samples to estimate the amount of non-conducting tissue within each tree, and applied a correction presented by Clearwater et al. (1999) to adjust for the difference. Due to the fact that the study trees are to be evaluated for long-term responses, tree-cores at this stage of the experiment could not be done, as the damage to the tree from the cores may have impact on the health of the trees and may impact the study. However, since McLaren et al., (2008) found little variability between the study trees (5-7 mm of non-conducting cambium), the same assumption was applied to all trees in this study.

Xylem sap flow was calculated using the methods presented in Granier (1987), using the following equations:

$$Ki = \frac{\Delta T_{\max i} - \Delta T_{ti}}{\Delta T_{ti}} \qquad (2)$$

$$Jsi = 0.119 x 10^{-3} Ki^{1.23} \qquad (3)$$

where ΔT_{ti} is the temperature differential at each time (t) for each sensor, $\Delta T_{max\,i}$ is the maximum temperature differential for each sensor, and K_i is the calculated dimensionless sap flow index, as discussed above. J_{si} is the sap flow velocity for each tree, measured in (m s^{-1}).

Sap flow velocity (J_{si}) for individual trees was first scaled-up to the cross sectional area of the stem using the sapwood area. Sapwood area was estimated by an allometric equation derived for this site by Peichl and Arain (2007) through a destructive harvesting experiment, and is presented in equation (4):

$$A_s = 0.0815 * DBH^{2.2254} \tag{4}$$

where A_s is the sapwood area (m^2), DBH is the diameter at breast height (m) and 0.0815 and 2.2254 are site-specific parameters. In order to calculate stand level canopy transpiration (E_c), tree sapwood area was further converted to sapwood per unit ground area using the following equation:

$$A_{si} : A_{gi} = BA * (A_{si} : A_{wi}) \tag{5}$$

where $A_{si} : A_{gi}$ is the ratio between sapwood area to ground area, BA is the site basal area (m^2) and $A_{si} : A_{wi}$ is the ratio of sapwood area to tree wood area (measured at breast height or 1.3m). Transpiration (E_T) for each individual tree (in kg m^{-2} s^{-1}) was calculated as:

$$E_{Ti} = \rho_w * J_{si} * (A_{si} : A_{gi}) \tag{6}$$

where ρ_w is the density of water (kg m^{-3}). Finally, half-hourly stand level transpiration per unit ground area (E_c) was calculated as:

$$E_c = \frac{\sum_{i=1}^{n} E_{Ti}}{n} \qquad (7)$$

where n denotes the number of trees sampled in each plot. E_c was then converted to half hourly hydrologic units (mm hh^{-1}).

In both the reference and the drought plots, dendrometer bands were installed on each of the study trees slightly below the sap flow sensors (~1.2-1.25 m agl) in order to measure their diameter growth throughout the season. The dendrometer bands were installed in early-March and the first set of measurements were taken on May 14th, followed by bi-monthly measurements of DBH increment to capture the rate of growth over the season by the two plots. At the end of the season, all trees within the measured plots including oak and understory saplings were measured in order to determine plot-scale basal area (BA), and total wood area contribution from both over-story and understory species.

2.4. Eddy Covariance Flux and Ancillary data

Half hourly fluxes of latent heat (*LE*), sensible Heat (*H*) and CO_2 (F_c) as well as other meteorological variables were measured on top of a 28 m scaffolding tower located about 50 m south of the drought plot. Details of the eddy covariance system and weather station are given in Arain and Restrepo-Coupe (2005) and Peichl et al. (2010).

Precipitation (PPT) was measured year-round about 2 km northeast of TP39 in an open area at Norman Dale Fish Hatchery using a weighted rain gauge (T200B, Geonor Inc.). In addition, a non-heated tipping bucket rain gauge (TE525, Texas Inst.) was also installed at this location along side the weighted rain gauge. A non-heated tipping bucket (CS700; CSI) was also installed on the top of the tower. The weighted gauge precipitation measurements were cross checked with the two tipping bucket rain gauges to ensure accuracy.

2.5. Data Quality Control and Gapfilling

Sap flow velocity and eddy covariance flux data was quality controlled for any possible spikes and missing periods. There was a large (10 days) gap in sap flow data in August due to power failure for sap flow system. Eddy covariance flux data had small gaps due periodic system maintenance, power failure, rain events and when turbulence was low (characterized when friction velocity, u^* < pre-defined threshold, u^*_{Th} = 0.25). We used a Neural Network Training Tool (nntraintool), in Matlab (The MathWorks Inc.) to fill gaps in sap flow and latent heat (*LE*) fluxes. Photosynthetically Active Radiation (PAR), vapour pressure deficit (VPD), soil temperature at the 5cm depth (T_s) and soil moisture averaged over the rooting zone ($\theta_{0\text{-}20cm}$) were used as training data for sap flow. For *LE*, the same environmental variables were used as training data, but also included windspeed (u). The Neural Network model simulated half-hourly sap flow values for each sensor, which were regressed against observed values. The output of this regression resulted in high goodness-of-fits for modeled data (slope = 1 and R^2=0.85), and thus, we opted for this method, as opposed to traditional multiple regression techniques.

To model transpiration, most studies have used a combination of the Penman-Monteith equation and the Jarvis-Stewart model, to derive stomatal conductance (g_c), and eventually, canopy transpiration (Whitley et al., 2009). However, according to a study by Rana et al., (2005) and a study by David et al. (1997), the Penman-Monteith equation has produced poor estimates of canopy transpiration under soil limiting conditions (particularly when E_c is low). To avoid this issue, we used the Neural Network tool, which modeled E_c well under all soil water conditions. The Neural Network (nntraintool) tool uses a Levenberg-Marquardt algorithm for optimization. The Levenberg-Marquardt algorithm (LMA) is the widely used optimization algorithm, for its robustness and accuracy (Ranganathan, 2004). The LMA minimizes a function using least-squares relationships or regressions (Lourakis, 2005). Prior to training, the training tool first randomly divides the data into three sets: 60% of the data is used for training the network, 20% is used to validate the outcomes of the model in order to prevent over-fitting the data (or fitting the random noise), and 20% of the data is reserved for a final test of the model output. Using the measured data, and the constraint variables, the neural network establishes the best fit for the data and generates outputs. These outputs are then used to fill the gaps in the E_c data, creating a continuous dataset.

In order to compare E_c from drought and reference plots, we obtained a ratio of BA/E_c, using plot specific Basal Area (Table 4). This ratio showed that both plots are very comparable with BA/E_c values of 0.23 for both drought and reference plots. Granier et al., (1987) showed that if the ratio of transpiration to Basal Area between the two plots is similar, then the transpiration per unit conductive sapwood area would be equivalent in each plot. The ratios in our plots are the same, and thus, the slightly greater wood area in drought plot can explain the difference in magnitude of sap flow in the drought plot. In order to remove the difference in sap flow magnitude between drought and reference plots and to analyze the impacts of the treatment (drought) on the transpiration rates, a normalization technique was applied by diving data from both treatment and reference plots with the maximum observed value.

$$Ec_{\_norm} = \frac{Ec}{Ec_{\_\max}} \qquad (8)$$

where E_{c_max} is the maximum observed half-hourly value of E_c for each plot. All data management and statistical analysis was conducted using Matlab software.

Chapter 3: Results

3.1. Meteorological and Soil Moisture Trends

Daily average trends of net radiation (R_n), air temperature (T_a), soil temperature at 5cm depth (T_s), and vapour pressure deficit (VPD) for 2009 are shown in Figure 1(a-e). During the winter, T_a remained below 0 ^oC consistently until mid-March (Figure 1-b), reaching a daily average minimum of -16.3 ^oC in February. By the end of March, T_a started to increase and steadily remain above 0 ^oC, increasing to a maximum of 25.3 ^oC by August. T_s followed the trend of T_a, except during winter months when T_s remained at 0 ^oC, due to the isothermal properties of the snowpack which insulated the soil and maintained a constant temperature with minimal diurnal variability. Once the snow pack melted, T_s increased and showed diurnal variability similar to T_a. The Annual average T_a for 2009 was 7.7 ^oC, which was similar to the 30-year (1971-2000) normal value of 7.8 ^oC for the region. T_s showed minimal variability between the two plots (Figure 1-b). VPD (Figure 1-c) responded to changes in incoming radiation and T_a. Daily average VPD never exceeded 1.2 kPa, however, half-hourly maximum VPD reached 2.5 kPa in the spring and early summer. Daily average values of VPD were fairly low during most of the summer months, with values rarely exceeding 1.0 kPa. Annual precipitation for 2009 was 995 mm, making 2009 an average precipitation year as compared to the 30-year mean precipitation of 1010 mm. Precipitation was evenly distributed throughout the year (Figure 1-e), with a small, natural dry period occurring in mid-September where rainfall did not occur for 12 consecutive days. This resulted in

September being one of the driest months for the year, with the highest number of dry days (Table 3). The through-fall exclusion period ran from April 1st until July 3rd, during which 270 mm of rainfall occurred at the site (Figure 1-e). With this considered, annual rainfall in the drought plot was reduced to 725 mm (397 mm for the growing season), representing a very dry year.

Root soil moisture was estimated over 0-20cm depth ($\theta_{0\text{-}20cm}$) in both plots, as the average of 5- and 20-cm probes. Since the majority of fine and small roots are located in the upper 20cm of the soil column (data not shown), we classified this as the root zone. From the beginning of the experiment, soil moisture values measured continuously at permanent monitoring location in the drought plot were lower than the values measured in the reference as shown in Figure 1-d. Regardless of a reduced continuous soil moisture trend in the drought plot, soil moisture during the through-fall exclusion period showed a steady decline in both continuous and manual measurements. It reached a minimum value of 0.053 m^3 m^{-3} and 0.056 m^3 m^{-3}, respectively. Differences between manual measurements and continuous measurements were not statistically different (Drought p = 0.13; Reference p = 0.27; Two-tailed student t-test), suggesting that the location of the continuous soil pit was representative of the spatial variability seen within each plot.

Soil moisture in the root zone expressed as Relative Extractable Water (REW) is shown in Figure 2. As soil moisture began to decline at the onset of the drought, REW dropped steadily from 0.8 to 0.4. Black (1979) found that when REW reached 0.4, transpiration in a Douglas-fir forest in western Canada started to decline. Other studies (including Breda et al., 1995; Granier et al., 2000; Calvet et al., 2004; Bernier et al., 2006) have also confirmed that REW at 0.4 is the point where the system expresses stress to water deficit. At this site, the drought plot reached 0.4 within 43 days following the onset of the induced drought. Both manual and continuous soil moisture measurements confirmed this period as being under this REW threshold. The drought plot continued to be under water stress for an additional 20 days following removal of the troughs. Throughout the rest of the summer and into the early fall, soil moisture increased, and values of REW returned to values above the water stress threshold point in both plots. In early September, however, a period of minimal rainfall occurred (Figure 1-e), and soil moisture in both the reference and drought plot started to show a steady decline (Figure 1-d). REW showed that both plots entered into a short 12 day, natural period of soil water deficit during this time.

3.2. Drought Impact on Transpiration

Daily values of transpiration (E_c) in the reference plot ranged from 0.01 to 1.52 mm d^{-1} throughout the growing season (April – November), while the daily values of E_c in the drought plot ranged from 0.01 to 1.94 mm d^{-1}, highlighting some dissimilarities in the magnitude of tree water loss between two plots (Figure 3a). Both plots showed significant similarity in E_c ($p = 0.46$; ANOVA) during the cool winter months and early spring (mid-April). After this time, the drought plot started to transpire more than the reference plot, showing significant deviation in magnitude until June 1st, 2009 ($p < 0.05$; ANOVA). In June, E_c in the drought plot gradually started to decline, and reached a minimum value of 0.32 mm d^{-1} on July 2nd , which as the end of the induced drought. On July 3rd, the throughfall displacement troughs were removed from the study area. Two days following the removal, a rainfall event occurred at the site, allowing for moisture replenishment of the upper soil layers. Soil moisture in the drought plot showed a quick response to the precipitation event (Figure 1-d), however, an increase in E_c lagged behind the change in soil moisture. 20 days following the removal of the troughs, E_c rates in the drought plot reached the same levels as the reference plot, and remained at the same level as the reference for the duration of the year. During this timeframe, the two plots were just significantly similar ($p = 0.06$; ANOVA). E_c in both plots remained high until late autumn, when the needles started to undergo senescence. Due to warm autumn temperatures, trees continued to transpire until the 5th of December.

Our biometric measurements in the two plots indicated that the basal area of the drought plot (44 m^2) was slightly higher than reference plot (43 m^2). Overstory wood area and sapwood area were also higher in the drought plot (Table 4). A higher conductive sapwood area provides a greater area for water movement in the trees and thus, a higher rate of transpiration would be expected (Granier et al., 2000). Since both components were greater in the drought plot, we attributed these ground conditions to the differences seen in the magnitude of E_c. Therefore, in order to remove bias in E_c rates between drought and reference plots we normalized in both plots, by the maximum observed E_c values (E_{c_max}) as shown in Figure 3b. A similar approach has been used in other studies, specifically when attempting to explore E_c from different species that transpire at different rates (Baldocchi et al., 2004; Gartner et al., 2009) or when looking at thinned vs non-thinned stands (Granier et al., 1987).

Normalized E_c data indicated that the magnitude of transpiration was statistically similar in both plots until May 5th ($p = 0.62$; ANOVA), at which point normalized E_c in the drought started to decline and deviate ($p < 0.05$; ANOVA) (Figure 3b). Contrary to non-normalized E_c, which showed response to the imposition of the throughfall displacement after about 60 days (Figure 3a), the normalized E_c showed this response within 34 days (Figure 3b). This delay in response was because of soil water storage availability after spring melt that was consumed by the trees prior to experiencing water stress.

Accumulated values of normalized E_c showed that both plots followed similar trends until mid to late-May, at which point the drought plot showed a rapid decline in the cumulative E_c value (Figure 4b). By the end of the year, the drought plot showed a cumulative decrease of 20% in normalized E_c as compared to reference plot. Annual total E_c from the reference plot was 191 mm, while total E_c from the drought plot was 194 mm, which was 39% and 40% of the annual total ecosystem ET values of 485 mm, respectively, as measured by the eddy covariance technique (Figure 5). This finding is similar to ET value reported by McLaren et al., (2008) at the same site in 2006, who found that E_c contributed ~47% to ET annually.

3.3. Environmental Controls on Transpiration

In order to explore the soil water stress threshold at our site, E_c normalized by E_{c_max} was plotted against REW for the duration of the drought period as well as 30 days following the drought, to account for the recovery period (Figure 6). As discussed above, in this study, we found that 43 days after the placement of the throughfall exclusion, REW reached 0.4. However, 34 days following the start of the exclusion, normalized E_c started to decline (Figure 3b), indicating that E_c started to decline at an earlier threshold than has been suggested by previous studies.

Normalized E_c showed a clear decline at our site when REW dropped below 0.53, which corresponds to volumetric soil moisture ~0.075 m^3 m^{-3}. REW in the reference plot only rarely reached REW levels as low as 0.53. Drought plot E_c linearly decreased as REW continued to decline to a minimum of 0.26 (R^2 = 0.51). The scatter in E_c vs REW data above 0.53 threshold, indicates that soil water content above this threshold, does not have a significant control on transpiration processes, and atmospheric processes, such as VPD, are likely controlling the variability in E_c.

In order to explore the impact of atmospheric controls and soil moisture stress on the diurnal trend of water loss, Figure 7 summarizes eight selected days throughout the imposed drought experiment and post drought period when rainfall had not yet occurred (April 27th – July 5th), and 4 days following the removal of the troughs (July 9th – August 6th). Early in the season when the weather was warm, soil moisture was non-limiting and VPD was high, normalized E_c in both the drought and the reference plot followed a very similar trend (Figure 7 a-b). In the morning hours, normalized E_c increased with increasing VPD until a maximum point was reached, at which point further increase in VPD no longer impacted E_c due to regulation of the stomata (Limousin et al., 2009). By May 4th, the drought plot started to show some decline in E_c maxima, as the E_c rate reached the same level as the reference plot (Figure 7b). The initial response of E_c to increases in VPD was linear, but when a VPD reached 1.0 kPa, E_c plateaued and stopped responding to further changes in VPD. The reference plot E_c increased at a slightly faster rate earlier in the day, and as a result, maximum E_c in the drought was reduced by 5% in comparison to the reference. Referring back to Figure 3b, May 4th was the point when E_c started to show reduction in total daily E_c, and REW was about 0.55. In the days following, a reduction in E_c in the drought plot continued, since shallower slopes in the morning hours lead to a reduced E_c maxima (Figure 7). The reduction in maximum E_c in the drought plot was 13, 20, 31, 33, 54 and 60% on May 24th, June 4th, June 12th, June 21st, June 27th, and July 5th, respectively (Figure 7c-h). In the four days following removal of the troughs, E_c started to recover from the extreme drought event. Figure 7(i-l) shows an increase in daily E_c maxima in the drought plot, relative to the reference, with increases in VPD.

In order to quantify the point where E_c maxima generally occurs, a linear relationship between daytime VPD and normalized E_c was established to measure the VPD threshold point. To determine whether this threshold varied throughout the drought period, the relationship between half-hourly E_c and daytime VPD (from 8:00 am to 4:00 pm) for each month of the peak growing season (May-October) for both the drought and reference plots is shown in Figure 8(a-f). Coefficients for each linear equation are summarized in Table 5. In May, both the drought and reference plots followed a similar pattern, with the drought plot slightly higher in E_c magnitude than the reference. The VPD threshold was the same in both plots, reaching an E_c maxima at 1.0 kPa (R^2 = 0.62, 0.72 for drought and reference respectively). In June, E_c in the drought plot started to show a reduction in E_c magnitude and VPD in both the drought and reference plots. The slope in the drought plot dropped by 35% relative to the reference (R^2 = 0.47, 0.54, respectively). In addition, the VPD threshold in both plots, dropped to 0.8 kPa. July included a combination of extreme drought stress and recovery. Between the two plots, the slope in the drought plot dropped by 37% relative to the reference R^2 = 0.48, 0.83, respectively), and the VPD threshold also declined to 0.5 kPa. The reference plot reached E_c maxima at a VPD threshold of 0.6 kPa. This change in threshold suggests that stomatal closure occurred sooner in the drought plot, in response to the severe soil moisture stress. In August and the following months, the drought plot started to return to higher levels of E_c, maintaining the same VPD threshold as the reference (0.60 kPa for all months), but failed to reach the same magnitude and pattern as the reference plot, which was seen in May. This suggests that the drought plot failed to recover to its full potential, even after 2 months of exposure to summer and early autumn precipitation events.

In the 2006 growing season, McLaren et al. (2008), explored the effect of early morning VPD (known as initial VPD or denoted here as VPD_{in}) on the E_c response patterns. Since atmospheric stability and low radiation occur during the morning hours at this site, it was decided that initial VPD could be used to characterize the weather conditions at the start of the diurnal transpiration cycle (McLaren et al., 2008). McLaren et al., 2008 also highlighted that soil moisture restrictions on E_c were more clearly evident when the VPD_{in} was accounted for. In 2006, however, only a short drought event occurred lasting a total of 15 days. Therefore, in order to explore the impact of extreme drought conditions, where we excluded throughfall to the root zone for 90 days, we re-visited the relationship between VPD_{In} and E_c. VPD_{in} is defined as the average VPD in the early morning (between 6:00 and 8:00 am), and is divided into three classes: low: $VPD_{in} < 0.02$ kPa; moderate: 0.02 kPa $< VPD_{in} > 0.05$ kPa; and high: $VPD_{in} > 0.05$ kPa. For the 2009 growing season, the majority of the days (56%) fell in the low category, where VPD_{In} was <0.02 kPa.

Figures 9(a-b) show the response of half hourly E_c to half hourly VPD in the drought and reference plots during days of low and moderate VPD_{in} respectively, from May 1st to September 30th. In the reference plot, when VPD_{in} values are low, E_c does not appear to be as restricted by VPD, as the rate of E_c increases rapidly and linearly (dashed line, slope = 0.76, $R^2 = 0.88$), to a maximum VPD of 0.8 kPa, at which point the E_c starts to plateau (Figure 9a). In contrast, when we evaluate the response of E_c to VPD during moderate VPD_{in} conditions (Figure 9b), we see a drop in slope (0.59) up to the VPD point of 0.8 kPa, at which point, E_c starts to show a plateau. However, the spread of the data is less as compared to Figure 9a, and thus the linear relationship is stronger ($R^2 = 0.94$).

Under low VPD_{in} conditions, the drought plot slope was reduced by 40% as compared to the reference (soild line, slope = 0.45, $R^2 = 0.51$). When VPD_{in} is in the moderate range, the separation between the drought and reference decreased. Again, E_c increases linearly with increases in VPD, however, the slope only decreased by 12% relative to the reference (slope = 0.52, $R^2 = 0.62$). Under periods of moderate VPD_{in}, E_c is more sensitive to the increases in VPD, and the stomata exert stronger control on transpiration, reducing the rate at which E_c increases to reach maximum E_c. Thus, we see the drop in slope in the reference between the low and moderate VPD_{in} categories. In the drought plot however, we do not see a large change in slope from low to moderate VPD_{in}. Soil moisture limitation, as seen above in Figure 8, reduces E_c magnitude and under extreme conditions can pull back the VPD threshold (July). We see the same trend in Figure 9(a-b) when considering VPD_{in}.

Under the high VPD_{in} conditions (Figure 9-c), the magnitude of E_c is still less in the drought plot than the reference. Similar to moderate VPD_{in}, the rate of increase in E_c between the two plots is much closer together, as compared to the low category. In the high category, drought E_c increases at a rate of 0.58 ($R^2 = 0.80$), and the reference E_c increases at a rate of 0.68 ($R^2 = 0.66$), resulting in a 15% decline in slope in the drought plot.

Overall, the drought plot does not show as much variability in slope under the different categories of VPD_{in} as compared to the reference, and actually shows an increase in slope from low VPD_{in} to high VPD_{in}. Since the drought was extreme and lasted for a long period of time, the soil moisture limitation in the drought plot appears to exert a stronger control on E_c magnitude than changes in VPD_{in}. Thus, as VPD_{in} became more extreme, E_c in the drought plot was already restricted due to limitations in the soil water content, and did not respond to changes in early morning atmospheric demand. In the reference plot, however, increases in E_c declined as the categories increased in intensity. This finding in the reference plot is similar to what was seen under both drought and normal conditions in McLaren et al., (2008), suggesting that E_c became less sensitive to mid-day VPD as early morning VPD increased. The drought plot, however, showed reverse findings to dry conditions in McLaren et al. (2008), as the slope increases from low to high VPD_{in}, suggesting that E_c increased in sensitivity to mid-day VPD.

3.4. Drought Impact on Tree Growth

In terms of the effects of the drought treatment on growth rates at our site, rate of change in tree growth (DBH) in two plots is shown in Figure 10. The trees that were measured for xylem sap flow in drought and reference plots, were selected to represent the range of tree diameters seen throughout the forest. Table 2 shows the distribution of the DBH at the start of the growing season between the two plots. The DBH distribution between plots was not statistically different (Table 4; $p = 0.14$; Two-tailed student t-test, $\alpha = 0.05$). Our measurements indicated that spatially, DBH growth increments between study trees showed more variation (CV = 87%) in the reference plot than in the drought plot (CV = 71%), when all banded trees were compared. The decreased variability was due to fewer trees experiencing growth within the drought plot. By the end of the growing period, the two plots had deviated significantly ($p < 0.05$; Two-tailed student t-test, $\alpha = 0.05$), and rates of DBH growth had reduced by 42% in the drought plot as compared to the reference plot. Figure 10 also highlights the time frame at which tree growth seized. In the reference plot, minimal growth continued until October 17th, suggesting that temperatures and soil moisture were adequate enough to promote growth. This is also supported with autumn transpiration values. However, in the drought plot, growth was no longer seen as of September 30th indicating an early termination of the tree growth as a result of the water restrictions in the spring.

Chapter 4: Discussion

Soil water stress occurs when growth and transpiration become restricted in response to a decline in soil moisture (Breda et al., 2006). In general, forests species (in particular, *Pinus*) have traits that have made them more drought tolerant than other plant species (Newton et al., 1991; Duursma et al., 2008). In the temperate region specifically, conifer forests seem to have adapted and developed more drought tolerant capabilities than deciduous species. For instance, in 2003, a severe drought event hit Europe, causing significant impact on forest ecosystems across the continent (Breda et al., 2006; Granier et al., 2007; Gartner et al., 2009). During this event, Spruce and Pine forests had less-severe overall responses to the drought, than the birch and aspen forests (Granier et al., 2007), indicating that the conifer species were more adaptable to drought conditions than the deciduous species. However, when drought events are severe, even drought adaptable forests are vulnerable to significant declines in their productivity and transpiration (Goldstein et al., 2000).

In eastern North America, white pine stands are considered drought tolerant species and can grow on sandy soils, which have low water holding capacity (Parker et al., 2001). It is considered a preferred native species for re-plantation or afforestation on cleared or marginal lands and has been widely planted in eastern North America in last few decades (Parker et al., 2001). However, the response of white pine forests to severe droughts, in particular to those occurring in spring and summer season due to recent changes in climate (IPCC, 2007; Piao et al, 2008) are not known. Our study strives to quantify the impact of prolonged and severe water stress occurring during the spring and summer on their growth and water loss. Our results show an annual decline of 20% in normalized E_c due to 90-day drought in the spring and early summer. This decrease in E_c is low as compared to other studies investigating drought effects on mature forest ecosystems. For instance, in the temperate Oak Forest at the long-term Walker Branch throughfall exclusion study, Wullschleger and Hanson in (2006) reported 11 to 30% reduction in annual E_c, throughout different years of their study. A 41-year old Scots Pine (*Pinus Sylvestris* L.) throughfall exclusion experiment in Europe, also showed a 30% reduction in annual E_c trends (Irvine et al., 1998), and a 35-year old Pinus laricio Poiret in Calabria, Italy saw a 50% reduction in annual E_c trends (Cinnirella et al., 2002). In the Boreal forest of Sweden, a three-month drought in 1994 resulted in a 41% decline in pine transpiration and a 46% decline in spruce transpiration (Cienciala et al., 1998). In a Boreal aspen forest, in central Saskatchewan, Canada, annual evapo-transpiration declined by 31% of the pre-drought mean (Krishnan et al., 2006). In the Amazon, a 2-year continuously compounded drought, excluding 50% of the throughfall had a 41% and 47% reduction in E_c (years 1 and 2 respectively) in comparison to the control plot (Fisher et al., 2007). A well-known drought tolerant *Q. ilex* forest in southern France (Damesin et al., 1998), exposed to a long-term (4-years) field manipulation, experienced a 23% reduction in transpiration, in response to a 29% reduction in throughfall input (Limousin et al., 2009). This overall decline suggests that our ecosystem is more drought adaptable than other mature forest ecosystems, including drought tolerant ecosystems, located in different parts of the world.

Apart from meteorological conditions, and soil moisture availability during the growing season, available soil water storage in the root zone prior to drought events play a key role in tree water loss and growth (Bovard et al., 2005; Limousin et al., 2009). Our results indicated that the diurnal variability of tree water loss (E_c) is strongly related to changes in meteorological conditions, in particular photosynthetically active radiation (used in the gap-filling procedure) and VPD. Similar controls have been observed by Granier et al. (1996); Irvine et al. (1998); Wullschleger et al. (2001); Bovard et al. (2005); Duursma et al. (2008); Leuzinger and Korner (2010) and Wallace and McJannet (2010). Half-hourly relationships between VPD and E_c in our forest indicated that the maximum daily E_c is strongly linked to changes in VPD and an affiliated VPD threshold point.

Although this VPD threshold point is variable, depending on the forest type, species composition and environmental conditions, it may range between 0.6 and 1.5 kPa (Granier et al., 1996; David et al., 2004; O'Brien et al., 2004; Barbour et al., 2005; Leuzinger et al., 2005; Bovard et al., 2005; McLaren et al., 2008; Kume et al., 2008). Under limited soil water conditions, Bovard et al., (2005) did not see an effect on the relationship between daily sap flow and cumulative daily PAR. However, sap flow sensitivity to VPD was influenced in certain species, as sap flow decreased at high VPD (above the 1.0 kPa threshold point) as compared to non-limiting conditions. In our study, we found that this threshold varied between months and under soil moisture conditions. When soil moisture restrictions were extreme (as seen in July), the VPD threshold between the two plots differed, with a reduced threshold due to moisture restrictions. However, under decreasing soil moisture this threshold did not vary between the two plots. McLaren et al., (2008) found that changes in VPD_{in} masked the effects of changes in soil moisture under increases in VPD, unless the relationships were separated out into three differing VPD_{in} categories. Under severe drought conditions, we found that soil moisture restrictions on E_c were evident regardless of VPD_{in} partitioning, as the slope between drought E_c and VPD did not show much variation as VPD_{in} increased. The opposite was seen with the reference plot, and our findings support that of McLaren et al., 2008, where reductions in soil moisture were masked until the data was broken down into VPD_{in} categories.

Similar to our findings, Bovard et al. (2005) found that 82% of variation in E_c was explained by PAR and VPD, and that soil moisture primarily affected the response of the stomata to increases in VPD by forcing an earlier closure of stomata. Limousin et al., (2009) also found that soil moisture significantly impacted stomatal closure patterns and reduced transpiration rates to prevent xylem embolism. Fisher et al. (2008) found that stored soil moisture had an influence on drought adaptability, and may over-ride the effects of drought by maintaining adequate plant available soil water during the initial growing period. However, if this soil water storage is depleted, a rapid decrease in E_c would occur. The clear separation of transpiration under limited and non-limited soil moisture, when investigating the response of E_c to VPD, suggested that while meteorological conditions may regulate the diurnal pattern of E_c, soil moisture appears to regulate the magnitude of water flux at our site. The results of our study, support the findings of Wallace and McJannet (2010) and Fisher et al., (2008), in that soil moisture under a site-specific threshold (in our case, of 7.5% (or REW = 0.53)) caused a decline in E_c, and ultimately affected the maximum E_c obtained at the transition point for the E_c-VPD relationship. The REW threshold point of 0.53, seen in our study, was much higher than the findings of many other studies, who have established an REW threshold of 0.4 (Black, 1979; Breda et al., 1995; Granier et al., 2000; Bernier et al., 2006). However, Krishnan et al., (2006) did see a reduction in stomatal conductance of a Boreal aspen forest, when REW reached a threshold of 0.65. Aspen trees have been well established as a drought-tollerant species, particularily in the Populus family (Lieffers et al., 2001). This further suggests that our forest stand is drought adaptable, with a high REW threshold, and responds to decreases in soil moisture early, to prevent excess water loss under periods of severe soil water limitation.

4.2. Response and Recovery Rates

Results of our experimental study indicated that transpiration in the drought plot, based on the normalized data, took 34 days to respond to the drought, however, once the decline started to occur, the cumulative reduction in E_c was 20% below that of the reference daily E_c value. Similar to our findings, Irvine et al., (1998) also noticed a long lag-period in the time it took for transpiration to decline as a result of soil moisture reductions. At the end of the growing season, the trees in the drought plot did not appear to fully recover, reaching maximum potential by early autumn and never exceeded the reference plot E_c. Krishnan et al., (2006) also saw a reduction in evapo-transpiration the two years following a drought event, where ET was 21% and 17% (year one and year two respectively) less than the pre-drought mean, suggesting that their site also did not fully recover to full potential. Breda et al. (1993) suggested that the reduction in transpiration from potential transpiration following drought removal could be linked to wounding to the fine root system in the shallow soil layers. As part of the adaptive qualities of trees, when drought stress becomes severe, resources are not allocated to fine root production and foliage, and more focus is placed on large root growth and basic maintenance for survival (Cinnirella et al., 2002; Breda et al., 2006). Thus, many fine roots suffer high mortality. Although fine-root biomass analysis was not conducted in our study, the similar results following trough removal suggest that this might be one possible explanation for the lower transpiration rates seen in our drought plot.

Following the removal of the troughs, E_c responded quickly to the precipitation input to the soil (lagging by a few hours). This fast response is similar to the findings of Granier et al., in 2007, where transpiration increases were seen following small precipitation pulses that occurred throughout the dry period (Granier et al., 2007), suggesting that increases in shallow soil moisture triggered a root response that signaled to the tree that it should transpire. However, maximum recovery of E_c was achieved after 30 days, when the magnitude of E_c from the drought plot became similar to E_c from the reference plot. This shows that the trees in the drought plot were able to sustain themselves under severe water limitation and achieved partial recovery in transpiration when moisture became available.

4.2. Drought and the potential influence on growth rates

Vegetation species that survive throughout the winter months (such as conifer trees) store carbon in various reservoirs located throughout the root, stem and branch system, to allow for winter maintenance and early spring start up production. During years of drought, it has been noticed that carbon sequestration patterns decline in response to severe soil water deficits (Irvine et al., 1998; Ogaya et al., 2003; Breda et al., 2006; Granier et al., 2007), and is highly variable depending on the individual tree species. However, because of the previous year storage, often the full effect of the drought event on tree stem growth is not seen until the year following the drought. At our site, stem biomass contributes 69% of the total tree biomass, while roots contribute 18% (Peichl and Arain, 2007). Therefore, impacts on stem-growth can have significant consequences on changes in overall tree biomass. In our study, we saw a difference of 42% in annual growth between the drought and reference plot trees. In addition, we noticed that the date for growth termination occurred earlier in the drought plot than the reference plot. Since the drought was considered very severe (90% exclusion for 90-days consistently), it is possible that the drought had an effect on the amount of growth occurring in the plot the year of the drought (2009), and it may show significant impacts on growth in the following growing season as well. As such, growth in this plot will be monitored closely to study the effects of the severe drought on tree succession in the post drought year.

Many studies have shown a decline in growth during and following a severe drought year. Granier et al., (2007) showed that annual biomass increments were reduced by 22 to 44% between different sites in Europe. A beech stand in Europe experienced a very significant decline in growth the year following the drought, showing 27% less growth than 2003, accounting for only 62% of the 2002 growth. Leuzinger et al. (2005) saw a 25% reduction in basal area increase the year following the 2003 drought event in Europe. An early termination (August) was also seen at this site. Irvine et al., (1998) saw a 14% reduction in basal area the year the drought occurred, and a 23% reduction, in comparison to the reference, the year following the drought, indicating that a compounded effect was occurring. Drought tolerant deciduous species, located in a mixed-forest in Spain, demonstrated significant variability within during a 2-year experimental drought from 1999-2001

(Ogaya et al., 2003). *A. unedo* and *Q. ilex* showed a reduction of 77%, and 55% respectively, while *P. latifolia* showed no reduction at all.

Conclusions

Currently, drought effects are not well understood in forest ecosystem, in particular in temperate conifer forests. Therefore, throughfall displacement experiments, such as the one described in this study, are critical for developing our understanding of what impact drought may have on temperate conifer forest ecosystem in a changing climate. This study indicated that a severe drought in the temperate region of eastern North America, will decrease annual transpiration by 20% and tree growth rates by 42%.

The diurnal course of transpiration was dominated in both the drought and reference plots by the diurnal trend of VPD. The relationship between VPD and E_c was linear until a transition point, or VPD threshold, which varied between months. Drought only influenced the VPD threshold point under severe drought conditions (when soil moisture had dropped under 0.06 m^3 m^{-3}, which occurred in July), reducing the threshold by 0.1 kPa from the reference plot in July. The decline in the transition point was likely a result of an earlier stomatal response due to changes in the hydraulic conductance along the soil-to-leaf pathway.

Transpiration was unaffected by soil water content above a soil water threshold (REW) of 0.53 (corresponding to volumetric soil moisture content of 0.075 m^3 m^{-3}), a threshold which is higher than findings reported in many other studies. Under this REW threshold, however, transpiration linearly declined with decreases in soil water content. The impact of reduced soil moisture altered the daily maximum E_c obtained in the drought plot. In the reference plot, when soil moisture was above the critical threshold, daily E_c maximum was dominated by the diurnal course of VPD, with distinct variability under differing VPD_{in} conditions. Since soil moisture dominated the maximum daily E_c in the drought plot, increases in VPD_{in} did not exert a change in daily maximum E_c.

Overall, this study highlights the impact a severe drought can have on canopy water fluxes and growth rates, in a single year. A reduction of 42% in growth, suggests that productivity in this forest, under a similar scenario, would have substantial influence on the carbon uptake processes of the ecosystem. In addition, the inabilities of transpiration in the drought plot to recover to full pre-drought potential. Thus this study provides new insight to how these forests would respond under a critical drought event occurring in the spring and early summer period.

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TABLES

Table 1: Site Characteristics

Stand Parameter	Condition
Location	42° 42' 55" N 80° 22' 20" W
Elevation	184 m
Overstory species	Whit Pine (Pinus Strobus)
Understory species	Young white pines, Black cherry, Hemlock, White birch and Black and white oak, Bracken fern, Poison ivy, Canada mayflower, Allegheny raspberry and Mosses
Leaf Area Index (LAI)	8.0 $m^2 m^{-2}$ *
Average Diameter at 1.3m or Breast Height (DBH)	35.5 cm (±5.9)**
Average Tree Base Diameter	39.4 cm (±7.9) **
Average Tree Height	21.8 m (± 1.7) **
Stem Density	421 trees ha^{-1} (± 166) **
Measured Basal Area	37.3 $m^2 ha^{-1}$ **
Wilting Point	0.01 to 0.040 $m^3 m^{-3}$
Field Capacity	0. 16 $m^3 m^{-3}$

* Chen et al., 2006
** Peichl et al., 2010

Table 2: Characteristics of the trees monitored in the drought and reference plots

Tree	Plot Location	DBH (m)	Wood Area (m^2)	Sapwood Area (m^2)
SF_1	Reference	0.371	0.108	0.0253
SF_2	Reference	0.262	0.0539	0.0117
SF_3	Reference	0.379	0.0113	0.0265
SF_4	Reference	0.488	0.187	0.0465
SF_5	Reference	0.430	0.146	0.0353
SF_6	**Drought**	**0.384**	**0.1170**	**0.0272**
SF_7	**Drought**	**0.335**	**0.0893**	**0.0202**
SF_8	**Drought**	**0.314**	**0.0785**	**0.0175**
SF_9	**Drought**	**0.409**	**0.1331**	**0.0315**
SF_10	**Drought**	**0.280**	**0.0624**	**0.0135**
SF_11	Reference	0.316	0.0795	0.0177
SF_12	Reference	0.378	0.1137	0.0264
SF_13	Reference	0.551	0.2416	0.0611
SF_14	Reference	0.451	0.1615	0.0390
SF_15	Reference	0.371	0.1092	0.0253
SF_16	Reference	0.456	0.1655	0.0401
SF_17	Reference	0.470	0.1758	0.0429
SF_18	Reference	0.364	0.1052	0.0242
SF_19	Reference	0.393	0.1226	0.0287
SF_20	Reference	0.375	0.1116	0.0259
SF_21	**Drought**	**0.404**	**0.1299**	**0.0306**
SF_22	**Drought**	**0.442**	**0.1551**	**0.0373**

Table 3: Growing season environmental conditions and water fluxes from drought (Dro) and reference (Ref) plots

Month	PPT_{Ref} (mm)	PPT_{Dro} (mm)	T_a (°C)	Mean $E_{c\,Ref}$ (mm d^{-1})	Mean $E_{c\,Dro}$ (mm d^{-1})	Total $E_{c\,Ref}$ (mm)	Total $E_{c\,Dro}$ (mm)	Dry Days	Wet Days**
April	142.9	0	7.4	0.44	0.64	12.3	19.2	16	14
May	38.8	0	13.1	0.98	1.22	29.1	37.8	20	11
June	70.7	0	17.0	0.97	0.78	27.3	23.4	18	12
July	93.0	89.0*	17.9	0.87	0.71	25.9	21.9	9	22
August	120.6	120.6	19.5	0.97	1.06	30.1	32.7	19	12
September	51.9	51.9	15.8	0.79	0.86	26.7	25.6	22	8
October	89.8	89.8	8.1	0.31	0.30	12.9	9.1	14	17
November	45.6	45.6	5.6	0.15	0.14	7.5	4.3	15	15
Seasonal average	**653.3**	**396.9**	**13.1**	**0.69**	**0.71**	**171.8#**	**174.0#**	**133**	**111**

* The drought was in place for the first three days of July until when 4 mm of rain fell.
**Wet day is defined when any precipitation event occurred (i.e. PPT >0 mm).
#Total E_c values are gapfilled.

Table 4: Biometric Characteristics of drought and reference plots

Parameter	Drought Plot	Reference Plot	p*
Average DBH (cm)	34.7 (±1.5)	38.1 (±2.6)	0.14
Overstory Wood Area (m^2)	1.83	1.72	0.08
Average Sapwood Area (m^2)	0.15	0.14	0.09
Understory Wood Area (m^2)	0.013	0.010	0.17
Basal Area (m^2)	44	43	0.35
BA/Annual E_c	0.23	0.23	
Annual growth rates (cm)	0.14 (±0.05)[&]	0.24 (±0.04)[%]	

* Results of a two-tailed student t-test, with $\alpha = 0.05$

[&] based on 7 trees

[%] based on 15 trees

Table 5: Coefficients for the linear relationship between monthly transpiration, E_c and vapor pressure deficit, VPD.

	Drought Plot			**Reference Plot**		
	β_1	β_0	R^2	β_1	β_0	R^2
May	0.40	0.020	0.62	0.40	0.023	0.72
June	0.28	0.018	0.47	0.43	0.036	0.54
July	0.41	0.004	0.48	0.66	0.087	0.83
August	0.61	0.006	0.65	0.59	0.075	0.54
September	0.76	0.034	0.55	0.67	0.059	0.50
October	0.47	0.050	0.60	0.60	0.034	0.58

FIGURES

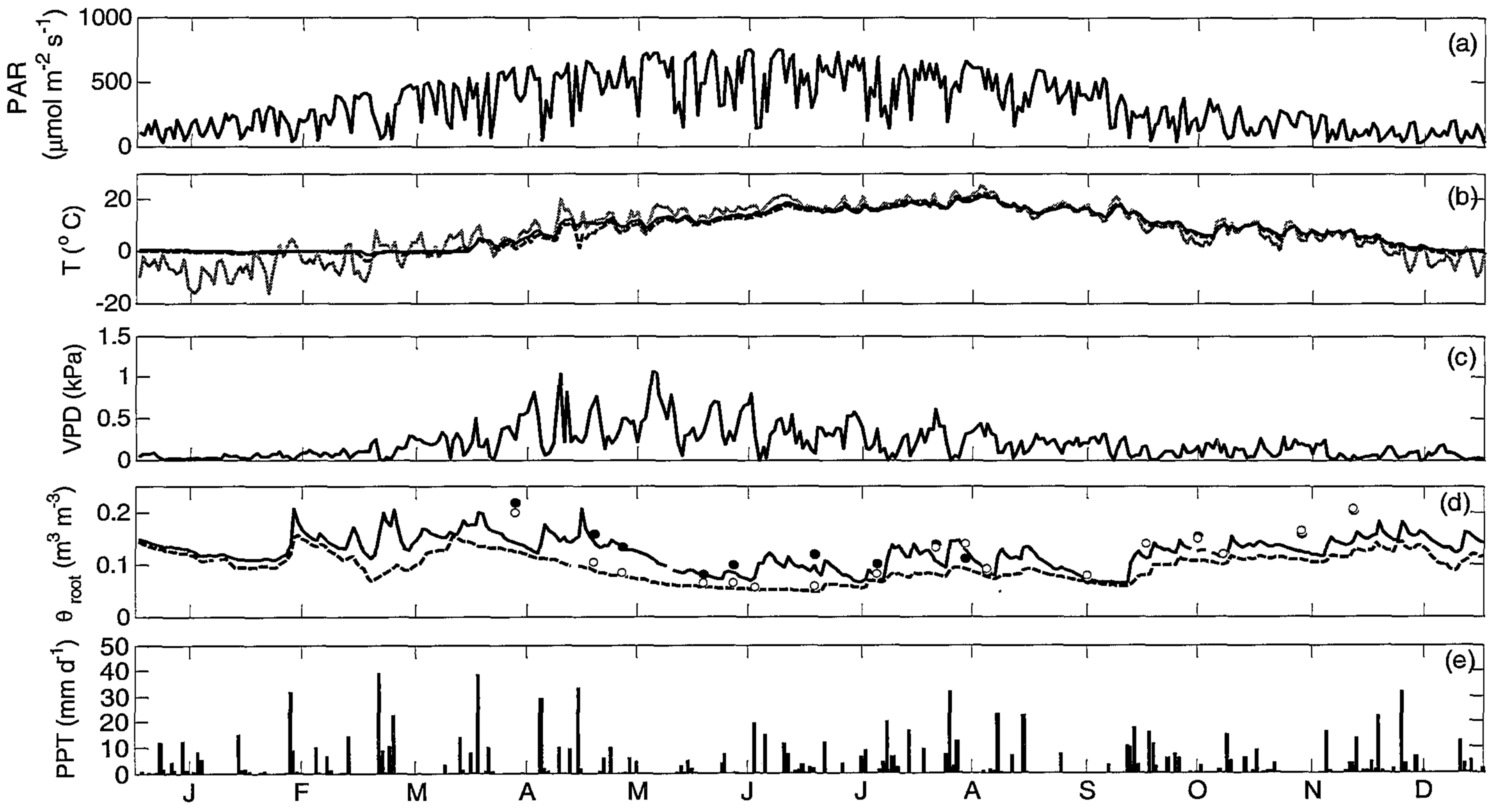

Figure 1: Daily mean values of (a) Photosynthetically Active Radiation, PAR (μmol m^{-2} s^{-1}), (b) air temperature (°C) (grey line) and soil temperatures at the 5cm depth (black line) in the drought (dashed) and reference (solid) plots, respectively, (c) vapour pressure deficit, VPD (kPa), (d) soil moisture in the root zone (0-20cm) in the drought (dashed line) and reference (solid line) plots; average of manual soil moisture measurements (n=54 per plot) are also shown (drought: open circle; reference: solid circle) and (e) daily precipitation (mm d^{-1}).

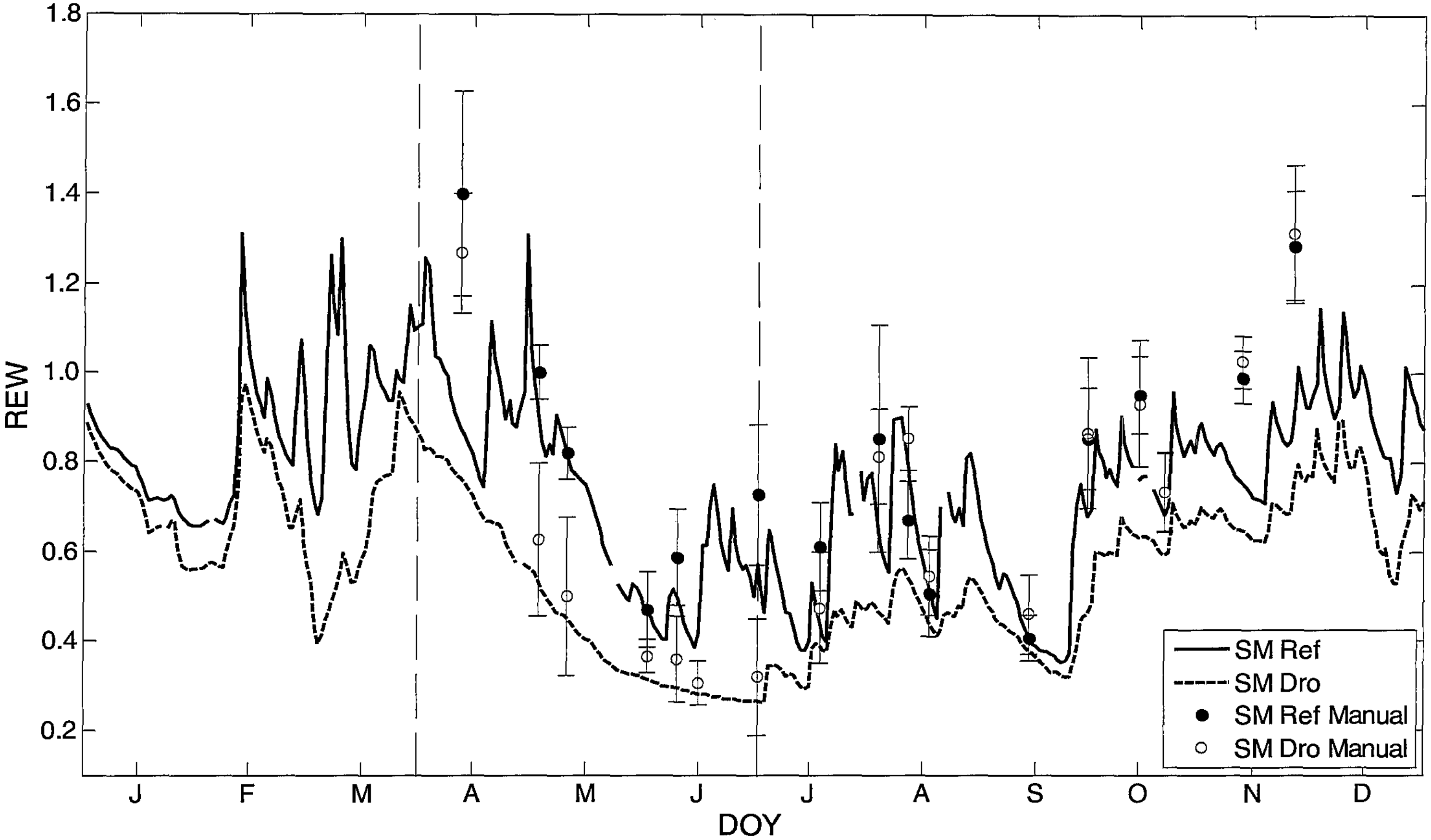

Figure 2: Relative extractable water (REW) for the drought (dashed line) and reference (solid line) in the top 20cm soil zone. REW calculated using 54 point measurements in drought (solid circle) and reference (open circle) are also shown. Error bars represent the standard deviation of each point.

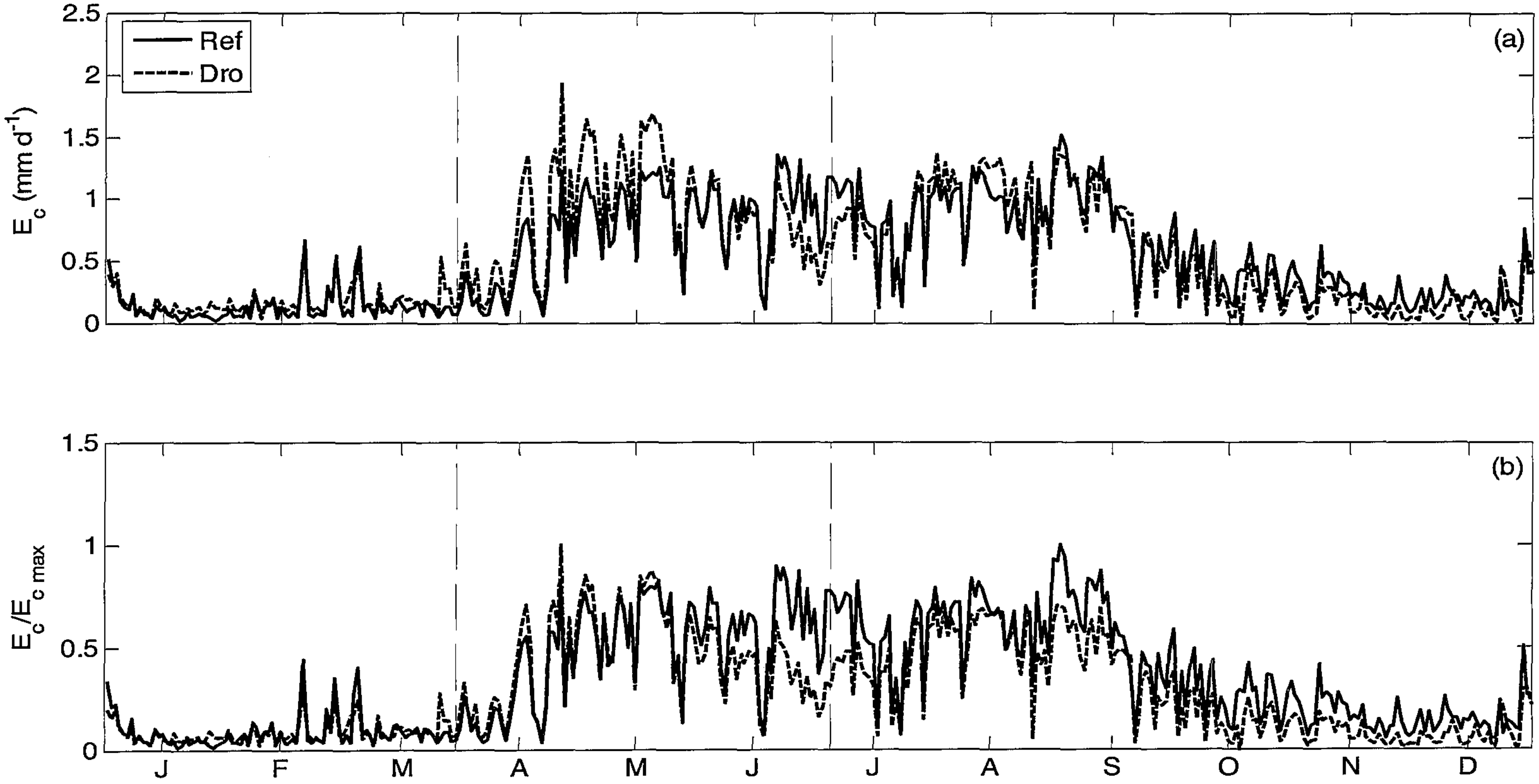

Figure 3: (a) Daily mean values of transpiration (E_c), calculated and scaled to stand level, in the drought (dashed line) and reference plots (solid line). (b) Normalized E_c vales using maximum daily E_c ($E_c/E_{c\,max}$) in the drought (dashed line) and reference (solid line) plots.

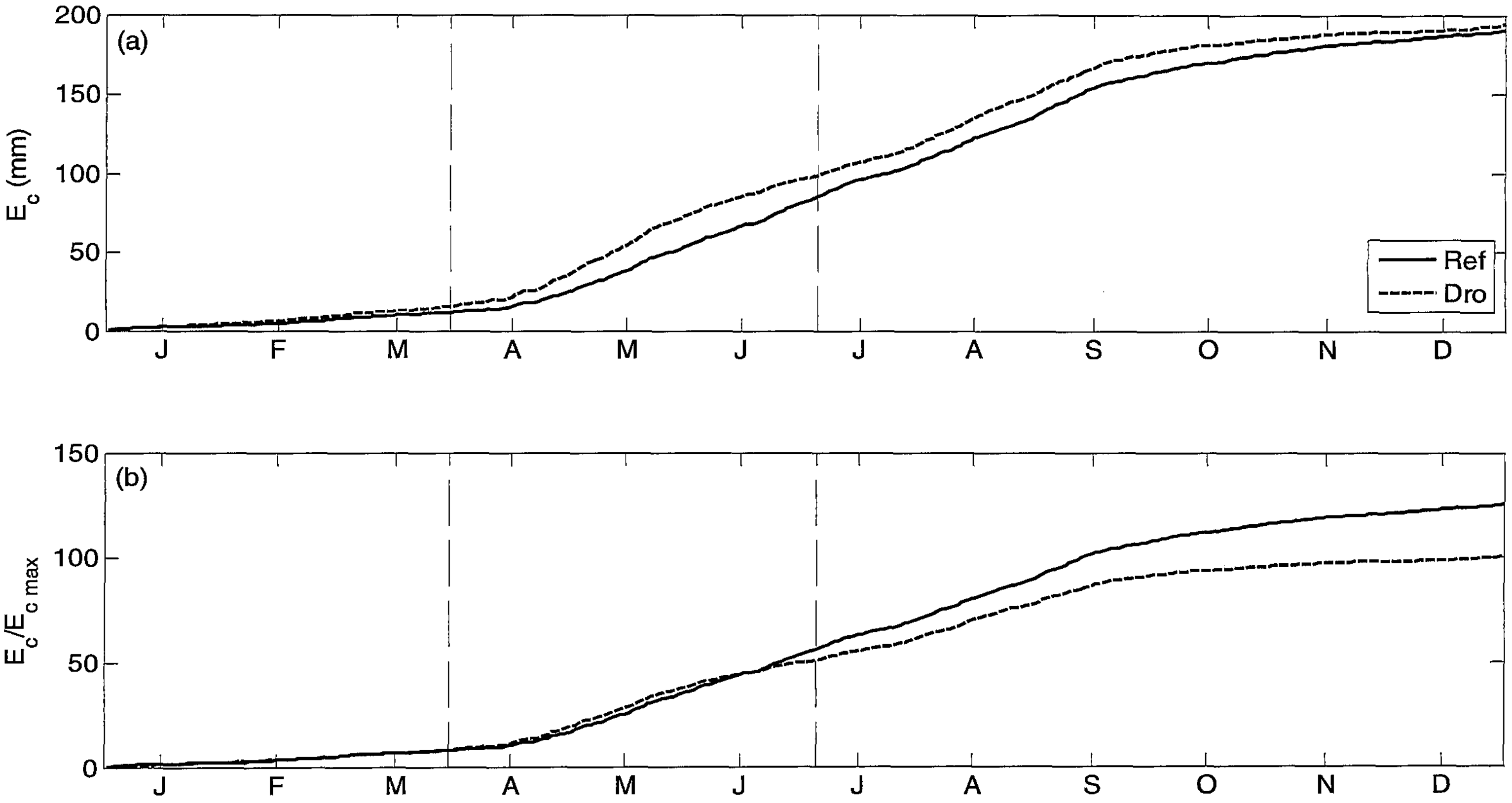

Figure 4: (a) Cumulative transpiration (E_c) in the drought (dashed line) and reference (solid line) plots. (b) Normalized cumulative E_c values using maximum daily E_c ($E_c/E_{c\,max}$) in the drought (dashed line) and reference (solid line) plots.

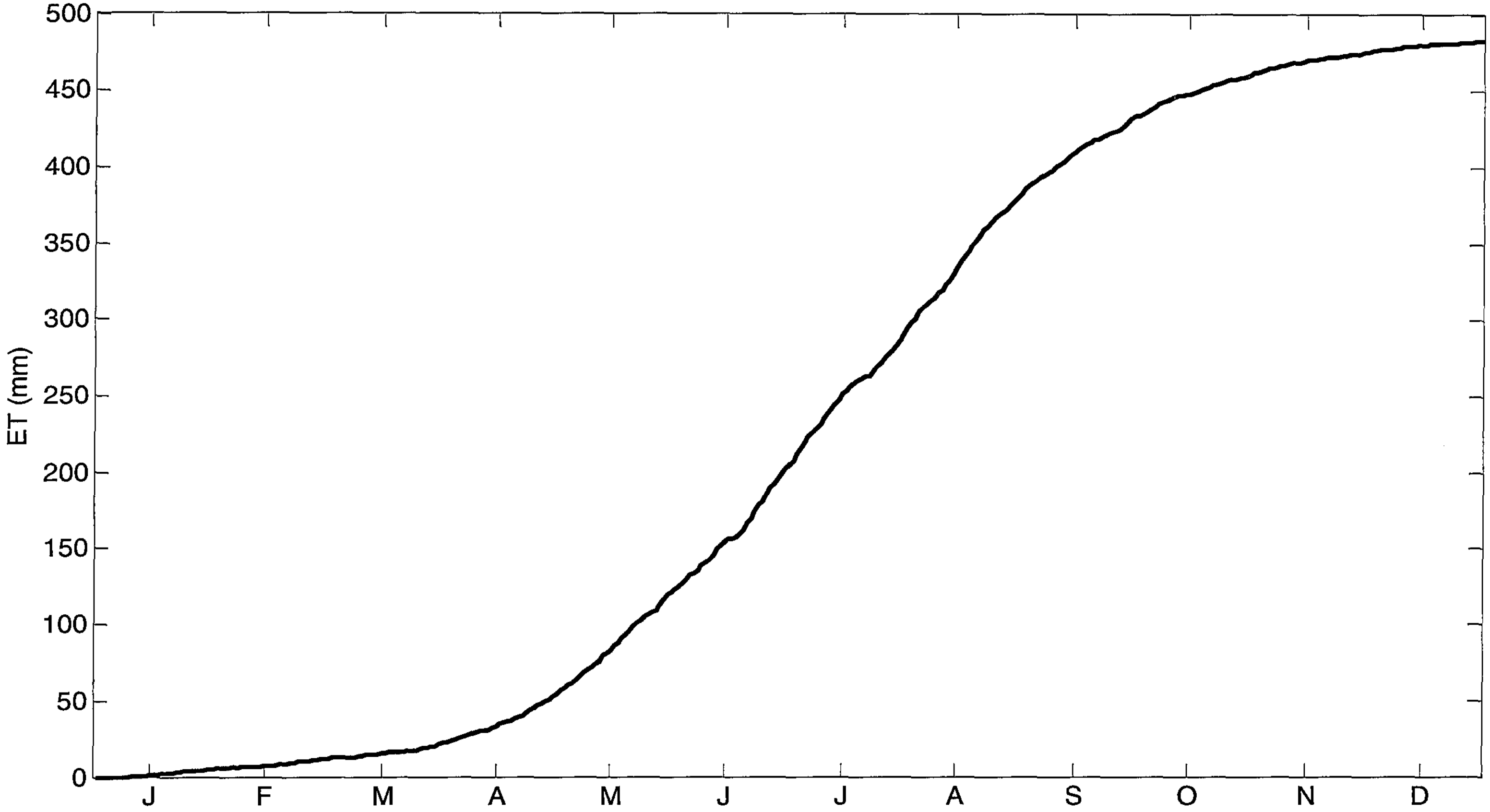

Figure 5: Ecosystem level evapotranspiration (ET) measured with the eddy covariance system.

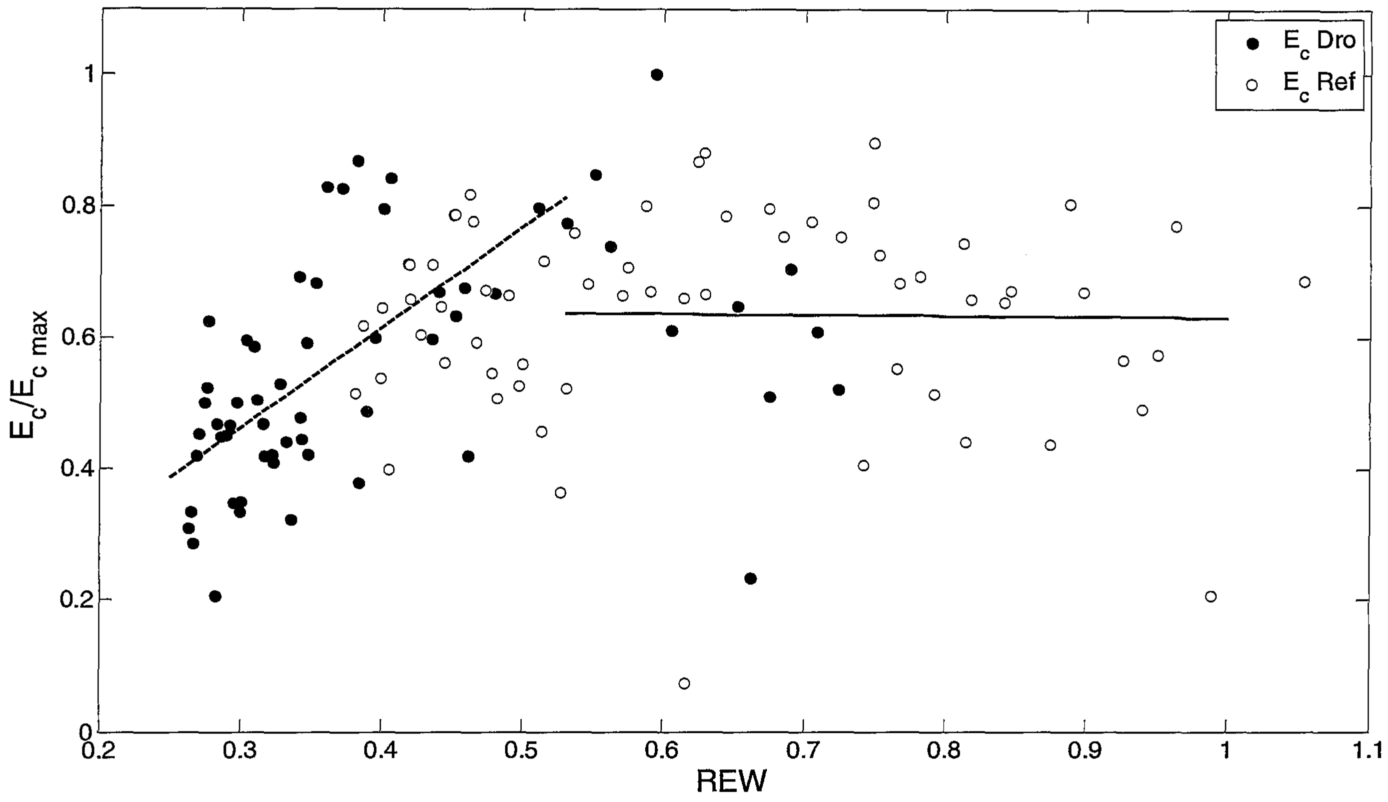

Figure 6: Relationship between normalized transpiration (E_c) and relative extractable water (REW) in both the drought (solid circles) and reference (open circles). At an REW threshold of 0.53, E_c starts to show a linear decline relative to decreases in REW. A line fitted to the E_c and REW relationship below a REW threshold values of 0.53 is defined as $y = 1.5x + 0.0062$ ($R^2 = 0.51$). The same relationship above an REW value of 0.53 is defined as $y = -0.011x + 0.64$ ($R^2 = 0.00$).

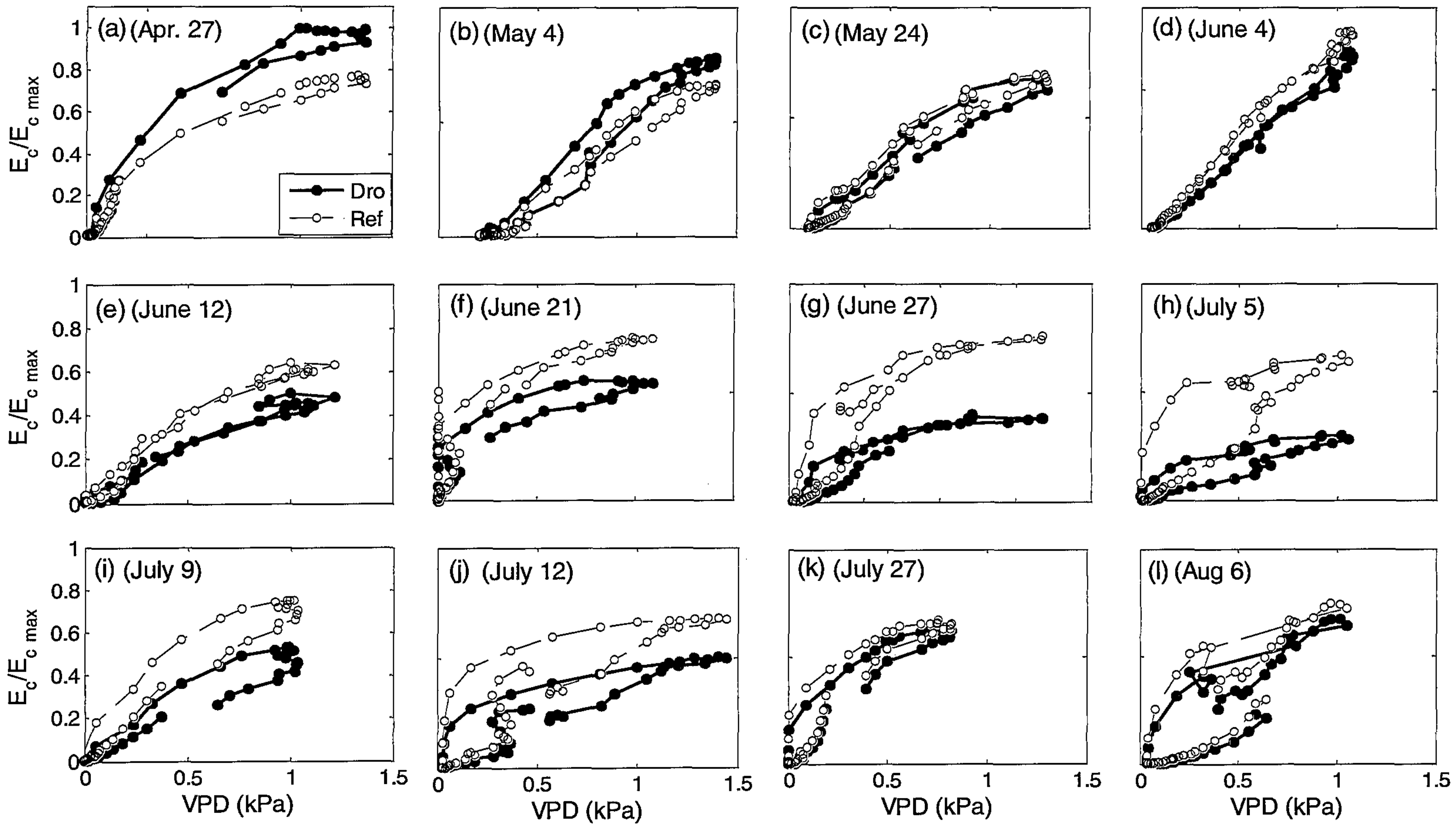

Figure 7: Diurnal trends of half-hourly vapor pressure deficit, VPD (kPa) and transpiration, E_c in the drought (closed circles) and reference (open circles) plots for select days during the drought (8 days; April 27 through July 5) and following the drought (4 days; July 9 through August 6).

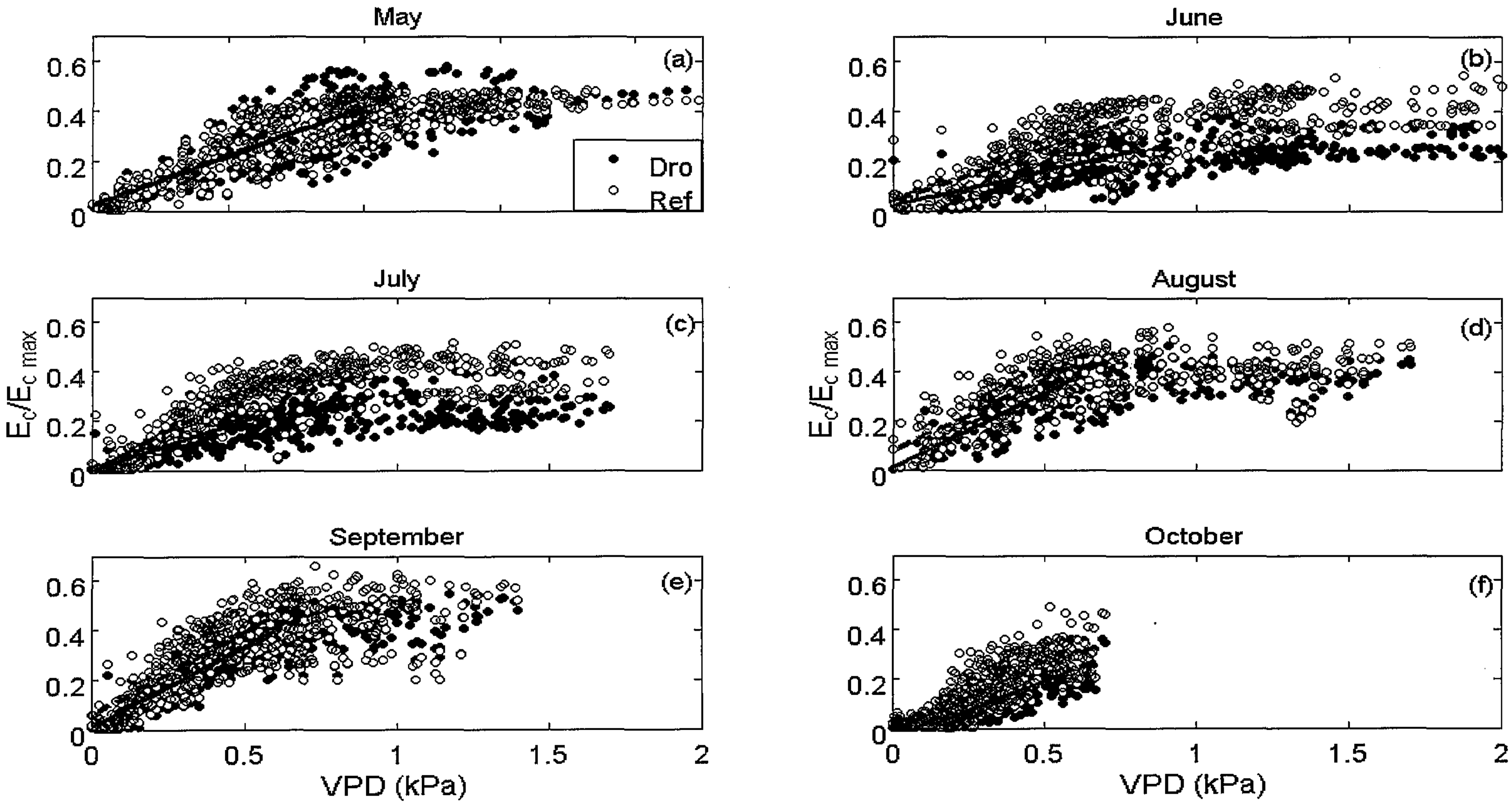

Figure 8: Half-hourly daytime vapor pressure deficit, VPD vs normalized transpiration, E_c for drought (filled circles) and reference (open circles) plot for each month; (a) May, (b) June, (c) July, (d) August, (e) September and (f) October, highlighting the change in VPD threshold as the drought progressed through the summer.

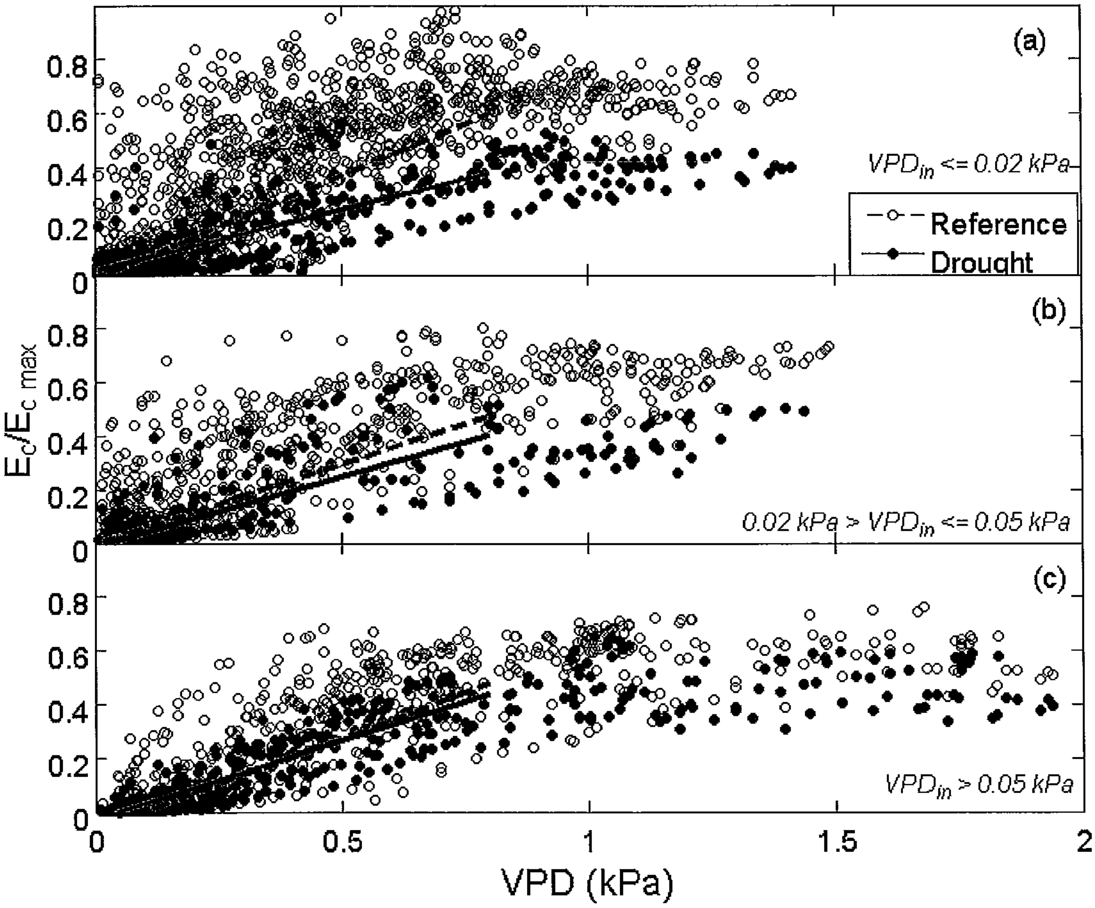

Figure 9 (a): Half hourly vapor pressure deficit, VPD vs normalized transpiration, $E_c/E_{c\,max}$ for the drought (when soil moisture, $\theta_{0\text{-}20cm}$ <0.07 $m^3\ m^{-3}$) and reference ($\theta_{0\text{-}20cm}$ > 0.07 $m^3\ m^{-3}$) conditions when early morning VPD (averaged between 6:00-8:00 am), VPD_{in} <= 0.02 kPa. A fitted line for drought conditions (solid line) is expressed as y = 0.45x + 0.0015 (R^2 = 0.51) and for reference conditions (dashed line) is expressed as y = 0.76x + 0.015 (R^2 = 0.88). **(b):** VPD vs $E_c/E_{c\,max}$ for drought ($\theta_{0\text{-}20cm}$ <0.07 $m^3\ m^{-3}$) and reference ($\theta_{0\text{-}20cm}$ > 0.07 $m^3\ m^{-3}$) conditions when: 0.02 > VPD_{in} <= 0.05 kPa. A fitted line for drought conditions (soild line) is expressed as y = 0.52x + 0.0016 (R^2 = 0.62) and for reference conditions (dashed line) is expressed as y = 0.59x + 0.005 (R^2 = 0.94). **(c):** VPD vs $E_c/E_{c\,max}$ for the drought plot ($\theta_{0\text{-}20cm}$ <0.07 $m^3\ m^{-3}$) and reference ($\theta_{0\text{-}20cm}$ > 0.07 $m^3\ m^{-3}$) conditions when: VPD_{in} > 0.05 kPa. A fitted line for drought conditions (soild line) is expressed as y = 0.68x + 0.069 (R^2 = 0.80) and for reference conditions (dashed line) is expressed as y = 0.58x - 0.029 (R^2 = 0.66).

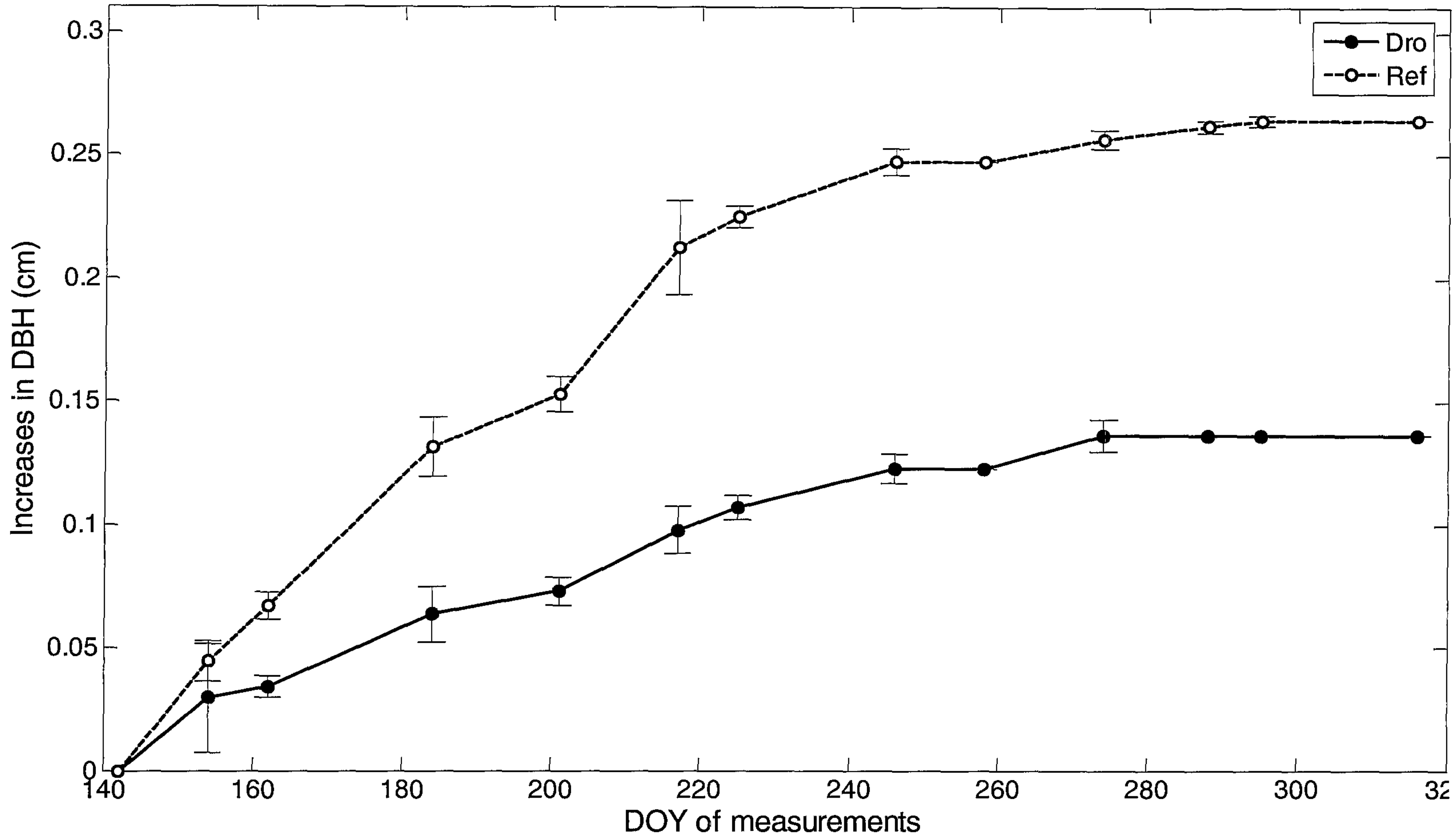

Figure 10: Cumulative growth rates in the drought (solid circles) and reference (open circles) plots. Standard Error for measurement points is also shown.