Evaluating and modeling long-term climate and disturbance impacts on evapotranspiration and canopy conductance in boreal aspen and black spruce stands

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The following individuals certify that they have read, and recommend to the Faculty of Graduate and Postdoctoral Studies for acceptance, the dissertation entitled:

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Abstract

Nearly one tenth of the world’s forest is located in Canada, with one third being boreal forest. Understanding how this biome is responding to climate change is important to global carbon (C) and water balances. Long-term climate and eddy-covariance (EC) measurements of C and water vapour fluxes were made on a mature deciduous aspen stand (old aspen, OA) and a mature coniferous black spruce stand (old black spruce, OBS) to determine the impact of climate variations and disturbances on the C and water fluxes, and test if commonly utilized models can successfully model these fluxes. The impact of a defoliation event at OA in the summer of 2016, due to forest tent caterpillar infestation, was investigated and annual GEP was found to be reduced by ~20% that year, leading to the most negative annual NEP (-72 g C m⁻² year⁻¹) over the observation period. Long-term trends in annual climate variables, along with trends in gross ecosystem production (GEP), ecosystem respiration (Rₑ), net ecosystem production (NEP), evapotranspiration (E), P – E, and water use efficiency (WUE = GEP/E) were investigated using 22 and 19 years of continuous data at OA and OBS, respectively. The impacts of growing season (GS) metrics on GS and annual NEP, GEP and E were investigated. Trends were also investigated at GS and monthly scales for climate variables and E, along with the impact of GS metrics on E at GS scale. The two stands showed varied responses to climatic variability, including responses to a multi-year drought that affected both sites but had a larger impact on the C and water fluxes at OA than OBS. The dependence of the canopy conductance (Gₑ) and E on their controlling variables was investigated at GS and monthly scales for both sites. The Jarvis-Stewart (JS) and modified Ball-Woodrow-Berry (MBWB) models were tested to estimate half-hourly Gₑ at each site and compute both Gₑ and E at seasonal to annual scales. This thesis demonstrates the importance of long-term observations in capturing variations in climate and
disturbances forests experience, that need to be further studied and modelled for improved understanding of their impacts.
Lay Summary

It is often said that forests are the lungs of the earth. Forests perform the vital function of creating oxygen from CO₂. The Boreal forest is particularly important as the second largest biome on earth. Due to increased CO₂ concentrations causing climate change, it is important to understand how forests are dealing with the changing environment. I studied the impact of changing climate by utilizing a long-term data set to look at how much carbon was taken up and released, and water used, by two forest stands over two decades. Like our lungs which can get infected impacting our overall health, forests can also be infected with insects affecting their health. Accordingly, I studied how one forest responded to being attacked by caterpillars during one summer. Knowing how the forest responds to climate change and insect infestation will help us predict responses to future climate change.
Preface

Chapters 2-5 are based on 22 and 19 years of measurements made in central Saskatchewan on a mature deciduous aspen stand (OA) and a mature coniferous black spruce stand (OBS). The Soil Physics and Biometeorology group led by Dr. Andy Black were involved in the setup of these sites and have led or been involved with the maintenance of the equipment and the data generated from the sites. I took over managing the equipment maintenance and data quality assurance and control for the sites in 2013 which I continued through 2017. For this work, I relied on the established data management system instituted by Zoran Nesic and Nicholas Grant, who taught me how to use and maintain it. Some of the code used for analysis in the chapters was generated by past members of the Soil Physics and Biometeorology Group, with most of these having been created by Zoran Nesic and Nicholas Grant. For this thesis, I conducted all analyses and wrote all text (except where specified otherwise below). Each chapter was guided and edited by Drs. Andrew Black, Rachhpal S. Jassal, Mark S. Johnson, and Andreas Christen with input from collaborators (Zoran Nesic, Nicholas J. Grant, Alan G. Barr, Warren D. Helgason, Andrew D. Richardson) at publication submission stages. A version of Chapter 2 has been published as: Jilmarie J. Stephens, T. Andrew Black, Rachhpal S. Jassal, Zoran Nesic, Nicholas J. Grant, Alan G. Barr, Warren D. Helgason, Andrew D. Richardson, Mark S. Johnson, Andreas Christen. (2018). Effects of forest tent caterpillar defoliation on carbon and water fluxes in a boreal aspen stand. Agricultural and Forest Meteorology. 253-54:176-189. The section on “Normalized difference vegetation index (NDVI)” was originally drafted by Mark S. Johnson and the section on “PhenoCam observations” was heavily modified by Andrew D. Richardson. The GCC data from the PhenoCam was processed
and sent to me by Andrew D. Richardson. The NDVI and Landsat8 figures were generated from analysis done by Mark S. Johnson.
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Figure 5.4 Measured rain-free half-hourly growing season $G_c$ vs. modelled Jarvis-Stewart (JS) and modelled modified Ball-Woodrow-Berry (MBWB) $G_c$ at Old Aspen (OA) ($n = 33,699$ for 11
years) and Old Black Spruce (OBS) \((n = 31,660 \text{ for 9 years})\). The black line is the 1:1 line, the blue and red lines are the regression for 11 years at OA and 9 years at OBS, respectively, with the equations given in the plots, and the grey lines are the regression lines for all the individual years tested at each site (1996:2017 at OA and 1999:2017 at OBS).

Figure 5.5 Daily ensemble averaged measured rain-free \(G_c\) (black circles), Jarvis-Stewart (JS) modelled \(G_c\) (blue squares), and Modified Ball-Woodrow-Berry (MBWB) modelled \(G_c\) (red stars) at OA (left column (a-e) May-Sept for 1996:2017) and OBS (right column (f-j) May-Sept for 1999:2017).

Figure 5.6 Measured rain-free growing season daily \(G_c\) vs. modelled Jarvis-Stewart (J-S) and modelled modified Ball-Woodrow-Berry (MBWB) \(G_c\) at Old Aspen (OA) \((n = 1203 \text{ for 11 years})\) and Old Black Spruce (OBS) \((n = 1795 \text{ for 9 years})\). The black line is the 1:1 line, the blue lines and red lines are the regression lines for 11 years at OA and 9 years at OBS, with the equations given in the plots, and the grey lines are the regression lines for all the individual years tested at each site (1996:2017 at OA and 1999:2017 at OBS).

Figure 5.7 Five-day 24-h averaged \(\text{CO}_2\) mixing ratio, 2-cm soil temperature \((T_s)\), air temperature \((T_a)\), photosynthetically active radiation \((Q)\), vapour pressure deficit \((D)\), cumulative precipitation \((P)\) and average (0-90-cm at OA and 0-60-cm at OBS) soil volumetric water content \((\theta)\) from 1996:2017 at Old Aspen (OA) by the red dot-dashed line and 1999:2017 at Old Black Spruce (OBS) by the blue dot-dashed line. Shaded red and blue areas denote \(\pm 1\sigma\) from the long-term mean at OA and OBS, respectively. This figure is the same as Fig. 4.1.

Figure 5.8 Mean annual five-day averaged measured rain-free \(G_c\), Jarvis-Stewart (JS) modelled \(G_c\), and Modified Ball-Woodrow-Berry (MBWB) modelled \(G_c\) at OA for 1996:2017 (a) and OBS
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(\(T_s\)), air temperature (\(T_a\)), downwelling photosynthetically active radiation (\(Q\)), vapour pressure
deficit (\(D\)), growing season precipitation (\(P\)) and average (0-90-cm depth at OA and 0-60-cm
depth at OBS) soil volumetric water content (\(\theta\)) from 1996 to 2017 at Old Aspen (OA) and
brown bar denotes the 2016 forest tent caterpillar (FTC) defoliation period at OA. This figure is
the same as Fig. 4.5).

Figure 5.10 Interannual variation in growing season measured rain-free \(G_c\) and \(E\) (black circles),
year round Jarvis-Stewart (JS) modelled \(G_c\) (a) and \(E\) (blue squares) (c), and Modified Ball-
Woodrow-Berry (MBWB) modelled \(G_c\) (b) and \(E\) (red stars) (d) at Old Aspen (OA) 1996:2017
and Old Black Spruce (OBS) 1999:2017, respectively.

Figure 5.11 Measured rain-free growing season mean \(G_c\) and \(E\) vs. modelled Jarvis-Stewart (JS)
and modelled modified Ball-Woodrow-Berry (MBWB) \(G_c\) and \(E\) at Old Aspen (OA) and Old
Black Spruce (OBS). The black line is the 1:1 line, the blue lines are JS regression lines and red
lines are the MBWB regression lines for 1996:2017 at OA and 1999:2017 at OBS, with the
equations given in the plots.

Figure 5.12 Interannual variation in annual mean measured rain-free \(G_c\) and \(E\) (black circles),
year round Jarvis-Stewart (JS) modelled \(G_c\) (a) and \(E\) (blue squares) (c), and Modified Ball-
Woodrow-Berry (MBWB) modelled \(G_c\) (b) and \(E\) (red stars) (d) at Old Aspen (OA) 1996:2017
and Old Black Spruce (OBS) 1999:2017, respectively.
Figure 5.13 Measured rain-free annual mean $G_c$ and $E$ vs. modelled Jarvis-Stewart (JS) and modelled modified Ball-Woodrow-Berry (MBWB) $G_c$ and $E$ at Old Aspen (OA) and Old Black Spruce (OBS). The black line is the 1:1 line, the blue lines are JS regression lines and red lines are the MBWB regression lines for 1996:2017 at OA and 1999:2017 at OBS, with the equations given in the plots.
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<thead>
<tr>
<th>Symbol</th>
<th>Units</th>
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<tr>
<td>$A$</td>
<td>$\mu$mol m$^{-2}$ s$^{-1}$</td>
<td>Rate of net CO$_2$ assimilation</td>
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<td>W m$^{-2}$</td>
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<td>°C$^{-1}$</td>
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<td>Mole fraction of CO$_2$ at the surface</td>
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<td>Specific heat of air</td>
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<td>mol CO$_2$ mol air$^{-1}$</td>
<td>CO$_2$ mole fraction at the leaf surface (Equation 5.2)</td>
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<td>kPa</td>
<td>Vapour pressure deficit</td>
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<td>mm year$^{-1}$ or mm day$^{-1}$</td>
<td>Evapotranspiration</td>
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<td>$g_s$</td>
<td>mol m$^{-2}$ s$^{-1}$ or mm s$^{-1}$</td>
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<td>mm s$^{-1}$ or mmol m$^{-2}$ s$^{-1}$</td>
<td>Aerodynamic conductance</td>
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<td>mm s$^{-1}$ or mmol m$^{-2}$ s$^{-1}$</td>
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<td>$G_{CC}$</td>
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<td>GEP($t$)</td>
<td>Time variation in GEP</td>
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<td>unitless ratio, Relative humidity at the leaf surface (Equation 5.10)</td>
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<td>unitless ratio, Relative humidity at the leaf surface (Equation 5.2)</td>
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<td>$H$</td>
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<td>mmol m$^{-2}$s$^{-1}$/μmol m$^{-2}$s$^{-1}$/(kPa mol CO$_2$ (mol air)$^{-1}$), Fitted parameter for Equation 5.11</td>
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<td>$P$</td>
<td>mm, Precipitation</td>
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<td>μmol photons m$^{-2}$s$^{-1}$, Downwelling photosynthetically active radiation</td>
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<td>$R_a$</td>
<td>W m$^{-2}$, Available energy flux</td>
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<td>$R_e$</td>
<td>g C m$^{-2}$ year$^{-1}$ or μmol m$^{-2}$s$^{-1}$, Ecosystem respiration</td>
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<td>$R_e(t)$</td>
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<td>$R_n$</td>
<td>W m$^{-2}$, Net radiation flux</td>
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<td>$s$</td>
<td>kPa °C$^{-1}$, Slope of the saturation vapour pressure curve</td>
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<td>$T_a$</td>
<td>°C, Air temperature</td>
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<td>$T_{min}$</td>
<td>°C, Minimum air temperature when $f(T_a)$=0</td>
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<td>Unit</td>
<td>Description</td>
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<tr>
<td>$T_{\text{max}}$</td>
<td>°C</td>
<td>Maximum air temperature when $f(T_a)=0$</td>
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<td>°C</td>
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<tr>
<td>$T_{\text{opt}}$</td>
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<td>Optimal temperature where $G_c$ is at its maximum</td>
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<td>°C</td>
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<tr>
<td>$u$</td>
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<td>$u_*$</td>
<td>m s$^{-1}$</td>
<td>Friction velocity</td>
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<td>$\alpha$</td>
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<td>Priestley-Taylor alpha</td>
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<td>$\lambda$</td>
<td>J kg$^{-1}$</td>
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<td>kPa °C$^{-1}$</td>
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<tr>
<td>$\rho$</td>
<td>kg m$^{-3}$</td>
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<td>Shortwave albedo</td>
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<tr>
<td>$\theta$</td>
<td>m$^3$m$^{-3}$</td>
<td>Volumetric soil water content</td>
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<td>$\Delta e_o$</td>
<td>kPa</td>
<td>$D$ at the surface</td>
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<tr>
<td>$\Delta S$</td>
<td>W m$^{-2}$</td>
<td>Rate of energy storage between EC sensor height and the ground (sensible heat (air and biomass), latent heat and photosynthetic energy)</td>
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<tr>
<td>$\Omega$</td>
<td></td>
<td>Decoupling coefficient</td>
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<tr>
<td>$\psi_m$</td>
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<td>Integral diabatic correction factor for momentum transfer</td>
</tr>
<tr>
<td>$\psi_h$</td>
<td></td>
<td>Integral diabatic correction factor for sensible heat transfer</td>
</tr>
<tr>
<td>$\Lambda$</td>
<td></td>
<td>Leaf area index</td>
</tr>
<tr>
<td>$\Lambda_{\text{max}}$</td>
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<td>Maximum observed leaf area index</td>
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## List of Abbreviations

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<tr>
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<th>Units</th>
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<tr>
<td>BERMS</td>
<td></td>
<td>Boreal Ecosystem Research and Monitoring Sites</td>
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<td>BWB</td>
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<td>Ball-Woodrow-Berry model</td>
</tr>
<tr>
<td>C</td>
<td></td>
<td>Carbon</td>
</tr>
<tr>
<td>CCP</td>
<td></td>
<td>Canadian Carbon Program</td>
</tr>
<tr>
<td>CCRN</td>
<td></td>
<td>Changing Cold Regions Network</td>
</tr>
<tr>
<td>CI</td>
<td></td>
<td>Confidence interval</td>
</tr>
<tr>
<td>CIPHA</td>
<td></td>
<td>Climate Change Impacts on Productivity and Health of Aspen</td>
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<tr>
<td>CO₂</td>
<td>µmol mol⁻¹ or ppm</td>
<td>Carbon dioxide</td>
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<td>DOY</td>
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<td>Day of the year</td>
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<td>EC</td>
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<td>Eddy-covariance</td>
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<td>FCRN</td>
<td></td>
<td>FLUXNET Canada Research Network</td>
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<td>FTC</td>
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<td>Forest tent caterpillar</td>
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<td>GEP</td>
<td>g C m⁻² year⁻¹ or µmol m⁻² s⁻¹</td>
<td>Gross ecosystem production</td>
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<td>GGML</td>
<td></td>
<td>Greenhouse Gases Measurement Laboratory</td>
</tr>
<tr>
<td>GS</td>
<td></td>
<td>Growing season</td>
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<td>JS</td>
<td></td>
<td>Jarvis-Stewart Model</td>
</tr>
<tr>
<td>LAI</td>
<td></td>
<td>Leaf area index</td>
</tr>
<tr>
<td>LFH</td>
<td></td>
<td>Litter-fermented-humic</td>
</tr>
<tr>
<td>MODIS</td>
<td></td>
<td>Moderate Resolution Imaging Spectroradiometer</td>
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<tr>
<td>MBWB</td>
<td></td>
<td>Modified Ball-Woodrow-Berry Model</td>
</tr>
<tr>
<td>Acronym</td>
<td>Definition</td>
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<tr>
<td>NDVI</td>
<td>Normalized difference vegetation index</td>
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<td>NEE</td>
<td>Net ecosystem exchange</td>
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<td>NEP</td>
<td>g C m$^{-2}$ year$^{-1}$ or μmol m$^{-2}$ s$^{-1}$ Net ecosystem production</td>
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<tr>
<td>NIR</td>
<td>Near infrared band Terra band 2 (841–876 nm)</td>
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</tr>
<tr>
<td>OA</td>
<td>Old Aspen</td>
<td></td>
</tr>
<tr>
<td>OBS</td>
<td>Old Black Spruce</td>
<td></td>
</tr>
<tr>
<td>PAR</td>
<td>μmol photons m$^{-2}$ s$^{-1}$ Photosynthetically active radiation</td>
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<tr>
<td>P-M</td>
<td>Penman-Monteith</td>
<td></td>
</tr>
<tr>
<td>PRT</td>
<td>Platinum resistance thermometer</td>
<td></td>
</tr>
<tr>
<td>RGB</td>
<td>Red-Green-Blue</td>
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<tr>
<td>WECC</td>
<td>Water, Ecosystem, Cryosphere and Climate</td>
<td></td>
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<tr>
<td>WUE</td>
<td>g C (kg H$_2$O)$^{-1}$ Water use efficiency</td>
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<tr>
<td>WUE$_i$</td>
<td>g C (kg H$_2$O)$^{-1}$ kPa Inherent water use efficiency</td>
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Lastly, I thank Luna for she loved me unconditionally and sat by my side through all the years of graduate school. Without her I would not have walked outside every single day of those years.
Dedication

To my family
Chapter 1: Introduction

1.1 Background and Motivation

Global climate change caused by increasing atmospheric CO$_2$ is altering earth ecosystems at a rapid rate, leading to an uncertain future climate (IPCC, 2013). Globally, averaged atmospheric CO$_2$ concentration has increased at a mean annual rate of 1.7 ppm y$^{-1}$ over the past three decades, with the warming and precipitation changes caused by the CO$_2$ increase being variable around the globe (IPCC, 2013). One of the ways atmospheric CO$_2$ concentration is reduced is through carbon (C) sequestration by forests. The C balance of an ecosystem results from the difference between CO$_2$ uptake by photosynthesis and CO$_2$ release by respiration. Studies have contrasting conclusions on the future C sink and source capabilities of forests under the impacts of climate change (Bonan, 2008, Keenan et al., 2012).

Since plants need CO$_2$ for photosynthesis, it is hypothesized that with increasing atmospheric CO$_2$ concentration, plants will become more productive and use less water (i.e. increase their water use efficiency), because stomata can take up more CO$_2$ per water molecule lost when the CO$_2$ concentration is high (Drake et al., 1997; Ward & Strain, 1999). Some multiyear free-air CO$_2$ enrichment (FACE) experiments with elevated CO$_2$ concentrations confirm this theory (Ainsworth & Rogers, 2007; Ward et al., 2012), while others disagree (Tor-ngern et al., 2015; Klein et al., 2016). A better understanding of the impact of environmental drivers on stomatal controls of transpiration can provide insight into the impact of changing environmental conditions on plant productivity in forests (Kropp et al., 2017).

The terrestrial C cycle is linked to the water cycle through evapotranspiration ($E$) at various temporal and spatial scales (Ball et al., 1987; Leuning et al., 1995). $E$ is the sum of water that is
evaporated from surfaces and transpired through plants; it has been extensively researched (e.g., Penman, 1948; Priestley and Taylor, 1972, Monteith, 1981, Su et al., 2007). $E$ is an important process that links major components of the energy and water balances of the Earth’s land surface (Su et al., 2007; Cheng et al., 2017). Climate influences $E$ through precipitation that supplies water available for uptake by plants to be transpired and providing the conditions for stomata to open for photosynthesis (Penman, 1948). Due to a constantly changing climate, $E$ is highly variable on diurnal to annual scales. Climate variables, such as air temperature, net radiation, vapor pressure deficit etc., are drivers of stomatal conductance and $E$, so if any were to change, the latter would be altered (Monteith, 1965; Jarvis, 1995; Berry et al., 2010). Katul et al. (2012) found that the Clausius-Clapeyron equation suggests the total water vapour in the atmosphere will increase by approximately 6.8% °C$^{-1}$ warming and if all this water is transformed into precipitation then the global precipitation and evapotranspiration will also increase by the same percentage.

The boreal forest ecosystem encompasses the land above 48°N, is second only to the world’s tropical forests in areal extent and occupies about 21% of its forested land surface (Arain et al., 2003). Nearly one tenth of all present-day global forest cover is located within Canada, with almost one third being boreal forest (FAO, 2015); making the latter important in its contribution to the global $C$ and water balances. The boreal forest is composed of varying vegetation due to differences in local climate, soil and topography. In North America the dominant vegetation type in slight lowland depressions is black spruce ($Picea mariana$ Mill.) forests, and well-drained loamy upland soils foster aspen ($Populus tremuloides$ Michx.) forests (Kljun et al., 2006; Barr et al., 2012). Black spruce forests occupy 39% of the area of the North American boreal forest and are the climax vegetation for these forests. Aspen forests occupy
21% and are particularly dynamic in their energy and water exchange because of the seasonal change in leaf area index (Barr et al., 2004; Black et al., 2005).

With the magnitude of global and northern hemispherical coverage, the boreal forest has a significant effect on global water, energy and C balances. It is thus important to understand the controlling variables of these processes and how they are changing over time. The boreal forest in Siberia and North America has relatively small $E$, even in the growing season (Jarvis et al., 1997; Yoshida et al., 2014). Boreal forest ecosystems experience large inter-annual variability in precipitation ($P$) so ecosystem $E$ is expected to be greatly variable between years, especially for dry regions which can have $E$ exceed $P$ in dry years (Zha et al., 2010). Ohta et al. (2008) suggested that the factors controlling forest $E$ may be dependent on the time scale used for analysis. In a Siberian forest, using long-term observation data, Yoshida et al. (2010) found that turbulent fluxes (the latent ($\lambda E$) and sensible ($H$) heat fluxes), and surface conductance responded differently to environmental factors at the diurnal, inter- and intra- seasonal, and interannual scales. Research on Canadian terrestrial ecosystems showed that stomatal conductance was the key determinant of $E$, and modelling stomatal conductance is the key to estimating $E$, at least for boreal coniferous forests (Brümmer et al., 2012), corroborating previous research (Jarvis, 1976; Kelliher et al., 1993). Accurate surface conductance models will enable scientists to better model $E$ projections under different climate conditions that may arise from climate change.

In order to create and test models, high quality measurements of climate and fluxes are needed. The use of the eddy-covariance (EC) technique to make H$_2$O and CO$_2$ flux measurements has increased rapidly in the past two decades, leading to over 900 active and historical flux sites worldwide (Chu et al., 2017). EC is popular because it can provide continuous, high temporal resolution data on the scale of half hours to years, and decades. The
EC method can be utilized to answer questions about ecological, biogeochemical and hydrological problems (Baldocchi, 2014). The data from the numerous worldwide sites have reached a large audience due to the work of regional flux programs such as AmeriFlux, Asiaflux, Fluxnet-Canada, and FLUXNET, which is a network of the networks, leading to a global flux network (Papale et al., 2012).

Before flux towers covered the globe, there were a limited number that were initiated the early to mid-90s and mostly located in forests in North America and Europe (Baldocchi et al., 2001). Through the Boreal Ecosystem-Atmosphere Study (BOREAS), an interdisciplinary experiment in the northern boreal forests of Canada, two large study areas, the Southern Study Area (SSA) a 130 km by 90 km area, just north of Prince Albert, Saskatchewan, and a similarly sized Northern Study Area (NSA), just north of Thompson, Manitoba were established to measure ecosystem fluxes (Sellers et al., 1997). Within the SSA, five towers were setup in stands of differing vegetation with one in a mature deciduous aspen stand called Old Aspen (OA) and another in a mature coniferous black spruce stand known as Old Black Spruce (OBS). At OA and OBS, flux measurements were first made during the fall of 1993 and much of 1994 and 1996. Following the end of BOREAS, the Boreal Ecosystem Research and Monitoring Sites (BERMS) program (Figure 1.1), which later became part of the FLUXNET Canada Research Network (FCRN) and the Canadian Carbon Program (CCP), continued EC measurements at these two sites.
Figure 1.1. Study area, showing the Canadian boreal forest (lower panel, shaded) and location of the Boreal Ecosystem Research and Monitoring Sites (BERMS) flux towers (+) (upper panel) from Barr et al., 2012. The extent of the study area is very similar to that of the BOREAS SSA Sellers et al., (1997).

Starting in 2013, BERMS became one of the 14 Water, Ecosystem, Cryosphere and Climate (WECC) Observatories included in the Changing Cold Regions Network (CCRN) (Figure 1.2). Continuous EC flux and climate measurements have been made since 1996 at OA (CA-Oas) and
1999 at OBS (CA-Obs). Through these multiple programs/campaigns, these sites have produced one of the longest continuous records of EC measurements in the world.

Figure 1.2 Map of the Changing Cold Regions Network (CCRN) study domain and primary Water, Ecosystem, Cryosphere and Climate Observatories (WECC) observatories with the square denoting the Boreal Ecosystem Research and Monitoring Sites (BERMS).

Since the initiation of these sites, researchers have utilized the data to study a wide range of scientific questions. In the early years, a lot of research focused on carbon (C) fluxes (Black et al., 1996; Sullivan et al., 1997; Goulden and Crill, 1997; Brooks et al., 1997; Kimball et al., 1997; Jarvis et al., 1997; Lavigne and Ryan, 1997; Chen et al., 1999; Rayment and Jarvis, 1999;
Over a decade of measurements at OA and OBS have been added since the aforementioned research was conducted, creating a long-term dataset that had only been partially analyzed. During the two decades of monitoring, two disturbance events of note were captured: 1) drought and 2) insect infestation. Western interior Canada including the BERMS sites experienced a drought from 2001-2003, which provided researchers with an opportunity to increase their understanding of the ecosystems’ response to water stress. In 1990, the Canadian government had established a research study called Climate Impacts on Productivity and Health of Aspen (CIPHA) to determine temporal variation in aspen stem growth. The network detected the impact of the drought as a 30% decrease in stem growth together with a greater than doubling in stem
mortality over the widespread aspen stands across Canada (Michaelian et al., 2011). Signs of water stress at OA started in June 2001 and lasted through 2003 (Krishnan et al., 2006). After the drought, reduced LAI was measured during 2004 and 2005 at OA (Barr et al., 2007). Due to this drought, widespread aspen dieback and mortality was observed from aerial surveys conducted in August 2004 in the most severely drought-affected areas, but was minor at OA (Hogg et al., 2005, 2008). Kljun et al. (2006) found that the drought had a greater impact on OA than OBS, pointing to the importance of topography, soil characteristics and the variability in precipitation in controlling the effect of drought on stand C sequestration.

Insect herbivores such as spruce budworm (Choristoneura fumiferana (Clem.)), the jack pine budworm (C. pinus Freeman), and the forest tent caterpillar (FTC) (Malacosoma disstria Hübner) damage the North American boreal forest more than any other insects (Volney and Fleming, 2000). Defoliation events by FTC, like the one observed at OA in 2016, are rarely fatal but the trees often demonstrate measurable growth reductions and become more susceptible to additional stress such as water limitations (Hogg et al., 2002). Pests are often a major, overlooked part of forest ecosystem dynamics that have a large impact on the structure and function of forests (Cook et al., 2008), and will be vital to include in models to secure future forest C dynamics.

One of the main goals and aspirations of EC flux sites is to collect time series that are long enough to detect temporal trends in fluxes, but until recently, the data sets were not long enough to separate natural variability and trends from sampling and measurement errors (Baldocchi et al., 2017). Baldocchi et al. (2017) found that records exceeding 20 years should be able to detect trends as small as 3 g C m⁻² y⁻¹ and ideally flux data should reach and exceed 30 years, the time
scale traditionally used in climate science trend analysis. The EC measurements at the BERMS sites have reached nearly two decades in length, making it long enough to start being able to detect any small trends in the fluxes and climate.

1.2 Research Objectives

This thesis presents four studies focused on evaluating the impact of climate variations and disturbances on the water fluxes ($E$ and $G_c$) and C fluxes at OA and OBS. The specific objectives were to:

1) Quantify the impact of a forest tent caterpillar (FTC) defoliation event in 2016 at OA by modelling what fluxes would have been without the defoliation, and compare the defoliation event fluxes with the long-term record, including the three-year (2001-2003) drought.

2) Investigate the dependence of rain-free daytime $G_c$ and $E$ on their controlling variables at the growing season and monthly time scales.

3) Detect any long-term trends at various time scales (e.g., monthly, growing season, annually) in climate variables, $E$, $P-E$, GEP, $R_e$, NEP, and WUE and determine the impact of the start date, end date and length of the growing season on annual NEP, GEP and $E$.

4) Test the ability of the Jarvis-Stewart (JS) and a modified Ball-Woodrow-Berry (MBWB) models to estimate half-hourly $G_c$ values in order to capture the seasonal and annual variations in $G_c$ and $E$. 
1.3 Thesis Overview

This dissertation contains six chapters, starting with an introduction covering the background and goals of this research, followed by four main research chapters presented as independent documents with their own specific introduction/ review of literature, methods, results and discussion sections. Chapter 2 presents 21 years of EC and climate measurements covering pre-infestation and infestation periods used to estimate the impact of a forest tent caterpillar (FTC) infestation on the $E$, NEP, and GEP at OA in 2016. This thesis places as much importance on C as water fluxes because the processes controlling both are closely related, both physically and physiologically (Campbell and Norman, 2012). Chapter 3 focuses on long-term variability in rain-free daytime growing season and monthly $E$ and $G_c$, along with their dependencies on controlling climate variables, at OA and OBS. Rain-free data enabled examination of the physiological controls of $G_c$ and $E$ without the complication of foliage wet from rainfall interception. Chapter 4 investigates the long-term trends in growing season and annual: climate, water and C fluxes at OA and OBS, with a particular emphasis on the C fluxes, and the impacts of the start date, end date, and length of the GS on NEP, GEP and $E$. Chapter 5 examines the ability of the JS and MBWB models to reproduce rain-free daytime $G_c$ at half-hourly, daily and annual time scales in order to capture the variation of rain-free $E$ over the two decades at each site. Chapter 6 summarizes key findings and conclusions of this research, presents limitations of the research, and potential future work is discussed.
Chapter 2: Effects of Forest Tent Caterpillar Defoliation on Carbon and Water Fluxes in a Boreal Aspen Stand

2.1 Introduction

Nearly a tenth of all present-day global forest cover exists within Canada, which extends across 38% of the country’s 9.1 million km$^2$ land area (FAO, 2015). Ecosystem disturbances such as wildfires, harvesting, insect outbreaks, and storms can have large effects on the C balance of these forests (Amiro et al., 2010). Impacts of insect outbreaks on C balance tend to vary greatly depending on the species of insects and their host vegetation. Two types of insects that are known to significantly alter C balance of a forest stand are: 1) Coleoptera (bark beetles) and 2) Lepidoptera (moths and butterflies) (Hicke et al., 2012; Peterson and Peterson 1992). The latter, which are defoliators (also known as folivores), feed directly on tree leaves, thereby reducing the leaf area and affecting tree growth and mortality (Cook et al., 2008; Hogg et al., 2008). Such insect herbivores are often host-specific at the level of tree genus. In aspen stands (Populus spp.), the primary species of Lepidoptera capable of defoliation are the forest tent caterpillar (FTC) (Malacosoma disstria Hübner), large aspen tortrix (Choristoneura conflictana), Bruce spanworm (Operophtera bruceata), aspen leaf miner (Phyllocnistis populiella), and gypsy moth (Lymantria dispar) (Peterson and Peterson, 1992). The FTC in particular has been characterized as the most consequential insect of trembling aspen in the prairie provinces (Brandt, 1995a), with several major outbreaks in the Canadian prairie provinces occurring between 1937 and 1990 (Brandt et al., 2003). FTC outbreaks tend to be periodic (separated by intervals of 9-13 years) and short-lived, lasting no longer than 1-2 years, though small areas of residual infestation...
can linger 4 years or longer (Cooke et al., 2009; Cooke and Lorenzetti, 2006). Despite the widespread, and sometimes severe, defoliation events caused by FTC, outbreaks rarely result in tree mortality on their own (Volney and Fleming 2000), with the exception of outbreaks in locations where unusually frequent, long-lasting defoliation has occurred (Man and Rice, 2010). When FTC defoliation coincides with or immediately follows drought, increases in tree mortality have been observed (Hogg et al., 2008).

The life cycle of FTC has been previously described by Ives and Wong (1988), but I provide a brief summary here. Larvae hatch early in spring, which coincides temporally with the flushing of aspen leaves. Larvae do not actually produce a silken “tent”, but instead leave trails of silk while traveling to feed and rest in small silken masses spun on tree trunks or larger branches. After approximately 5 weeks, mature larvae form silken cocoons and pupate for about 10 days before emerging as moths. They then go on to lay eggs, which become larvae 4 weeks later but do not hatch until the following spring.

The impact of transient defoliation by insect herbivory on short-term fluxes has been the focus of some recent studies (e.g., Clark et al., 2010; Cook et al., 2008; Schafer et al., 2010). Here, I examine an FTC infestation in 2016 that occurred at the boreal Old Aspen (OA) flux tower site in Saskatchewan (Fluxnet ID "CA-Oas") for the first time in the 21-year period of long-term flux monitoring at this site. The infestation led to a complete defoliation of the stand as shown in Figure 2.1. Motivated by the unique opportunity afforded by a FTC defoliation event occurring in an intensively-instrumented forest stand, I have examined the impacts of this transient disturbance on seasonal and annual C and water fluxes. Quantification of the impact of FTC on C and water fluxes in 2016, compared to pre-disturbance measurements from 1996 to 2015, required the separation of the FTC impact from climate effects during 2016. This was
achieved by simulating the fluxes for the FTC-infestation period assuming there was no infestation, and determining the impact by subtracting the measured fluxes.

Figure 2.1 Photos of the forest tent caterpillar (FTC) defoliation event at the Old Aspen (OA) Fluxnet site taken on 16/06/2016 from atop the tower within (a) and above the canopy (b). Panel (a) shows the branches stripped to petioles with the FTC silken webs. In panel (b), the defoliated stand (over and understory) allows the green shrubbery on the forest floor to be seen.
2.2 Materials and Methods

2.2.1 Site Description

The OA study site is a mature deciduous broadleaf forest located near the southern edge of the boreal forest in Prince Albert National Park, Saskatchewan, in the Boreal Plains ecozone (53.62889°N, 106.19779°W, WGS-84). The forest consists of trembling aspen (*Populus tremuloides* Michx.) with scattered (~10%) balsam poplar (*Populus balsamifera* L.) overstory and a hazelnut (*Corylus cornuta* Marsh.) understory. The understory accounts for 50% of the total leaf area (Arain *et al.*, 2002; Barr *et al.*, 2004). The stand is a uniformly aged stand that regenerated after a natural fire in 1919. The canopy height in 2002 was 21 m (Barr *et al.*, 2012) and currently has a stem density of 486 trees ha\(^{-1}\) (personal communication: Jay Maillet 3/3/2017). The soil, an Orthic Gray Luvisol, has developed on clay-rich glacial till that occurs below an 8-10-cm thick LFH (litter-fermented-humic) layer and a 30-cm-thick silt loam layer (Barr *et al.*, 2012). Mean (1960-2000) annual precipitation and air temperature from the closest long-term climate stations - Waskesiu Lake (53.55°N, 106.04°W, 532 m elevation) and Prince Albert Airport (53.13°N, 105.67°W, 428 m elevation) - are 422 mm and 0.6°C, and 408 mm and 0.9°C, respectively.

2.2.2 Climate Measurements

A suite of climate variables were measured and reported as half-hourly average values. Air temperature was measured with temperature/humidity sensors (model HMP45C, Vaisala Oy, Finland), which were housed in aspirated radiation shields at a height of 37 m. Air temperature was also measured with a *platinum resistance thermometer* (PRT) and a 36-gauge chromel-constantan thermocouple (Omega Engineering Inc., Laval, Quebec), both housed in an aspirated radiation shield (model 076B, Met-One Instruments Inc., Grants Pass, OR) at 36 m. Precipitation
was measured using both a tipping bucket rain gauge (model TR-525, Texas Electronics Inc., Dallas, TX, USA or model CS700, Campbell Scientific Inc. (CSI), Logan, UT, USA) and a weighing rain gauge (model 3000 with an Alter shield, Belfort Instruments, Baltimore, MD, USA) which were located at a height of ~2 m on a raised platform in the center of a natural clearing approximately 50 m northeast of the tower. Antifreeze was added in winter to prevent freezing and motor oil was added in summer to minimize evaporative losses from the weighing rain gauge. Shortwave and longwave radiation were measured at the 36-m (downwelling) and 30-m height (upwelling) with paired pyranometers (model CM11, Kipp & Zonen BV, Delft, The Netherlands) and paired pyrgeometers (model PIR, Eppley Laboratory Inc., Newport, RI, USA), respectively. Upwelling and downwelling components of photosynthetically active radiation (PAR) were measured at the same heights with paired quantum sensors (model LI-190SA, LI-COR Inc., Lincoln, NE). About 95% of the down-facing radiometers’ canopy view would be within 43 m of the tower (Reifsnyder, 1967). Two profiles of soil temperature were measured at six depths (2, 5, 10, 20, 50, and 100 cm) with copper-constantan thermocouples.

2.2.3 Eddy-Covariance Flux Measurements

Year-round eddy-covariance (EC) measurements of fluxes of CO₂, water vapor, and sensible heat were made. These fluxes were measured using instruments mounted on a scaffold tower 39 m above the ground, including a tri-axial sonic anemometer (model R2 (1996-1999) or R3 (1999- present) Gill Instruments Ltd., Lymington, UK) and a closed-path, temperature-controlled infrared gas (CO₂/H₂O) analyzer (model LI-6262 or LI-7000, LI-COR Inc.). Air was drawn through a heated sampling tube (4 m length; 4 mm inner diameter Synflex 1300 tube (Saint-Gobain, Performance Plastics, Wayne, NJ)) by a diaphragm pump (model DOA-V191-AA, Gast Inc., Dayton, OH) at a flow rate of 10 L min⁻¹ for the LI-6262 and 15 L min⁻¹ for the
LI-7000 (Krishan et al., 2006; Barr et al., 2007, 2012). Daily automatic calibrations to correct CO₂ concentration measurements for zero and span shifts were implemented using CO₂ standard gases from the Greenhouse Gases Measurement Laboratory (GGML) of Environment and Climate Change Canada in Downsview, ON, Canada (Krishnan et al., 2006). The heated sample tube was replaced every 6 months to improve response times in H₂O and CO₂ sampling that are reduced due to dust, pollen, smoke particles or condensation in the tube. Half-hourly CO₂, water vapour, sensible heat, and turbulent fluxes were calculated from the covariance of fluctuations in the vertical wind component and the scalar quantity of interest (i.e., mole mixing ratios of CO₂ or water vapour, and air temperature (Webb et al., 1980)) measured at 20 Hz and computed directly on the computer located at the site. Further details on the experimental setup, calibrations, calculations of fluxes and flux footprint analysis can be found in Griffis et al. (2003), Barr et al. (2004), Krishnan et al. (2006), Zha et al. (2010) and Chen et al. (2012).

2.2.4 PhenoCam Observations

The PhenoCam Network (http://phenocam.sr.unh.edu) is a continental-scale network that provides automated, high-frequency near-surface remote sensing of canopy phenology. A PhenoCam is a high-resolution digital camera that takes photos every half hour and uploads them to the PhenoCam server, where images and derived data are made publicly available in near-real time. A PhenoCam has been monitoring canopy phenology at OA since 2011. The camera has a 1/2.5” CMOS imaging sensor, with a standard Bayer filter and is mounted at a height of approximately 32 m with a tilt angle, looking north such that the camera views about 20% sky, 80% canopy over an area of approximately 720 m². There have been two cameras mounted on the tower, PhenoCam1 from 2011-2016 and PhenoCam2 from June 2016 to present. PhenoCam1 had a 4-10 mm zoom lens with a field of view of approximately 105°, while PhenoCam2 has a
fixed 6.2 mm lens with a field of view of approximately 80°. Images are recorded at 1296 x 960 pixel resolution, as standard 3-layer red-green-blue (RGB) JPEG files with 8 bits per channel. Image processing consists of extracting RGB color channel information from the digital images, using methods described previously (Richardson et al., 2007; Sonnentag et al., 2012).

“Chromatic coordinates”, indicating the relative intensity (pixel value, a digital number) of one channel against the overall intensity of all three channels together, termed as green chromatic coordinate ($G_{CC}$) can be readily calculated as $G_{CC}=G_{DN}/[R_{DN}+G_{DN}+B_{DN}]$, where $G_{DN}$, $R_{DN}$ and $B_{DN}$ represent the green ($G$), red ($R$), and blue ($B$) digital numbers, respectively. $G_{CC}$, widely-used in the phenological literature, is the product of the amount of foliage present and the color of individual leaves (Keenan et al., 2014). In a deciduous forest such as ours, increasing canopy greenness in spring is driven by the unfolding and expansion of new foliage, and consequently an increase in photosynthetic activity. Previous studies have linked canopy greenness indices (e.g., $G_{CC}$) to seasonal changes in net ecosystem C exchange and canopy photosynthesis (Richardson et al., 2007, 2009; Toomey et al., 2015). While $G_{CC}$ tends to saturate at modest values of leaf area index (Keenan et al., 2014), the index has been successfully used to track canopy damage in response to extreme disturbance (Hufkens et al., 2012).

2.2.5 Normalized Difference Vegetation Index (NDVI)

Daily normalized difference vegetation index (NDVI) values corresponding to the OA tower location were obtained from the MODIS Terra platform for the 2001-2016 period using Google Earth Engine. Here, NDVI represents $(\text{NIR} - \text{Red}) / (\text{NIR} + \text{Red})$ computed from the 7-band daily 500 m MOD09GA MODIS surface reflectance product (Vermote et al., 2015), where the red (Red) band is Terra band 1 (620–670 nm) and the near infrared (NIR) band is Terra band 2 (841–876 nm). Daily NDVI data were processed using the phenex package (Lange and Doktor,
This consisted of correcting and modeling the raw data using an asymmetric Gaussian function applied individually to each year to derive the long-term mean and standard deviation for each day of year for the 2001-2016 period. The corrected data for 2016 are presented with the long-term data set, also using the asymmetric Gaussian correction that has been shown to be the most effective for reducing noise in MODIS NDVI data for the boreal forest region (Hird and McDermid, 2009).

2.2.6 Data Processing and Quality Control

Measurements and calibrations were checked daily (as part of a quality control/assurance routine) using a Matlab (Version 7.5, The Mathworks, Natick, MA, USA) program. Raw data went through three stages of cleaning before being used in calculations. In the first stage, data values with faulty measurements were removed but not replaced or interpolated. In the second stage, faulty measurements from specific sensors were replaced with the best available alternative measurements from redundant on-site instruments. Finally, in the third stage, temporal interpolation and gap filling based on diurnal variations was performed. All data cleaning procedures directly follow those described in Krishnan et al. (2006).

In the third data cleaning stage, net ecosystem production (NEP), gross ecosystem production (GEP) and ecosystem respiration ($R_e$) were calculated. NEP was determined using $\text{NEP} = -\text{NEE}$, where NEE is the net ecosystem exchange of CO$_2$ obtained directly from measurements of surface CO$_2$ flux corrected for the rate of change in air column CO$_2$ storage (I ignored negligibly small losses of dissolved organic C at the site). NEP is defined as the difference between C gained by GEP and C losses as a result of $R_e$. By this convention, NEP is positive for a C sink and negative for a C source.
I followed the Fluxnet-Canada Research Network (FCRN) procedure to estimate annual NEP, GEP and \( R_e \) as described in Barr et al. (2004) which is summarized below. \( R_e \) was estimated from NEP when GEP was known to be zero (nighttime and during the cold-season when both air \( (T_a) \) and soil \( (T_s) \) temperatures were < 0°C). An empirical annual relationship between half hourly \( R_e \) and half hourly near-surface (2-cm) \( T_s \) for a friction velocity \( (u_*) \) < \( u_* \) threshold of 0.35 m s\(^{-1}\) (Barr et al., 2004) was used to fill nighttime gaps and to estimate daytime \( R_e \). GEP was estimated as NEP + \( R_e \) (daytime) or zero (nighttime and during the cold-season, and gaps were filled using the rectangular hyperbolic relationship of GEP to PAR (i.e., the Michaelis-Menten light response equation). Gaps in NEP were then filled with the difference between the estimated GEP and \( R_e \). To account for changes in other environmental variables such as soil moisture or vapor pressure deficit \( (D) \), a time-varying parameter was developed for each empirical relationship using a moving temporal window (Barr et al., 2004). This parameter is defined as the slope of the linear regression between estimated and measured values of \( R_e \) and GEP.

Uncertainty in annual NEP was quantified using three steps: (1) random error from each half-hour flux was estimated by adding a 20% random error per half hour as described in Morgenstern et al. (2004); (2) gap-filling procedure uncertainty was assessed by removing up to 40% of the data annually using a uniformly discrete random number generator, with 500 randomly selected continuous gap lengths ranging from a single missing half hour period to 10 days of data (480 half-hourly periods); (3) systematic bias due to the variation of the chosen \( u_* \) threshold was estimated by varying it by ± 20% of our chosen 0.35 m s\(^{-1}\) threshold and then recalculating NEP. Total random error by taking the sum of squares of error from steps 1 and 2 was ± 17 g C m\(^{-2}\) year\(^{-1}\). The systematic error from step 3 was ± 36 g C m\(^{-2}\) year\(^{-1}\). Since the
systematic error from choosing $u_*$ will have a similar magnitude and direction each year, it is not random, and thus was added directly to the random error rather than using the sum-of-squares. The overall estimated uncertainty of annual NEP was $\pm 53 \, \text{g C m}^{-2} \, \text{year}^{-1}$. These values are comparable to those reported by Krishnan et al. (2006) using 11 years of data at this site. The same procedure was followed to calculate the uncertainty in annual GEP and $R_e$. The total random error from steps 1 and 2 was $\pm 21 \, \text{g C m}^{-2} \, \text{year}^{-1}$ and $\pm 20 \, \text{g C m}^{-2} \, \text{year}^{-1}$ for GEP and $R_e$, respectively. The systematic error from step 3 was $\pm 53 \, \text{g C m}^{-2} \, \text{year}^{-1}$ for GEP and $\pm 89 \, \text{g C m}^{-2} \, \text{year}^{-1}$ for $R_e$. The overall estimated uncertainty of annual GEP was $\pm 74 \, \text{g C m}^{-2} \, \text{year}^{-1}$ and for $R_e$ was $\pm 109 \, \text{g C m}^{-2} \, \text{year}^{-1}$.

The same procedure as for the C fluxes was followed to estimate the uncertainty in annual $E$. The gap filling in step 2 for $E$ relied on estimates of sensible and latent heat using a moving window based on Amiro et al. (2006). The total random error by taking the sum of squares of error from steps 1 and 2 was $\pm 7 \, \text{mm year}^{-1}$. The systematic error from step 3 was $\pm 2 \, \text{mm year}^{-1}$. The sum of these two errors produced an overall estimated uncertainty in annual $E$ of $\pm 9 \, \text{mm year}^{-1}$.

2.2.7 Estimating the Impact of the FTC Infestation on Carbon and Water Fluxes

Data from four years (1998, 2001, 2006, and 2010) with early growing season onset within a week of the 2016 onset date (DOY 126) were chosen to parameterize the simulation of C and water fluxes in 2016 assuming there was no FTC infestation (see below). Growing season onset was defined as the calendar day when the daily average GEP made a significant jump (from $<0.8 \, \mu\text{mol m}^{-2} \, \text{s}^{-1}$ winter levels to $>1 \, \mu\text{mol m}^{-2} \, \text{s}^{-1}$) and was followed by a rapid increase thereafter. For the four years (1998, 2001, 2006, 2010), the onset dates were DOY 123, 125, 127, 133 with three of the years having growing season onsets within $\pm 3$ days of that for 2016. The growing
season onset was checked by calculating cumulative growing-season degree days following the method of Barr et al. (2004). Using the day of the year when 100 degree days were reached to define the start of the growing season, it also occurred on DOY 126 in 2016. Following this method for the four years, the growing season onset dates were DOY 123, 132, 120, 134 (in close agreement with the observed onset dates listed above) are within ± 8 days of that for 2016.

To calculate what the 2016 C fluxes would have been in the absence of an FTC outbreak, I used the same physiological equations to estimate \( R_e \) and GEP as in the FCRN gap filling procedure (Barr et al., 2004). I applied the procedure to the complete gap-filled record from each of the four years listed above to retrieve parameters for the empirical relationships and the time varying parameters in Equations (2.1) and (2.2) below to calculate half-hourly values of \( R_e \) and GEP in \( \mu \text{mol m}^{-2} \text{s}^{-1} \) for 2016 using, respectively:

\[
R_e = R_e(t) \frac{b_1}{1+\exp(b_2(b_3-T_s))} \tag{2.1}
\]

where \( R_e(t) \) is the time variation in \( R_e \) (see below) which accounted for the seasonal variations in other climate variables (e.g., soil moisture), \( T_s \) is the half-hourly value of 2-cm soil temperature (°C) and \( b_1 \) (\( \mu \text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1} \)), \( b_2 \) (°C\(^{-1} \)) and \( b_3 \) (°C) are fitted parameters (Table 2.1); and

\[
GEP = GEP(t) \frac{c_1 Q}{c_2 + Q} \tag{2.2}
\]

where GEP(t) is the time variation in GEP (see below) which accounted for the seasonal variations in other climate variables, \( Q \) is half-hourly downwelling PAR (\( \mu \text{mol photons m}^{-2} \text{s}^{-1} \)) for 2016, and \( c_1 \) (\( \mu \text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1} \)) and \( c_2 \) (\( \mu \text{mol photons m}^{-2} \text{s}^{-1} \)) are fitted parameters that vary with light (Table 2.1). I found that the model performed better when applied separately for low light (PAR <800 \( \mu \text{mol photons m}^{-2} \text{s}^{-1} \)) and high light (PAR >800 \( \mu \text{mol photons m}^{-2} \text{s}^{-1} \)) conditions.
Table 2.1 Fitted parameter values for Eq. 2.1 for $R_e$ and Eq. 2.2 for GEP under low light (PAR <800 μmol photons m$^{-2}$s$^{-1}$) and high light (PAR >800 μmol photons m$^{-2}$s$^{-1}$) for individual years and the average of the four years.

<table>
<thead>
<tr>
<th>Year</th>
<th>$R_e$</th>
<th>GEP</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$b_1$ (μmol CO$_2$ m$^{-2}$ s$^{-1}$)</td>
<td>$b_2$ ($^\circ$C$^{-1}$)</td>
</tr>
<tr>
<td>1998</td>
<td>11</td>
<td>0.24</td>
</tr>
<tr>
<td>2001</td>
<td>8</td>
<td>0.25</td>
</tr>
<tr>
<td>2006</td>
<td>11</td>
<td>0.24</td>
</tr>
<tr>
<td>2010</td>
<td>12</td>
<td>0.24</td>
</tr>
<tr>
<td>Average</td>
<td>10</td>
<td>0.25</td>
</tr>
</tbody>
</table>

In the estimation of different parameters in Equations (2.1) and (2.2), first $b_1$, $b_2$, $b_3$ and $c_1$ and $c_2$ were estimated achieving the best fit to measured $R_e$ and GEP data, respectively. Then $R_e(t)$ and GEP(t) were calculated as the ratios of the respective measured values to those estimated by using the fitted parameters ($b_1$, $b_2$, etc.) using a moving window. The optimal window size was found to be 100 data points (~2 days). Figure 2.2 shows the average values of the two time-varying parameters obtained using the moving-window procedure.
Figure 2.2 Average values of the two time-varying parameters, $R_e(t)$ and GEP$(t)$ vs. day of year (DOY). Each value is the average of 4 values for the 4 years (1998, 2001, 2006, and 2010).

Then NEP was calculated from $\text{NEP} = \text{GEP} - R_e$. The simulation uncertainties associated with annual estimates of $R_e$ and GEP were assessed by varying the simulation parameters ($b_1$, $b_2$, $b_3$ and $R_e(t)$) for $R_e$ and $c_1$, $c_2$ for both light levels, and GEP$(t)$ for GEP by $\pm$ 10% to simulate new half-hourly values and summed to provide new annual estimates.

To estimate the values of $E$ that would have occurred without FTC infestation, I used the Priestley-Taylor approach (Priestley and Taylor, 1972). Daily average climate was used to calculate daily values of the Priestley-Taylor alpha ($\alpha$) for each of the four years, which were averaged to obtain mean daily (24-hour) $\alpha$ values, using

$$\alpha = \frac{\lambda E}{[s/(s+y)]R_a}$$ (2.3)

where $E$ is the daily (24 hour) water vapour flux (evapotranspiration) (kg m$^{-2}$ day$^{-1}$ or mm day$^{-1}$), $R_a$ is the available energy flux (W m$^{-2}$), which is given by $(R_a = R_n - G)$ (neglecting energy...
storage change in the air column beneath the flux measurement sensors on the tower) where $R_n$ is daily net radiation (W m$^{-2}$), $G$ is daily soil heat flux (W m$^{-2}$), $s$ is the slope of the saturation vapor pressure curve (kPa °C$^{-1}$), $\lambda$ is the latent heat of vaporization (J kg$^{-1}$), and $\gamma$ is the psychrometric constant (kPa °C$^{-1}$). The three latter variables were evaluated at half-hourly scales and then averaged to daily values. $\alpha$ values were calculated using two methods: using Eq (2.3) and replacing $R_n - G$ with $H + \lambda E$ where $H$ is the daily sensible heat flux and $\lambda E$ is the daily latent heat flux. The latter method was used by Krishnan et al. (2006) to avoid issues of energy-balance non-closure, since the substitution of $H + \lambda E$ has the same effect on $\alpha$ as adjusting $H + \lambda E$ to force energy balance closure (Barr et al., 2002). The mean daily $\alpha$ values were then used to simulate $E$ for 2016 as if there had been no FTC infestation, using

$$E = \alpha \left( \frac{sR_n}{s + \gamma} \right) \left( \frac{1}{\lambda} \right)$$

(2.4)

$E$ was calculated using the same two methods used to calculate $\alpha$. To account for the change in shortwave albedo ($\rho_s$) due to the defoliation, the average daily $\rho_s$ values from the four years were used to estimate what daily $R_n$ would have been during 2016 without defoliation. The simulation uncertainty in estimating annual $E$ was determined by varying $\alpha$ by 10% and summing to retrieve new values.

2.3 Results

2.3.1 Climate Measurements

Figure 2.3 shows the interannual variation in the annual average $T_a$, PAR, $D$, and $T_s$. The values of several climate variables in 2016 exceeded ± 1 standard deviation relative to the long-term mean of the observed record at OA. 2015 and 2016 exhibited the highest annual $T_a$ on record (3.49°C (>+1σ) in 2016 versus a long-term (1996-2015) mean of 2.28°C). Since 2008,
there was a slightly decreasing trend in PAR, and the 2016 mean value was the lowest on record (243 μmol m⁻² s⁻¹ (<-1σ) versus a long-term mean of 266 μmol m⁻² s⁻¹). The same trend, and the lowest value on record, was observed in the downwelling shortwave radiation. Mean value of D in 2016 was the third highest on record (0.42 kPa (>+1σ) in 2016 versus a long-term mean of 0.37 kPa). In 2016, the mean annual Tₛ of 5.23°C was among the 5 warmest years in terms of Tₛ at the 2-cm depth in the last 21 years. P over the 1996-2016 period of record exhibited high inter-annual variability (range 237-710 mm; standard deviation 128 mm), with the three drought years during 2001 to 2003 (Krishnan et al., 2006). Average annual P increased by 21.4% from 433 mm for the pre-drought years (1996-2000) to 538 mm in the post drought years (2004-2015) (Figure 2.5b). This increase in annual P is consistent with the observed wetting of Northern Hemisphere mid-latitudes (30°N to 60°N) between 1901-2008 (Stocker et al., 2013). In 2016, P at OA (457 mm) was 10% lower than in the previous 4 years.
Figure 2.3 Annual average 24-h averaged air temperature \((T_a)\), downwelling photosynthetically active radiation \((Q)\), vapour pressure deficit \((D)\), 2-cm soil temperature \((T_s)\) and annual precipitation \((P)\) from 1996 to 2016 with the 21-year mean shown by the black line.

Figure 2.4 shows how temporal variation in climate variables in 2016 compared with those for 1996-2015. \(T_a\) mostly followed the well-defined seasonal cycle observed in prior years, and was generally within one standard deviation of the long-term mean. However, there were several notable departures from the mean \(T_a\) during key time periods—including one at the start of the growing season in late April, indicating a rapid spring warm up. PAR values in 2016 were below the average values for most of the year except for early April, which was likely related to the
rapid warming at this time and the overall early start of the growing season. $D$ generally tracked $T_a$, although in this case the April anomaly was even more pronounced.

Soil temperature at the 2-cm depth in 2016 was above the 20-year mean, with the initial spring warming spike in late April falling well outside one standard deviation from the mean. The 2016 winter and early spring were wetter than usual, but by April cumulative $P$ plateaued,
remaining depressed throughout the growing season and did not return to the long-term mean until mid-October yielding an annual total (457 mm) only slightly less than the 1996-2015 average value (465 mm).

2.3.2 Long-term Carbon and Water Fluxes

For nearly all of the years in 1996-2015, prior to the FTC-induced defoliation event in 2016, OA had been a moderate C sink (NEP = 118 ± 53 (mean ± average uncertainty) g C m$^{-2}$ y$^{-1}$ (Figure 2.5a)), with mean GEP and $R_e$ of 1058 ± 74 g C m$^{-2}$ y$^{-1}$ and 941 ± 109 g C m$^{-2}$ y$^{-1}$, respectively. The two exceptions were in 2004 and 2007. In 2004, following the three-year drought, near-zero NEP (0 ± 32 g C m$^{-2}$ y$^{-1}$) resulted from a cool spring and the combination of a large decrease (296 g C m$^{-2}$ y$^{-1}$) in GEP and only a small decrease (179 g C m$^{-2}$ y$^{-1}$) in $R_e$ compared to the long-term means (Barr et al., 2007). In 2007 NEP was well below zero (-34 ± 25 g C m$^{-2}$ y$^{-1}$) with slightly below-average GEP (978 ± 46 g C m$^{-2}$ y$^{-1}$) but above-average $R_e$ (1013 ± 67 g C m$^{-2}$ y$^{-1}$). In 2016, the NEP value (-72 ± 59 g C m$^{-2}$ y$^{-1}$) was far below the second lowest value of -34 g C m$^{-2}$ y$^{-1}$ in 2007. The extremely low NEP value in 2016 resulted from the different responses of GEP and $R_e$ to defoliation (Figure 2.12). The value of GEP in 2016 (878 ± 77 g C m$^{-2}$ y$^{-1}$) was similar to the 2004 value, despite the near-total defoliation during mid-May to mid-June in 2016. The early spring rise in GEP in 2016, associated with a warm spring and early leafout, partly offset the reduction in GEP by defoliation. In contrast to the below-average GEP in 2016, $R_e$ remained near normal (940 ± 123 g C m$^{-2}$ y$^{-1}$).

Interannual variation in annual $E$ was, in general, closely linked to the variation in annual $P$ (Figure 2.5b), although somewhat subdued. While $P$ in 2016 was 10% lower than the previous 4 years, 2016 $E$ (332 mm) was well within the previously observed range and not nearly as low as observed during the 2001-2003 drought years. Furthermore, $P - E$ (precipitation excess)
increased slightly in 2016 due to a small drop in $E$. Note that $P - E$ is a relative rather than an absolute index of water excess, because of the lack of closure in the surface energy balance; applying an energy-closure fraction of 0.88 to $E$ (as reported by Barr et al. (2012) at this site) would increase $E$ and reduce $P - E$ by ~50 mm y$^{-1}$. 
Figure 2.5 1996-2016 annual values of a) gross ecosystem production (GEP) (red circles), ecosystem respiration ($R_e$) (blue squares), net ecosystem production (NEP) (black diamonds) and b) evapotranspiration ($E$) (red circles), precipitation ($P$) (blue squares) and precipitation excess ($P - E$) (black diamonds) with magnitudes of the uncertainty bars calculated as described in Section 2.6. Note that uncertainty bars are present in panel b, but are not visible because the magnitude of uncertainty spans a smaller range than the markers.
2.3.3 Defoliation Dynamics

The start of the 2016 growing season was among the earliest in our 21-year record (ranked = 4th by flux method or tied for 3rd using growing degree days). In May 2016, the FTC attack caused complete defoliation of the stand including the hazelunt understory (Figure 2.1b) with subsequent recovery to near normal greenness near the end of the growing season. This progression of phenological changes was tracked by the PhenoCam, as shown in Figure 2.6.

Figure 2.6 PhenoCam photographs taken from the top of the flux tower on 13 May 18:00 CST (a), 27 May 16:00 CST (b), 1 June 15:00 CST (c), and 24 July 15:00 CST 2016 (d).
Unfortunately, due to malfunctioning of the PhenoCam I do not have photographs, and therefore measured $G_{CC}$ values, for the initial stage (29 April (DOY 120) to 13 May (DOY 134)) of the 2016 growing season and again later in the growing season from 2 June (DOY 154) to 16 June (DOY 168). For this reason, I also present $\rho_s$ and NDVI values, derived from MODIS, which are described below. I gap filled the measured $G_{CC}$ values by fitting a cubic polynomial between $G_{CC}$ and the $\rho_s$ during the green-up period (DOY 126-150) with $R^2$ of 0.88 and RMSE of 0.012. Between 2012 and 2015, $G_{CC}$ before the start of canopy green-up had an average value of 0.310. In 2016, it was 0.313 on 29 April (DOY 120), but by 13 May (DOY 134), it had already increased to 0.371 (Figure 2.7a). The gap-filled $G_{CC}$ values reached a maximum of 0.387 on 15 May (DOY 136) which was 84% of the seasonal amplitude progressing to the average maximum $G_{CC}$ (0.402). In comparison, the average value from the past four years (0.326) only reached 17% of the seasonal amplitude by 15 May (DOY 136). The difference between 2016 and the past four years (2012-2015) could be due to the uniquely early start of the growing season in 2016. During the defoliation event, $G_{CC}$ dropped to a minimum value of 0.322 on 18 June (DOY 170) and subsequently started to recover. Upon stand refoliation, the maximum 2016 $G_{CC}$ value was 0.387, which was $\sim 96\%$ of the average maximum $G_{CC}$ (0.402), and occurred about a month later than is typical (Figure 2.7a).

The seasonal progression of $\rho_s$ from 2012-2016 showed the impact of an early growing season start and defoliation in 2016 on the stand’s radiation dynamics (Figure 2.7b). Change in $\rho_s$ is highly correlated to that of $G_{CC}$, as expected from the high $R^2$ and low RMSE between the two variables during the green-up period, and shows the gap filling approach captured the timing and magnitude of change quite well. $\rho_s$ does have a greater increase in magnitude past 16 May (DOY137) compared to $G_{CC}$ and reached a maximum value of 0.13 on 21 May (DOY 142).
compared to the maximum $G_{CC}$ on 15 May (DOY136). The minimum $\rho_s$ value of 0.097 occurred on 14 June (DOY 166) four days earlier than the minimum value recorded by the two PhenoCams. If either PhenoCam had been functional during that period then possibly the occurrence date of the minimum would be in agreement. $\rho_s$ stopped increasing on July 2 (DOY184) when it reached 0.128 falling directly in the middle of the spread of values in the previous four years on that date (0.122-0.141).
Figure 2.7 Growing season progression of the green chromatic coordinate \((G_{CC})\) (a) and shortwave albedo \((\rho_s)\) (b) for 2012 to 2016. PhenoCam1 was the camera that had been running since 2012 and PhenoCam2 was installed on 16 June 2016. The asterisk values are gap-filled by a cubic polynomial of the relationship between green-up \(G_{CC}\) values and shortwave albedo. The grey bar indicates the duration of the defoliation event.
Daily NDVI values were aggregated into long-term means for each DOY in order to compare the 2016 infestation period to typical land surface phenology (Figure 2.8). The 2016 NDVI values exhibited an earlier than average increase in NDVI due to the early growing season start and an unusual decline within the growing season starting at DOY 140, as with $G_{cc}$ and $\rho_s$, corresponding to the FTC infestation.

Figure 2.8 NDVI values for a 500-m MODIS pixel representing the Old Aspen tower location. The black squares correspond to NDVI values for 2016, fit with a LOWESS smoothing function (black line). The blue line represents the mean NDVI values for each day of year over the 2001 – 2016 period with the shaded blue area corresponding to ± 1 standard deviation from the mean for each day of year. The grey bar indicates the duration of the defoliation event.

The NDVI shows the effect of the defoliation but may blunt it due to coarse pixel resolution and by not covering the same flux footprint area as the tower. Chen et al. (2011) found 90% annual
flux footprint from 1.2 km during 2006 at OA. Kljun et al. (2006) found that under convective conditions the 90% flux footprint was typically 450-550 m at OA, while during stable or neutral conditions it was typically 900 m. This research indicates that the MODIS NDVI pixel is only capturing a fraction of the flux footprint. Landsat8 NDVI was used to help quantify the extent of defoliation attack within the flux footprint using 3 dates (Figure 2.9): 18 June 2015 (one year before the attack), 16 May 2016 (maximum green-up prior to attack, though not yet to anticipated peak greenness), and 17 June 2016 (date of maximal influence of attack on NDVI as determined from MODIS derived values, Figure 2.8). The median NDVI values for the three dates were 0.79, 0.54 and 0.21, indicating that the defoliation event decreased the NDVI by 73% compared to nearly the same June day value in 2015. The majority of the Landsat data for the 2 km by 2 km area corresponding to the flux tower footprint has an NDVI less 0.3 by 17 June 2016, excluding two areas: one located north and another in the south to south-west. Landsat8 has a finer spatial resolution, 30 m by 30 m, but has a lower temporal resolution (8-day compared with the daily MODIS data), so it is useful to see the spatial heterogeneity of the attack, but not the temporal dynamics. Visual observations on site showed the defoliation to be most extreme at the tower site, tapering off from the tower Figure 2.10.
Figure 2.9 NDVI data from the Landsat8 platform, which has a pixel size of 30 m x 30 m, centered on the tower and covering an area of 2 km$^2$ on 16 June 2015, 16 May 2016 and 17 June 2016.

Figure 2.10 Photographs of the forest tent caterpillar (FTC) defoliation event at the Old Aspen (OA) Fluxnet site taken on 16 June 2016 from atop the tower starting north and turning in approximately 45° increments for the full 360°.

2.3.4 Simulation Validation

To evaluate the method used to estimate what the C fluxes would have been without defoliation, the method was applied to each of the reference years (1998, 2001, 2006, and 2010). I compared simulated and observed C and water fluxes for the four years, both as a four-year
average and for each year individually by using average climate and parameter values and individual-year values, respectively. For the individual-year simulations, the parameters used were the average of the three values from the three other years, to ensure independence. Results (Table 2.2) showed that daily average simulated GEP either over or underestimated (+11% to -1%) measured GEP for individual years. The simulated annual GEP for individual years deviated from the measured GEP by an average of 53 g C m\(^{-2}\) y\(^{-1}\) which falls within the average measurement uncertainty of 95 g C m\(^{-2}\) y\(^{-1}\) for those years.

Table 2.2 Summary of the comparison of simulated and measured annual values of GEP and \(R_e\) for individual years (1998, 2001, 2006, and 2010) and the 4 year average.

<table>
<thead>
<tr>
<th></th>
<th>GEP</th>
<th>(R_e)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Percent error</td>
<td>11% to -1%</td>
<td>18% to -8%</td>
</tr>
<tr>
<td>Difference (g C m(^2) y(^{-1}))</td>
<td>84 to -64 (avg. = 53)</td>
<td>58 to -15 (avg. = 32)</td>
</tr>
<tr>
<td>Measurement uncertainty (g C m(^2) y(^{-1}))</td>
<td>115 to 63 (avg. = 95)</td>
<td>157 to 98 (avg. = 134)</td>
</tr>
<tr>
<td>Slope + Intercept of 4 year average (g C m(^2) y(^{-1}))</td>
<td>1.00 + 0.04</td>
<td>1.03 -0.02</td>
</tr>
<tr>
<td>4-year average difference (g C m(^2) y(^{-1}))</td>
<td>10</td>
<td>19</td>
</tr>
</tbody>
</table>

The results include the correction factor of 0.90 applied to the simulated \(R_e\).

However, when parameter values averaged over the four years were used, the model yielded a slope of 1.00 between the measured and the modeled GEP values as shown in Figure 2.11a. The simulated annual GEP from the average of the four years was only 10 g C m\(^{-2}\) y\(^{-1}\) less than the average of the measured GEP from the four years. Simulated \(R_e\) was either over or underestimated for individual years (+18% to -8%) with the average of the four years being overestimated by 9% and yielding a slope of 1.09 between the average of the measurements and the simulated results. \(R_e\) was systematically overestimated for years with larger (>1500°C days) cumulative growing degree days and underestimated for years with smaller cumulative growing degree days. The long-term mean cumulative growing degree day total was 1453 ± 159 °C days.
I attempted to improve the $R_e$ simulation by stratifying on $T_s$ similar to the method used for GEP, but the method did not work well. The lack of improvement in this method is likely due to heterotrophic respiration being more affected by soil moisture variation which is not accounted for here, compared to autotrophic respiration and GEP which have similar response to temperature variations. Thus, I found it necessary to correct the $R_e$ simulation by multiplying simulated $R_e$ output by the slope of the linear regression between the measured and simulated $R_e$, which resulted in a new slope of 1.03 (Figure 2.11b). Consequently, the corrected simulated annual $R_e$ from individual years differed from measurements by an average of 32 g C m$^{-2}$ y$^{-1}$ while the average measurement uncertainty was 134 g C m$^{-2}$ y$^{-1}$. The simulated $R_e$ from the average of the four years was 19 g C m$^{-2}$ y$^{-1}$ less than the average of the measured $R_e$ for the four years.

The simulated annual values of GEP and $R_e$ led to the calculated NEP for individual years deviating on average 52 g C m$^{-2}$ y$^{-1}$ from the measured value, which was within the 60 g C m$^{-2}$ y$^{-1}$ average measurement uncertainty for these years. The calculated NEP from the simulation ran on the average of the four years resulted in simulated NEP being 10 g C m$^{-2}$ y$^{-1}$ greater than the average measured NEP for the four years. For simulated $E$, the average Priestley-Taylor $\alpha$ during most of the growing season (June – Sept) was greater than 1 reaching a maximum of 1.18 (Figure 2.11c). The small variation in $\alpha$ between years led to a slope of 0.99 in the linear regression (not shown) between simulated and measured $E$ with an $R^2$ of 0.99.
Figure 2.11 Daily average measurements (average of the 4 validation years) versus simulated gross ecosystem production (GEP) (a) and ecosystem respiration ($R_e$) (b) ($n = 365$). Panel (c) shows five-day averaged Priestley-Taylor alpha ($\alpha$) from the four years (1998, 2001, 2006, and 2010) with the standard deviation indicated by the blue shading.
2.3.5 Impact of FTC Infestation on Carbon and Water Fluxes

The 2016 growing season, delineated using daily GEP, began with a strong GEP of 2.1 g C m$^{-2}$ d$^{-1}$ (24-h average) on 6 May (Figure 2.12a). Measured GEP continued to increase to 7.7 g C m$^{-2}$ d$^{-1}$ until 21 May but then dropped to 1.3 g C m$^{-2}$ d$^{-1}$ on 11 June and remained below 2 g C m$^{-2}$ d$^{-1}$ until 17 June as a result of canopy defoliation. On refoliation, GEP quickly increased once again, reaching 9.6 g C m$^{-2}$ d$^{-1}$ three and a half weeks later (14 July). Unlike the measured values, the simulated FTC-free GEP values continued to increase after 11 May, reaching a maximum value of 17.5 g C m$^{-2}$ d$^{-1}$ on 30 June and then declining to match the measured flux on 3 July. It either matched or was slightly lower than the measured values for the rest of the year. Our results show that the FTC attack depressed GEP for five weeks during the usually productive early portion of the growing season (Figure 2.12a).

The difference between measured and simulated FTC-free $R_e$ was significantly less than that for GEP (Figure 2.12b). The two values began to diverge after 14 May, becoming considerably larger after 22 May when measured $R_e$ began to decrease while simulated $R_e$ continued to increase (Figure 2.12b). After 11 July, measured $R_e$ decreased while simulated $R_e$ continued to increase. This difference was likely due to low $P$ during July and August (Figure 2.4). The two traces remained divergent until 15 August. Both measured and simulated NEP (Figure 2.12c) were negative (as low as -3.9 g C m$^{-2}$ d$^{-1}$ on 5 May) and remained comparable until 21 May when they diverged, with simulated NEP quickly becoming increasingly positive and measured NEP returning to negative values. Simulated NEP reached a maximum value of 10.7 g C m$^{-2}$ d$^{-1}$ on 23 June while measured NEP was negative (-1.9 g C m$^{-2}$ d$^{-1}$) so that, like
GEP, they did not match again until 3 July. Simulated NEP was less than measured NEP (Figure 2.12c) because simulated $R_e$ was much higher than measured $R_e$ from 11 July to 10 August.

Figure 2.12 Temporal progression of three-day averaged measured (red line), simulated (black dashed line), and the 1996-2015 mean (blue dashed line) for (a) gross ecosystem production (GEP), (b) ecosystem respiration ($R_e$), (c) net ecosystem production (NEP), and (d) evapotranspiration ($E$). Grey shaded areas indicate ±1σ from the long-term mean. Note the shaded area for pannel d is not visible because the magnitude of deviation spans a range of similar sizing to the lines.
The impact of the defoliation on $E$ was much subtler than on C fluxes (Figure 2.12d). Starting on 3 May 2016, measured $E$ was 0.93 mm day$^{-1}$ increasing to 2.5 mm day$^{-1}$ on 21 May and subsequently decreasing to less than 2 mm day$^{-1}$ for the next 17 consecutive days. Then it slowly increased to its growing season maximum of 5.7 mm day$^{-1}$ on 25 July and steadily decreased thereafter. Simulated $E$ remained somewhat lower than measured $E$ until 24 May, at which point simulated $E$ increased to 1.5 to 2 times greater than measured $E$ for a 4-week period (Figure 2.12d).

These differences in the temporal progression of measured and simulated fluxes led to a significant difference in annual C fluxes, but not in annual $E$ (Figure 2.13). Measured GEP values during 2016 summed to $877 ± 77$ g C m$^{-2}$ y$^{-1}$, while simulated values assuming no FTC infestation summed to $1098 ± 130$ g C m$^{-2}$ y$^{-1}$. Thus, the FTC infestation reduced 2016 annual GEP by $~20\%$ relative to what it would have been without FTC infestation. In contrast, $R_e$ was depressed by only $6\%$ by the attack (measured $940 ± 123$ g C m$^{-2}$ y$^{-1}$ and simulated $1003 ± 42$ g C m$^{-2}$ y$^{-1}$). In our analysis, FTC-infestation decreased NEP from $95 ± 91$ g C m$^{-2}$ y$^{-1}$ (simulated) to $-72 ± 59$ g C m$^{-2}$ y$^{-1}$ (measured), indicating that the stand likely would have been a C sink in 2016 without the FTC infestation. The small differences between measured and simulated $E$ values led to the annual totals being insignificantly different (measured $332 ± 7$ mm y$^{-1}$ and simulated $339 ± 61$ mm y$^{-1}$, respectively).
Figure 2.13 Annual measured (FTC attack) in blue compared to simulated (no FTC attack) in hatched green, and the 20-year mean, in white dots on pink background, gross ecosystem production (GEP), ecosystem respiration ($R_e$), net ecosystem production (NEP) and evapotranspiration ($E$).

2.4 Discussion

The impact of the FTC defoliation at OA started in early May and lasted until early July. Cook et al. (2008) also observed their stand defoliated from May to June by a single generation of FTC larvae that fed on newly emerged leaves. They observed defoliation of 37% drop in leaf area index (LAI) while I found a 83% drop in $G_{CC}$ and 75% in $\rho_s$ by mid-June before the refoliation of the stand. It is typical for trees to refoliate a few weeks after defoliation and for the
leaves to remain smaller than leaves in years without attack (Wargo, 1981). The smaller leaves in the refoliated stand may account for the observed decrease in $G_{CC}$ after refoliation. Although the OA stand did refoliate following the FTC attack, it did not recover to the maximum $G_{CC}$ normally achieved at the peak of the growing season. Schafer et al. (2010) found that after a complete defoliation event (lasting 2-3 weeks), the stand refoliated to 50% of the two previous growing seasons’ foliage level. I found a much greater refoliation with our stand recovering to 96% of the average maximum $G_{CC}$ and $p_s$ reaching typical values by the end of June. A small secondary rise in $G_{CC}$ also occurred in the second week of September 2016, just prior to canopy senescence. I note that this difference could potentially have been caused by sensor discontinuity because a new PhenoCam was in use during the end of the 2016 season and the previous camera was decommissioned and was therefore unavailable for direct comparison.

The 2016 defoliation suppressed GEP by more than 75% from early May to mid-June, but the second leaf flush in June caused GEP to recover to near-normal values for the remainder of the growing season. Despite this recovery, the annual total GEP was reduced by ~20% compared to what it would have been without the FTC infestation. Cook et al. (2008) found that despite a re-flush of leaves following FTC defoliation, GEP remained suppressed for the rest of the growing season leading to a 24% decrease in annual GEP compared to the mean of 6 years of non-disturbed flux tower observations. I found that the reduction in measured $R_e$ was about 30% smaller during the period from early May to early August, which resulted in an annual total that was approximately 6% lower than simulated $R_e$ without the defoliation event. However, Cook et al. (2008) found $R_e$ in the attack year to be about 6% greater than in the two non-attack years. Amiro et al. (2010) reported that during the year of a gypsy moth and FTC infestation in oak-pine and pitch pine-scrub oak stands, both GEP and $R_e$ decreased. I found that the resulting NEP
in 2016 was greatly decreased from early May to mid June but was slightly higher than simulated from mid July through August, due to simulated FTC-free $R_e$ being much higher than measured $R_e$ during that time. Schafer et al. (2010) found that despite a 50% refoliation of the stand, modelled net canopy assimilation was reduced by 75%. In our study, annual NEP was reduced from $95 \pm 91$ g C m$^{-2}$ y$^{-1}$ to $-72 \pm 59$ g C m$^{-2}$ y$^{-1}$ by the defoliation event. These results that an FTC infestation switched the stand from a C sink to a C source are consistent with those observed by Hicke et al. (2012) for severe insect outbreaks.

The defoliation event caused the site to become a C source for the second time on record, but with the most negative annual NEP ever recorded at the site. The significant decrease in GEP while $R_e$ remained slightly below the long-term mean, led to extremely low annual NEP. The year 2016 was very warm, with the highest $T_a$ on record (1997-2016) and among the 5 warmest years in terms of $T_s$ in the 1996-2016 observation period. Despite these warm temperatures and the early start to the growing season, the growing degree day total in 2016 was only the 4th highest on record. The early growing season start, due to warm spring temperatures, led to early foliation, which partially offset the decrease in GEP by the defoliation. The FTC-free simulation indicated that without the defoliation, annual GEP in 2016 would have been greater than the long-term mean. Surprisingly, annual $R_e$ in 2016 was slightly lower than the long-term mean, despite the unusually warm air and soil temperatures in 2016. If the attack had not occurred, $R_e$ would have been greater than the long-term mean.

Despite the large impact on C, the FTC infestation had a minimal effect on annual $E$. One might hypothesize that a significant alteration to the C fluxes would also be observed in the water fluxes, but previous studies have shown why this may not be the case. Using soil moisture, radial bole growth, and xylem pressure potential measurements, Stephens et al. (1972) showed
that one of the physiological impacts of a 40% defoliation event of gypsy moth on deciduous trees is reduced water loss and stress during the period when leaves are absent. Quentin et al. (2011) observed a short-term decrease in water flux after manual defoliation of eucalyptus but rates of water use in the defoliated trees where similar to the control trees when the leaf area recovered. Similar to the results of Stephens et al. (1972) and Quentin et al. (2011), after defoliation $E$ decreased by one third to one half of simulated levels that would have occurred without the defoliation and then recovered so that they closely matched for the remainder of the year, resulting in very similar annual total $E$. The capability for increased transpiration by refoliated stands is explained by the increased stomatal conductance to transpiration of the secondary foliage compared to the primary foliage that escaped folivory (Stephens et al., 1972), or utilization of increased soil moisture later in the growing season due to decreased $E$ during the defoliation. A defoliation of 40% of the total plant leaf area in sugar cane increased stomatal conductance resulting in whole plant evapotranspiration and leaf water potential of the remaining leaf area being of similar magnitude to pre-defoliation levels (Meinzer and Grantz 1990). Improved water use efficiency during defoliation and increased stomatal conductance upon refoliation are important results since it is often thought that defoliation would reduce transpiration and therefore could significantly alter stand water balances (Cunningham et al., 2009).

In eastern Alberta and western Saskatchewan several years of consecutive FTC infestations were recorded in the late 1980s (Brandt 1995) and the defoliation during this period was associated with two major collapses in growth, observed using tree-ring analysis in Saskatchewan (Hogg and Schwarz 1999). Hogg et al. (2002) found similar results with tree-ring analysis in the Grande Prairie area of northwestern Alberta. In 2000, the Climate Change Impacts
on Productivity and Health of Aspen (CIPHA) program established forest health monitoring from northeastern British Columbia to the Northwest Territories and to southern Manitoba. During the period 1951-2000, insect defoliation was the second strongest influence on the inter-annual variation in regional-scale aspen growth, and when combined with drought produced a major collapse in aspen stands (Hogg et al. 2005, 2008). In 2012, 8.6 million hectares of forests in Canada were damaged by insects, with 3 million impacted by bark beetles and the remainder affected by spruce budworms and FTC (The State of Canada’s Forests: Annual Report 2014). Defoliators have impacted more than 100 Mha of forest in Canada and the USA combined over the past six decades (Kautz et al., 2017). The extent and impact of the combined effects of insect defoliation events and drought indicates the need of incorporating them in national- to global-scale models of forest growth and C cycling (Kurz and Apps, 1999).

With expected climate change, the capacity of forests to be C sinks is becoming even more uncertain. Forest disturbance by insects has already been shown to be impacted by human-induced climate change (Kurz et al., 2008). The majority of insect disturbances have been limited to the southern region of Canada, but with warming temperatures, expansion into areas where insects have historically not been able to thrive could lead to large alterations to the C cycle (Kurz et al., 2013). Couture et al. (2015) found that negative impacts of herbivorous insects on NEP more than doubled under elevated CO₂ concentrations, suggesting that herbivorous insects may limit the capacity of forests to be C sinks in a high CO₂ world. For every 1 g C m⁻² year⁻¹ change in net C flux from Canada’s boreal forest, the total change in the boreal forest C balance will be 2.7 Tg C year⁻¹, showing that a small change in flux over such a large area has implications for the global C cycle (Kurz et al., 2013). Since widespread outbreaks
of defoliating insects are common, failure to measure such events and assess the effects on C exchange can lead to large errors in regional and continental C budgets.

2.5 Conclusions

1. During the FTC infestation period in 2016, NEP and GEP were greatly reduced, while $R_e$ was slightly reduced with all three fluxes recovering to near normal levels before the end of the growing season.

2. FTC infestation resulted in observed $E$ being one half to two thirds of simulated $E$ for a 4-week period during the defoliation period but had little effect on annual $E$.

3. FTC infestation in 2016 resulted in the most negative annual NEP (-72 g C m$^{-2}$ year$^{-1}$) observed over the 1996-2016 period of flux monitoring at the OA site.

4. The OA stand, which has been generally a C sink since 1996, would also have been a C sink in 2016 without the FTC infestation.

5. Combining remote sensing indices with tower-based fluxes and indices provides verification in quantifying the intensity and extent of such a defoliation event.

6. Insect caused defoliation events can result in substantial but short-term impacts to water and C fluxes, with annual net C uptake decreasing more than the decrease caused by a three-year drought.
Chapter 3: Long-term Variability and Trends in Rain-Free Daytime Growing Season and Monthly Evapotranspiration and Conductance, and Their Controls in Boreal Aspen and Black Spruce Stands

3.1 Introduction

Many eddy-covariance (EC) studies have focused on the annual and seasonal variations of C exchange due to climatic variability at boreal aspen and conifer sites (Baldocchi et al., 2001, 2008; Barr et al., 2004, 2007; Black et al., 2000; Dunn et al., 2007; Kljun et al., 2006). Some of these studies have looked at water fluxes only in relation to C fluxes. There have been many studies looking at the climate controls on evapotranspiration ($E$) in aspen stands over a period of 1-5 years (Brown et al., 2014; Blanken et al., 2001), while there have been fewer studies on coniferous stands (Zha et al., 2010; Brümmer et al., 2012).

How relationships between controlling variables such as vapor pressure deficit ($D$) change with $E$ and canopy conductance ($G_c$) change over longer time scales is crucial to understanding ecosystem responses to global change, and is also important for inputs into ecosystem and global climate models. With increased atmospheric CO$_2$ concentrations across the globe, gross ecosystem production (GEP) is increasing but without a significant increase in $E$, thereby leading to increasing water use efficiency ($WUE = \text{GEP}/E$) at the global scale (Cheng et al., 2017). However, this trend is not consistent across all biomes and latitudes (Keenan et al., 2013; Ohta et al., 2014).

The present study focuses on analysis of 22 and 19 years of climate and flux measurements in two southern boreal forest stands, a mature deciduous aspen stand (OA) and a mature...
coniferous black spruce stand (OBS). Specifically, I investigated: (i) the long-term variability in climate variables, including air temperature ($T_a$), net radiation ($R_n$), photosynthetically active radiation (PAR), vapour pressure deficit ($D$), CO$_2$ concentration, precipitation ($P$), and volumetric soil water content ($\theta$), (ii) the relationships between monthly and growing season $G_c$ and the controlling variables ($T_a$, $R_n$, PAR, $D$, CO$_2$ concentration, $P$, and $\theta$), (iii) the relationships between monthly and growing season (~May-Sept) $E$ and the controlling variables, including $R_n$, PAR, $D$, CO$_2$ concentration, $P$, $\theta$, and (iv) the trends in WUE and inherent water use efficiency ($WUE_i = WUE \times D$) (the latter to account for variable evaporative demand). The objectives of the study were to detect if there were any trends, and quantify the variability, in the climate variables, $E$, $G_c$, and WUE over two decades of measurements, and determine the relationships between $E$ and $G_c$ at monthly and growing season scales.

3.2 Materials and Methods

3.2.1 Site Descriptions

OA (CA-Oas) and OBS (CA-Obs) are located near the southern edge of the boreal forest in central Saskatchewan in the Boreal Plains ecozone. Continuous measurements have been made since 1996 at OA and 1999 at OBS as part of the Boreal Ecosystem Research and Monitoring Sites (BERMS) program and the FLUXNET Canada Research Network (FCRN)/Canadian Carbon Program (CCP). Starting in 2013, BERMS became one of the 14 Water, Ecosystem, Cryosphere and Climate (WECC) Observatories included in the Changing Cold Regions Network (CCRN). OA is a mature deciduous broadleaf forest located in Prince Albert National Park (53.62889°N, 106.19779°W, WGS-84). OBS is a mature evergreen forest located approximately 100 km NE of Prince Albert, near White Swan Lake (53.98°N, 105.12°W). Both sites have uniformly aged stands that regenerated after natural fires, in 1919 at OA and in 1879 at
OBS (Barr et al., 2012). OA is dominated by trembling aspen (*Populus tremuloides* Michx.) with a scattered (~10%) balsam poplar (*Populus balsamifera* L.) overstory and a hazelnut (*Corylus cornuta* Marsh.) understory, while OBS consists of black spruce (*Picea mariana*) with a sporadically distributed tamarack (*Larix laricina* Du Roi) overstory and a sparse understory of shrubs such as *Ledum groenlandicum* Retzius and *Vaccinium vitisidaea* L. The stands are 21 m and 14 m high, respectively, and are highly coupled to the atmosphere (decoupling coefficient (Ω) for OA and OBS of 0.13 and 0.15, respectively). The Orthic Gray Luvisol soil at OA consists of an 8-10 cm thick LFH (litter-fermented-humic) layer and a 30-cm-thick silt loam layer on glacial till parent material (Barr et al., 2012). The soil is moderately well drained with high available soil water storage capacity in the root zone and a water table depth of approximately 3 m (Kljun et al., 2006). The soil at OBS is a Peaty Orthic Gleysol with a 20-30-cm thick surface layer comprising hummocky peat (*Sphagnum* spp.) in wet areas and feather mosses (*Hylocomium Splendens*) and lichens (*Cladina* spp.) in drier areas (Arain et al., 2002). The peat is above a waterlogged sandy clay mineral soil with poor drainage and a shallow water table that ranges between 0 and 1 m below the surface. The terrain is generally level at OA while OBS has a slight slope (<2°) from north to south. The sites have a uniform fetch of 3 km in all directions and 1.2 km in the prevailing wind directions. Flux footprints (90%-isopleth along the wind direction) under convective conditions were typically 450-550 and 200-300 m, and 900 and 500 m during stable and neutral conditions at OA and OBS, respectively (Kljun et al., 2006). Both the daytime and nighttime flux footprints at each site were significantly within the uniform fetch around the towers.
3.2.2 Climate Measurements

Air temperature was measured at a height of 37 m at OA and 25 m at OBS with temperature/humidity sensors (model HMP45C, Vaisala Oy, Finland) enclosed in aspirated radiation shields (model 076B, Met-One Instruments Inc., Grants Pass, OR). Air temperature was also measured at the height of 36 m at OA and 24 m at OBS with a platinum resistance thermometer (PRT) and a 36-gauge chromel-constantan thermocouple (Omega Engineering Inc., Laval, Quebec); both enclosed in aspirated radiation shields. Shortwave and longwave radiation were measured with paired pyranometers (model CM11, Kipp & Zonen BV, Delft, The Netherlands) and paired pyrgeometers (model PIR, Eppley Laboratory, Newport, RI, USA) at 36-m (downwelling) and 30-m (upwelling) heights at OA and 25-m (downwelling) and 20-m (upwelling) heights at OBS. At the same heights, upwelling and downwelling components of photosynthetically active radiation (PAR) were measured with paired quantum sensors (model LI-190SA, LI-COR Inc., Lincoln, NE). $P$ was measured using both a tipping bucket rain gauge (model TR-525, Texas Electronics Inc., Dallas, TX, USA or model CS700, Campbell Scientific Inc. (CSI), Logan, UT, USA) and a weighing rain gauge (model 3000 with an Alter shield, Belfort Instruments, Baltimore, MD, USA or a model T-200B3, Geonor, Augusta, NJ, USA). At OA the precipitation gauges were located in the center of a natural clearing approximately 50 m northeast of the tower on a raised platform at a height of ~2 m, while at OBS the weighing gauge was mounted on top of the instrument hut (height of 3.5 m) to reduce under-catch at high wind speeds. In winter, antifreeze was added to prevent freezing and in summer motor oil was added to minimize evaporative losses from the weighing rain gauges. At both sites two profiles of soil temperature ($T_s$) were made at six depths (2, 5, 10, 20, 50, and 100 cm) with copper-constantan thermocouples. At OA $\theta$ was measured using two profiles of soil water reflectometers (model CS
615, Campbell Scientific Inc.) at the depths of 2.5, 7.5, 22.5, 45 and 60 cm along with TDR probes (Moisture Point type B, Gabel Corp., Victoria, Canada) at depths of 0-15, 15-30, 30-60, 60-90, and 90-120 cm. At OBS $\theta$ was measured using two profiles of soil water reflectometers (model CS 615, Campbell Scientific Inc.) at the depths of 2.5, 7.5, 22.5, 45 and 60 cm.

3.2.3 **Eddy-Covariance Flux Measurements**

Continuous eddy–covariance (EC) measurements of fluxes of water vapour, CO$_2$, and sensible heat were made half hourly at 39 and 27 m above ground for OA and OBS, respectively. The fluxes were measured using a tri-axial sonic anemometer (model R2 (1996-1999) or R3 (1999- present) Gill Instruments Ltd., Lymington, UK) and a closed-path, temperature-controlled infrared gas (CO$_2$/H$_2$O) analyzer (IRGA) (model LI-6262 or LI-7000, LI-COR Inc.). A diaphragm pump (model DOA-V191-AA, Gast Inc., Dayton, OH) pulled air through a heated sampling tube (4 m length; 4 mm inner diameter) at a flow rate of 10 L min$^{-1}$ and 15 L min$^{-1}$ for the LI-6262 and LI-7000 IRGAs, respectively (Krishnan *et al*., 2006; Barr *et al*., 2007, 2012). Daily calibrations to correct CO$_2$ concentration measurements for zero and span shifts were implemented automatically using CO$_2$ standard gases from the Greenhouse Gases Measurement Laboratory (GGML) of Environment and Climate Change Canada in Downsview, ON, Canada (Krishnan *et al*., 2006). Heated sample tubes (to prevent condensation) were replaced every 6-12 months to improve the response times in H$_2$O and CO$_2$ sampling that get reduced due to the build up of dust, pollen and smoke particles on the tubing walls. Half-hourly fluxes were derived from 20 Hz measurements, calculated following Webb *et al*., (1980), and stored directly on the computers located at the sites. Further details on the experimental setup, calibrations and calculations of fluxes can be found in Arain *et al*., (2002), Griffis *et al*., (2003), Barr *et al*., (2004), Krishnan *et al*., (2006; 2008), and Zha *et al*., (2010).
3.2.4 Data Processing and Quality Control

Daily checks of measurements and calibrations were performed as part of a quality control/assurance routine using Matlab (Version 8.5, The Mathworks, Natick, MA, USA). After being received via telemetry, the raw data went through three stages of cleaning before being used in calculations. In the first stage, faulty measurements were identified removed; in the second stage those values were replaced by the best available alternative measurements from the other replicated on-site instruments. Gaps were then filled based on temporal interpolation or diurnal variations. In the final stage, the gross ecosystem production (GEP) was calculated.

Data were filtered to obtain rain-free periods and calculate daytime growing season values. To determine rain-free periods, rain events (precipitation > 0.1 mm within 30 mins) and the next 24 hours were removed. Then remaining data were filtered for daytime periods with sufficient light (photon flux density > 200 µmol m\(^{-2}\) s\(^{-1}\)) (Blanken and Black, 2004; Krishnan et al., 2006). This was necessary to restrict to periods of physiological controls of water vapour fluxes, i.e. to those dominated by transpiration. The growing season (GS) was defined following Wu et al. (2013) where the GS start and end were the days when the smoothed daily GEP had reached 10% of the annual maximum smoothed GEP. This allowed the GEP threshold to vary between sites and annually (Wu et al., 2012). Daily GEP was smoothed using a local regression using a 1st degree polynomial model and weighted linear least squares that assigns lower weight to outliers in the regression. This method leads to a similar fit as the spline smoothing used by Richardson et al. (2010) to find the GS start and end dates.

3.2.5 Calculated Variables

Stand WUE (g C (kg H\(_2\)O\(^{-1}\)) was calculated half-hourly as

\[
WUE = \frac{GEP}{E} \quad (3.1)
\]
and WUE$_i$ (g C (kg H$_2$O)$^{-1}$ kPa) was obtained by multiplying Eq (3.1) by $D$

$$WUE_i = WUE \times D$$  \hspace{1cm} (3.2)

to account for the effects of atmospheric evaporative demand (Beer et al., 2010; Keenan et al., 2013; Zhou et al., 2017).

Half-hourly $G_c$ (m s$^{-1}$) was calculated using the inverted version of the Penman-Monteith (P-M) equation as follows (Jarvis and McNaughton, 1986):

$$\frac{1}{G_c} = \frac{\rho c_p D}{\gamma \lambda E} + \frac{1}{G_a} \left[ \frac{s}{\gamma} \left( \frac{R_a}{\lambda E} - 1 \right) - 1 \right]$$  \hspace{1cm} (3.3)

where $\lambda$ is the latent heat of vaporization (J kg$^{-1}$) ($\lambda E$ is the latent heat flux), $R_a$ is the available energy flux (W m$^{-2}$) and is equal to $R_n$ (net radiation) (W m$^{-2}$) minus $G$ (soil surface heat flux) (W m$^{-2}$) minus $\Delta S$ (rate of energy storage between EC sensor height and the ground) (W m$^{-2}$), $\rho$ is the air density (kg m$^{-3}$), $c_p$ is the specific heat of air (J kg$^{-1}$ K$^{-1}$), $s$ is the slope of the saturation water vapour pressure versus air temperature curve (kPa °C$^{-1}$), $\gamma$ is the psychrometric constant (kPa°C$^{-1}$); $D$ is the vapour pressure deficit (kPa) and $G_a$ is the aerodynamic conductance (m s$^{-1}$) for sensible heat and water vapour transfer. $G_a$ is given by:

$$\frac{1}{G_a} = \frac{u}{u^*} + \frac{1}{k u^*} (2 + \psi_m - \psi_h)$$  \hspace{1cm} (3.4)

where $u$ is the wind speed (m s$^{-1}$), $u^*$ is the friction velocity (m s$^{-1}$), $k$ is the von Karman constant (= 0.4) and $\psi_m$ and $\psi_h$ are the integral diabatic correction factors for momentum and sensible heat transfer, respectively, with the coefficient of 2 (= $kB^{-1}$) recommended for all vegetated surfaces (Garratt, 1978; Hicks et al., 2018).

Yearly anomalies in measured variables relative to long-term means were calculated using two approaches. If a variable had a significant linear trend over time, then anomalies were
calculated as the difference between the observed value and the value predicted from a linear regression fit to the values as defined below,

\[ A_i = x_i - f_{(year,i)} \]  \hspace{1cm} (3.5)

where \( A_i \) is the annual anomaly of the variable, \( x_i \) for the year \( i \), and \( f_{(year,i)} \) is the value predicted from the linear regression fit. If a variable did not have a trend, then the anomalies (i.e., interannual variability) were calculated from the difference between the observed value and the mean value using

\[ A_i = x_i - X_{mean} \]  \hspace{1cm} (3.6)

where \( X_{mean} \) is the mean value for the entire observation period (Wu et al., 2013). The trends and relationships were determined using the Nelder-Mead simplex (direct search) method to minimize the deviation of the desired M-estimate using the fit of ordinary least square regression to the data. The Matlab function regstats was used to obtain the diagnostic statistics for the regression such as the \( t \)-statistic.

3.3 Results

3.3.1 Climate Measurements

Figure 3.1 shows the long-term record of, and interannual variability in, GS rain-free daytime (PAR>200 \( \mu \)mol \( m^{-2} s^{-1} \)) mean \( CO_2 \), \( T_a \), downwelling photosynthetically active radiation (\( Q \)), \( D \), \( P \), and \( \theta \) integrated over the 0-90 cm depth for OA (1996-2017) and over the 0-60 cm depth for OBS (1999-2017). Data from each site indicated a significant and increasing trend in \( CO_2 \) concentration of \( \sim 2 \mu mol \ mol^{-1} \ y^{-1} \) (slope = 1.4 \( \mu mol \ mol^{-1} \ y^{-1} \), \( R^2 = 0.48 \), \( p < 0.001 \) at OA and slope = 2.0 \( \mu mol \ mol^{-1} \ y^{-1} \), \( R^2 = 0.92 \), \( p < 0.001 \) at OBS), which is consistent with other long-
term CO\(_2\) dataset collected around the world. The long-term GS mean at OA was 374 \(\mu\text{mol mol}^{-1}\) while at OBS it was 383\(\mu\text{mol mol}^{-1}\).

There were no significant long-term trends in \(T_s\) at OA or OBS. The long-term GS mean \(T_s\) at OA was 10.9\(^\circ\text{C}\) and at OBS it was 7.4\(^\circ\text{C}\). The GS \(T_s\) anomalies ranged from -1.1 to 1.6\(^\circ\text{C}\) at OA and -0.96 to -1.1 \(^\circ\text{C}\) at OBS. The warmest GS \(T_s\) occurred in 2006 with 12.5\(^\circ\text{C}\) at OA while at OBS it occurred in 2001 with 8.4\(^\circ\text{C}\). The coldest \(T_s\) occurred in 2005 with 9.8\(^\circ\text{C}\) at OA but occurred in 2010 at OBS with 6.4\(^\circ\text{C}\).

At both sites, there was no significant long-term trend in \(T_a\). The long-term GS mean \(T_a\) at OA was 17.0\(^\circ\text{C}\) and at OBS it was 14.3\(^\circ\text{C}\). The GS \(T_a\) anomalies ranged from -1.5 to 1.6\(^\circ\text{C}\) at OA and -1.8 to 2.1\(^\circ\text{C}\) at OBS. The warmest year occurred in 2003 with 18.6\(^\circ\text{C}\) at OA but occurred in 2006 with 16.3\(^\circ\text{C}\) at OBS. At OA, the coldest year with 15.5\(^\circ\text{C}\) was in 2000 while at OBS it occurred in 2009 with 12.5\(^\circ\text{C}\).

Both sites showed a decreasing trend in GS \(Q\) with a greater decrease at OBS (slope = -4.57 \(\mu\text{mol m}^{-2}\text{s}^{-1}\text{y}^{-1}\), \(R^2 = 0.41\), \(p = 0.003\)) than at OA (slope = -2.83 \(\mu\text{mol m}^{-2}\text{s}^{-1}\text{y}^{-1}\), \(R^2 = 0.21\), \(p = 0.03\)). Long-term means were 872 and 851 \(\mu\text{mol m}^{-2}\text{s}^{-1}\) at OA and OBS, respectively. The highest measured half-hourly \(Q\) occurred in 2006 at both sites with values of 944 \(\mu\text{mol m}^{-2}\text{s}^{-1}\) and 904 \(\mu\text{mol m}^{-2}\text{s}^{-1}\) at OA and OBS, respectively. The lowest \(Q\) occurred at OBS in 2017 with 738 \(\mu\text{mol m}^{-2}\text{s}^{-1}\) and at OA in 2016 with 786 \(\mu\text{mol m}^{-2}\text{s}^{-1}\).

There were no trends in GS mean \(D\) at either site with long-term means of 1.00 and 0.91 kPa and anomalies ranging from -0.20 to 0.28 and -0.16 to 0.16 kPa for OA and OBS, respectively. The year of highest daytime average \(D\) coincided with the year of the highest \(T_a\) at each site, with values of 1.3 and 1.1 kPa at OA and OBS, respectively.
There was no significant trend in GS P at either site. I measured a long-term GS mean of 330 and 363 mm with anomalies ranging from -179 to 177 and -165 to 149 mm at OA and OBS, respectively. The large difference in GS P at the sites, especially during the 2001-2003 drought, was due to the longer GS at OBS than OA. The lowest GS P at OA occurred in the first year of the drought with 151 mm, while the lowest at OBS occurred in the last year of the drought with 198 mm.

There was a significantly increasing trend at the 95% CI in \( \theta \) (slope = 0.0041 m\(^3\) m\(^{-3}\) y\(^{-1}\), \( R^2 = 0.30, p = 0.012 \)) at OA, and at OBS, there was also a significantly increasing trend but at the 90% CI (slope= 0.0021 m\(^3\) m\(^{-3}\) y\(^{-1}\), \( R^2 =0.20, p = 0.074 \)). The long-term mean values of \( \theta \) at both sites were very similar, for the different root zone depths, at 0.33 and 0.31 m\(^3\) m\(^{-3}\) with anomalies ranging from -0.08 to 0.05 and -0.05 to 0.03 m\(^3\) m\(^{-3}\) y\(^{-1}\) for OA and OBS, respectively. At both sites, \( \theta \) decreased during the 2001-2003 drought but with a greater decrease from the mean at OA than OBS. The lowest annual \( \theta \) of 0.24 m\(^3\) m\(^{-3}\) at OA occurred in 2002, a year after the lowest \( P \), while the lowest \( \theta \) of 0.25 m\(^3\) m\(^{-3}\) at OBS occurred in the lowest \( P \) year.
Figure 3.1 Rain-free daytime (PAR>200 µmol m⁻² s⁻¹) growing season averaged: CO₂ mixing ratio (CO₂), 2-cm soil temperature (Tₛ), air temperature (Tₐ), downwelling photosynthetically active radiation (Q), vapour pressure deficit (D), growing season precipitation (P) and average integrated (0-90 cm at OA and 0-60 cm at OBS) soil volumetric water content (θ) from 1996 to 2017 at Old Aspen (OA) and 1999-2017 at Old Black Spruce (OBS).
3.3.2 Trends in, and Interannual Variability of, Rain-Free Daytime $E$ and WUE

There were no significant trends in GS or monthly rain-free daytime average $E$ at OA (Figure 3.2a,c). There was, however, large variability in values of monthly average $E$ over the observation period, particularly between May and July. The long-term monthly daytime (PAR>200 µmol m$^{-2}$ s$^{-1}$) GS means were 0.08, 0.18, 0.23, 0.21, and 0.14 mm hr$^{-1}$ for May, June, July, August, and September, with the long-term mean of the GS average values being 0.18 mm hr$^{-1}$ (3.6 mm day$^{-1}$). Similar to OA, there were no significant trends in either GS or monthly average $E$ at OBS (Figure 3.2b,d). The variability in monthly average $E$ was much smaller at OBS than OA with long-term (over the years of EC measurements) monthly means of 0.09, 0.12, 0.16, 0.15, and 0.11 mm hr$^{-1}$ for May, June, July, August, and September. The small variation and low values of monthly average $E$ translated to a small long-term GS average $E$ of 0.11 mm hr$^{-1}$ (2.2 mm day$^{-1}$). At both sites, the July and August long-term inter-annual variability pattern matched closely with that of the mean GS values. The pattern observed for the other months were less similar to the pattern of the mean GS values, with May and September being especially distinct.
Figure 3.2 Long-term and inter-annual variation in rain-free daytime (PAR>200 µmol m\(^{-2}\) s\(^{-1}\)) growing season averaged \(E\) at OA (a) and OBS (b) with inter-annual variation in monthly averaged \(E\) from 1996 to 2017 at OA (c) and 1999 to 2017 at OBS (d).

There were no significant trends in GS rain-free daytime (PAR>200 µmol m\(^{-2}\) s\(^{-1}\)) GEP at OA or OBS despite the trend of increasing CO\(_2\) concentration observed at each site (Figure 3.3). The long-term mean GS rain-free daytime GEP at OA was 645 g C m\(^{-2}\) y\(^{-1}\) vs 521 g C m\(^{-2}\) y\(^{-1}\) at OBS, with the greater values at OA due to the differing physiology for the evergreen vegetation.
at OBS compared to the deciduous trees predominant at OA. The annual anomalies in GEP ranged from -206 to 340 g C m⁻² y⁻¹ at OA and -118 to 136 g C m⁻² y⁻¹ at OBS. Drought conditions during 2001-2003 caused GEP at both sites to decrease, but with a greater impact at OA than at OBS. For 2013 and 2017, rain-free daytime growing season GEP and $E$ accounted for approximately 85% of the annual GEP and $E$. 

Figure 3.3 Inter-annual variation in rain-free daytime (PAR>200 µmol m$^{-2}$ s$^{-1}$) growing season averaged gross ecosystem production (GEP) (a) and evapotranspiration ($E$) (b) from 1996 to 2017 at OA and 1999 to 2017 at OBS.
The lack of long-term trend in both $E$ and GEP led to a lack of trend in GS rain-free daytime WUE or WUE$_i$ at OA or OBS (Figure 3.4). The long-term mean GS rain-free daytime WUE was 6.0 g C (kg H$_2$O)$^{-1}$ at OA and 5.5 g C (kg H$_2$O)$^{-1}$ at OBS while WUE$_i$ means were 5.9 and 5.1 g C kPa (kg H$_2$O)$^{-1}$ at OA and OBS, respectively. The maximum WUE and WUE$_i$ at OA occurred in 2003 with 7.4 g C (kg H$_2$O)$^{-1}$ and 9.5 g C kPa (kg H$_2$O)$^{-1}$, respectively. In 2003, the GS rain-free daytime GEP was 586 g C m$^{-2}$ y$^{-1}$, below the long-term mean while the GS rain-free daytime $E$ was the fourth lowest on record with 316 mm. At OBS, the maximum WUE occurred in 2014 with 5.9 g C (kg H$_2$O)$^{-1}$ and the WUE$_i$ maximum occurred in 2006 with 6.0 g C kPa (kg H$_2$O)$^{-1}$. GS rain-free daytime GEP for 2014 in OBS was 600 g C m$^{-2}$ y$^{-1}$ (the fourth highest GS on record for that site), while the GS $E$ that year was the fifth highest with 404 mm, slightly above the long-term GS $E$ mean of 378 mm. The minimum value of WUE of 5.3 g C (kg H$_2$O)$^{-1}$ occurred in 2007 at OA and 5.2 g C (kg H$_2$O)$^{-1}$ in 2008 at OBS. At OA, the 2006 GS GEP had the fifth highest GEP on record at 711 g C m$^{-2}$ y$^{-1}$, while GS $E$ of 479 mm was greater than the long-term mean of 408 mm. In 2008, the year with the minimum WUE at OBS, GS GEP was the seventh lowest at 547 g C m$^{-2}$ y$^{-1}$ while GS $E$ that year was fourth highest at 424 mm. The minimum WUE$_i$ occurred in 2007, the same year as the minimum WUE, at OA with 5.1 g C kPa (kg H$_2$O)$^{-1}$ and the minimum at OBS was in 2009 with 4.0 g C kPa (kg H$_2$O)$^{-1}$. In 2009 at OBS, GS GEP was the highest on record with 647 g C m$^{-2}$ y$^{-1}$ and the GS $E$ was the second highest with 497 mm.
Figure 3.4 Long-term trends and inter-annual variation in rain-free daytime (PAR > 200 µmol m² s⁻¹) growing season averaged water use efficiency (WUE) (a) and inherent water use efficiency (WUEᵢ) (b) from 1996 to 2017 at OA and 1999 to 2017 at OBS.
3.3.3 Environmental Controls on Rain-Free Daytime Monthly and Growing Season $E$

No significant relationships between rain-free daytime GS average $E$ and GS average $T_a$ were observed at either OA (Figure 3.5a) or OBS (Figure 3.5b). The GS average $E$ and $T_a$ values were lower at OBS, which had a longer GS, including most of May and September. Also, the difference in the coniferous tree physiology compared to deciduous trees causes $E$ to be lower at OBS than at OA (Arian et al., 2002). Unlike at the GS scale, relationships between $E$ and $T_a$ were significant ($p < 0.001$) at the monthly scale for both sites (Figure 3.5c,d). Despite the differences in physiology between the sites, the relationships had similar linear fits and $R^2$ values, with a slightly higher $R^2$ at OA than at OBS. The only months that had a significant relationship between $E$ and $T_a$ was September for OA (slope = 0.10, $R^2= 0.34$, $p = 0.01$) and May for OBS (slope = 0.03, $R^2= 0.39$, $p = 0.01$) (Table B1).
Figure 3.5 Panels (a) and (b) show the relationship between rain-free daytime (PAR>200 μmol m⁻² s⁻¹) growing season average daily evapotranspiration (E) and air temperature (Tₐ) at OA (a) and OBS (b). The black lines are the linear regression relationships (equations shown). Panels (c) and (d) show the relationships between E and Tₐ for individual growing season months for OA and OBS, respectively. The colored lines are the linear regressions for the individual months while the black line is the regression line for all months combined (equations shown).

At the GS scale, there were no significant relationships between E and the climate variables (D, Rᵣ, PAR, P and θ) at the 95% CI at either site. However, at the 90% CI, there was a
significant relationship with \( \theta \) (slope = 0.27, \( R^2 = 0.18 \), \( p = 0.06 \)) at OA (Table 3.1). At the monthly scale, there were significant relationships between \( E \) and several climate variables at OA, but not as many as for OBS. The relationship between \( E \) and \( D \) was significant (slope = 0.07, \( R^2 = 0.20 \), \( p < 0.001 \)) at OBS while it was not at OA. At OA, the relationship between \( E \) and \( R_n \) was significant (slope = 0.00, \( R^2 = 0.08 \), \( p = 0.00 \)), while it was not significant at OBS. Similar to \( R_n \), \( Q \) had a significant relationship with \( E \) at OA (slope = 0.00, \( R^2 = 0.08 \), \( p = 0.00 \)) and not at OBS. Lastly, \( E \) also had a significant relationship with \( P \) at OA (slope = 0.00, \( R^2 = 0.10 \), \( p = 0.00 \)) but not at OBS. At both sites, \( \theta \) did not exhibit a significant control on \( E \) at the monthly scale. For the individual months, the relationships between \( E \) and several climate variables (\( T_a \), \( D \), \( P \), and \( \theta \)) were not significant at either site (Table B1). The relationship between \( E \) and \( R_n \) was significant only for the month of September (slope = 0.00, \( R^2 = 0.49 \), \( p = 0.00 \)) at OA and for none of the months at OBS. Similarly, there was also a significant relationship with \( Q \) at OA for only September (slope = 0.00, \( R^2 = 0.49 \), \( p = 0.00 \)) and no individual month at OBS.
Table 3.1 Parameter values for linear relationships between mean monthly and growing season rain-free daytime (PAR>200 µmol m\(^{-2}\) s\(^{-1}\)) evapotranspiration (E) (mm d\(^{-1}\)) and each of the following variables: air temperature (\(T_a\)), vapour pressure deficit (\(D\)), net radiation (\(R_n\)), downwelling photosynthetically active radiation (\(Q\)), cumulative growing season precipitation (\(P\)), and integrated (0-90 cm at OA and 0-60 cm at OBS) soil volumetric water content (\(\theta\)) at Old Aspen (OA) and Old Black Spruce (OBS). Red \(p\) values statistically significant at 95% CI.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Growing Season</th>
<th>Monthly</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
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<td>(T_a) (°C)</td>
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<td>(D) (kPa)</td>
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<td>OBS -0.021</td>
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<tr>
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<td>OBS 0.000</td>
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<td>OBS 0.000</td>
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<td>(P) (mm)</td>
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<td>OBS 0.105</td>
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3.3.4 Environmental Controls on Rain-Free Daytime \(G_c\)

\(G_c\) is an important control on \(E\), and so it is necessary to look at the long-term monthly and GS relationships between \(G_c\) and climate variables. The strongest relationship for GS \(G_c\) occurred with \(D\) at both sites (slope = -12.4, \(R^2 = 0.66\), \(p < 0.001\) at OA and slope = -6.8, \(R^2 = 0.52\), \(p < 0.001\) at OBS) (Figure 3.6a,b). The relationship at the monthly scale was also significant at both sites (slope = -5.6, \(R^2 = 0.11\), \(p < 0.001\) at OA and slope = -1.6, \(R^2 = 0.04\), \(p < 0.001\) at OBS) (Figure 3.6c,d). The negative relationship was consistent at the two time scales, and for both sites, despite the difference in physiology. The slope is almost twice as steep at OA as at OBS indicating the stronger sensitivity of the \(G_c\) at OA to \(D\) than that at OBS. For the individual months, \(G_c\) values for May are low and have the lowest \(R^2\) of all the months at both sites showing it to be quite distinct from the rest of the GS months (Table B2).
Figure 3.6 Panels (a) and (b) show the relationship between rain-free daytime (PAR>200 µmol m\(^{-2}\) s\(^{-1}\)) mean growing season canopy conductance (\(G_c\)) and vapor pressure deficit (\(D\)) at OA and OBS, respectively. Panels (c) and (d) show the relationships between monthly mean rain-free daytime (PAR>200 µmol m\(^{-2}\) s\(^{-1}\)) conductance and \(D\). The colored lines are the linear regressions for the individual months while the black line is the regression line for all months combined (equations shown).

Table 3.2 shows the relationships between mean GS and monthly \(G_c\) and environmental variables. At OBS, the linear relationship between GS \(G_c\) and \(T_a\) was significant at the 95% confidence level (slope = -0.49, \(R^2 = 0.33\), \(p = 0.02\)), while at OA, it was significant only at the
90% CI (slope = -0.94, $R^2 = 0.16$, $p = 0.08$). The linear relationship between GS $G_c$ and $R_n$ was not significant at either site, but the relationship between GS $G_c$ and $Q$ was significant at the 90% CI at OBS (slope = -0.02, $R^2 = 0.36$, $p = 0.01$) and at the 90% CI at OA (slope = -0.02, $R^2 = 0.19$, $p = 0.06$). The other significant relationship for both the sites at the GS scale was between $G_c$ and $\theta$ at the 95% CI (slope = 19.9, $R^2 = 0.27$, $p = 0.03$) at OBS and the 90% confidence level (slope = 15.2, $R^2 = 0.16$, $p = 0.08$) at OA. At the monthly scale, the relationship between $G_c$ and $\theta$ was significant at OA at the 90% CI (slope = 11.7, $R^2 = 0.03$, $p = 0.09$).

At the monthly scale, the relationship between GS $G_c$ and $T_a$ was significant at OA (slope = 0.52, $R^2 = 0.20$, $p < 0.001$), but not at OBS. For the individual GS months, OA showed significant relationships for August and September while OBS had significant relationships for all months except May (Table B2). Unlike at the GS scale that had no significant relationship between $G_c$ and $R_n$ at either site, the relationship was significant at the monthly time scale for OBS (slope = -0.01, $R^2 = 0.10$, $p = 0.00$). While OA had no significant relationship between $G_c$ and $R_n$ at the GS or monthly scale, the relationships were significant for the individual months of May and June. On the other hand, OBS showed significant relationships between GS and monthly $G_c$ and $R_n$ but not for the individual months (Table B2). At the monthly scale, only OBS had a significant relationship between $G_c$ and PAR (slope = -0.01, $R^2 = 0.28$, $p < 0.001$), which was also observed for the individual months of May, June and August. This relationship was significant for May and June at OA, similar to those observed for $R_n$. The relationship between $G_c$ and $P$ at the monthly scale was significant at both sites (slope = 0.03, $R^2 = 0.15$, $p < 0.001$ at OA and slope = 0.00, $R^2 = 0.04$, $p = 0.08$ at OBS), but for the individual months, it was not significant for any month at both sites. At the monthly scale, the relationship between $G_c$ and $\theta$ was significant at the 90% CI at OA (slope = 11.73, $R^2 = 0.03$, $p = 0.09$), and just outside that
threshold for OBS ($p = 0.11$) for OBS. The relationship between $G_c$ and $\theta$ was also significant at the 90% CI for May and July at OA. For individual months, the relationship between $G_c$ and $\theta$ at OBS was significant only for July.

Table 3.2 Parameter values for linear relationships between mean monthly and growing season rain-free daytime (PAR>200 µmol m$^{-2}$ s$^{-1}$) conductance ($G_c$) (mm s$^{-1}$) and the following environmental variables: air temperature ($T_a$), vapour pressure deficit ($D$), net radiation ($R_n$), downwelling photosynthetically active radiation ($Q$), total growing season precipitation ($P$), integrated (90 cm at OA and 60 cm at OBS) soil volumetric water content ($\theta$) at Old Aspen (OA) and Old Black Spruce (OBS). Red $p$ values statistically significant at 95% CI.

<table>
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<th>Growing Season</th>
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<td>Slope</td>
<td>Intercept</td>
</tr>
<tr>
<td>$T_a$ (ºC)</td>
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<tr>
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3.4 Discussion

3.4.1 Climate Trends

Research has shown Northern Hemisphere land masses warming annually and for all seasons except winter, which has no significant trend or sometimes a negative trend, since 1987 (Cohen et al., 2012). For Canada the annual mean temperature increased by 1.5ºC over 1950-2010, with the largest increase of 2.3ºC in winter and smaller warming in winter but still an increase of 1.7ºC (Vincent et al. 2012). I have not seen a significant trend in warming in the GS
(i.e., no increase in \( T_a \)) during 1996-2017 at OA or 1999-2017 at OBS. Mekis and Vincent (2011) reported annual rainfall in Canada increased by 12.5% from 1950-2009, with total rainfall increasing in all season, with the largest increase observed during the spring. No trends in GS \( P \) were observed at OA or OBS.

3.4.2 Rain-Free Daytime \( E \) and WUE

At OA and OBS, no trends in GS average \( E \) or monthly average \( E \) were detected. GS \( E \) at OA mostly comes from transpiration, with 5% of it coming from evaporation from the soil surface and about 6% from wet leaves (Blanken and Black, 2004; Krishnan et al., 2006). At 10 out of the 14 FLUXNET sites studied by Keenan et al. (2013), they found a decreasing trend in ecosystem \( E \). One of the four sites not showing the decreasing trend was the northern black spruce site (NOBS) of the BOREAS northern study area. My observation of no trend in \( E \) at OBS matches that found at NOBS. Keenan et al. (2013) found a significant \((p = 0.02)\) decrease in GEP of average 2.60% y\(^{-1}\) at NOBS. However, I found no increasing long-term trend in GEP at OA or OBS. In a Siberian larch stand, Ohta et al. (2014) found that GEP increased from 2004 to 2007 but then decreased and remained constant from 2008 to 2011. They also noted that \( E \) increased from 2004 to 2007 but at slower rate than GEP increased, and remained at a higher constant from 2008 to 2011.

The response of ecosystem WUE to changes in climate variables depends on the tradeoff between water loss and C uptake. Keenan et al. (2013), using long-term EC measurements from FLUXNET sites, found an overall significant increase in WUE in temperate and boreal forests in the Northern Hemisphere over the past two decades. They found there was no significant trend in daytime summer (J,J,A) WUE at NOBS from 1993-2004. Our results agree with these findings since we found no significant trends in GS rain-free daytime mean WUE at OBS and OA. At
OA, the maximum value of WUE occurred in 2003 at the height of the 2001-2003 drought, when GS total $E$ was the fourth lowest on record, consistent with results from earlier studies observing increased WUE with increased drought stress (Krishnan et al., 2006; Baldocchi 1997). Unlike at OA, maximum WUE at OBS did not occur during the drought but rather in 2014 with above average GS GEP and $E$. Ohta et al. (2014) observed decreasing WUE from 2004-2011 in their Siberian larch stand due to the increasing GEP with a larger rater of increase in $E$ in the early years and then GEP decreased and remained at a relatively constant GEP in the later years while $E$ maintained a higher constant value after 2008. Others (e.g., Dekker et al., 2016; Frank et al., 2015) have found that EC data alone were not able to completely constrain the CO$_2$ sensitivity of WUE because the data records were too short to detect significant changes in CO$_2$ so they relied on longer time series of tree ring or C-isotope data. Cheng et al. (2017), using an analytical WUE model, found WUE at 11 sites with 6 years of continous EC data to increase on average by 14.7 ± 9.0 mg C mm H$_2$O y$^{-1}$, which was consistent with the in situ observed mean trend of 12.6 ± 11.4 mg C mm H$_2$O y$^{-1}$ at the same sites.

Dietrich et al. (2016) found that boreal jack pine WUE$_i$ was positively correlated with atmospheric CO$_2$ concentration and increased over time. Frank et al. (2015), using stable C isotope measurements ($\delta^{13}$C), found that for every 1 ppmv rise in atmospheric CO$_2$, intercellular CO$_2$ ($c_i$) increased by ~0.76 ppmv such that WUE$_i$ increased on average 14 ± 10% in broadleaf stands and 22 ± 6% in conifer stands in the twentieth century from the 1901-1910 reference period. These trends of increasing WUE$_i$ were not observed at either OA or OBS.

3.4.3 Relationships Between Rain-Free Daytime $E$ and Controlling Variables

At the GS scale, I found the strongest control on $E$ was $\theta$ at both sites. At the annual time scale at OA, Barr et al. (2006) found the strongest relationship for $E$ versus climate variables to
be with the sum of the current and the previous year precipitation. Ohta et al. (2008) reported that the interannual variation in $E$ followed the variation of soil water content but Ohta et al. (2001) found the daily $E$ to be strongly controlled by VPD and poorly coupled with surface moisture while Dolman et al. (2004) also reported on the importance of $D$ for $E$ at the half-hour scale at the same site. Therefore, Ohta et al. (2008) suggested that the variables controlling $E$ can differ depending on the time scale analysed. Baldocchi et al. (2001) found a spectral peak in fluxes at the seasonal to semi-annual time scale due to the distinct differences in climate during the seasons and the approximately half-year duration of the GS. They also found a spectral gap at the monthly scale, which they attributed to the lack of meaningful biological or meteorological factors at that scale. Kelliher et al. (1993) found if water is limiting, $\theta$ becomes the major control on $E$ such that the ratio of evaporation rate to the available energy tends to decrease linearly with decreasing soil water content. Using nine years of data, Yoshida et al. (2010) showed $Q$, $D$, and $\theta$ to be main drivers of $E$ at diurnal, intra-seasonal and inter-seasonal scales in a Siberian larch forest. They determined that $E$ was correlated with $Q$ on hourly to intra-seasonal timescales, with $D$ and $T_a$ on intra- to inter-seasonal timescales, and with $\theta$ on inter-seasonal to inter-annual timescales. I also observed a shift in the correlation between $E$ and the climate variables with temporal scale. At the GS scale, I found the strongest relationships to be with $D$, $P$ and $\theta$, while at the monthly time scale, $T_a$ had the highest $R^2$ of the climate variables. For OBS Zha et al. (2010) found that at the monthly time scale there was no significant inter-annual dependence of $E$ on $\theta$ during the summer (June to August), causing low interannual variability in $E$. Brümmer et al. (2012) also found significant linear relationships between monthly $E$ and $D$ in both deciduous and coniferous forests. They found that for five boreal coniferous sites, the decoupling
coefficient ($\Omega$) (McNaughton and Jarvis, 1983) had values less than 0.2, showing that the stomatal conductance, and not $G_a$, was the key determinant of $E$.

### 3.4.4 Relationships Between Rain-Free Daytime $G_c$ and Climate Variables

Considering the major role of $G_c$ in determining $E$, it is important to investigate the drivers of change in $G_c$. Yoshida et al. (2010) found that $G_c$ was controlled by $Q$ at diurnal and inter-seasonal to interannual scales due to changes in plant physiology, while $D$ was controlling at the intra-seasonal scale due to meteorological changes. They showed $T_a$ and $\theta$ altered $G_c$ on inter-seasonal to interannual scales. Ohta et al. (2014) found no significant relationship between growing season (JJA) mean $G_c$ and downwelling shortwave radiation but found negative relationships between $G_c$ and $T_a$ and $D$, with no clear relationship to $\theta$. I did not investigate the role of shortwave radiation in controlling $G_c$ but considered $Q$ (which is highly correlated to shortwave radiation), and found $Q$ had significant relationships at both sites at the growing season scale and the strongest relationship with $G_c$ at the monthly time scale at OBS. I found significant negative relationships between $G_c$ and $D$, similar to Ohta et al. (2014) and Brümmer et al. (2012), at both sites at the GS and monthly time scales. I also found significant negative relationships at the 90% CI between $G_c$ and $T_a$ at the GS scale at both sites, but only at OA at the monthly time scale. Unlike Ohta et al. (2014), I found significant positive relationships at the 90% CI between $G_c$ and $\theta$ at both sites at the GS scale but only for OA at the monthly time scale.

### 3.5 Conclusions

1. The environmental controls of rain-free daytime (PAR>200 µmol m$^{-2}$ s$^{-1}$) $G_c$ were time scale dependent, and were distinct between sites at the monthly scale. At the GS scale, the strongest control on $G_c$ was $D$ for both sites. At the monthly scale at OA, $T_a$ had the strongest relationship with $G_c$ while at OBS it was $Q$. 

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2. The environmental controls on $E$ varied with the time scale. The strongest control on $E$ at the growing season scale was $\theta$ at both sites, and $T_a$ at the monthly time scale.

3. With no long-term trend in rain-free daytime (PAR $> 200 \, \mu\text{mol m}^{-2} \, \text{s}^{-1}$) GS averaged $E$ or GEP observed at either site, there were no trends observed in rain-free daytime GS averaged WUE or WUE$_i$ at either site.

4. These sites have experienced no significant trend in their long-term rain-free daytime GS averaged climate and fluxes.
Chapter 4: Interannual Variability and Long-Term Trends in Climate, Water, and Carbon Fluxes in the Southern Boreal Old Aspen and Old Black Spruce Stands

4.1 Introduction

Nearly one tenth of all present-day global forest cover is located within Canada, with almost one third being boreal forest (FAO, 2015); making the latter important in its contribution to the global C and water balances. Understanding how this biome is responding to climate change is vital for future ecosystem modelling. An ecosystem experiences the effects of the variation of solar radiation due to the change in the sun’s position at the monthly and seasonal time scales. With the changing of the seasons, ecosystem phenology differences add to the effects of micrometeorological variation. At the interannual scale, growing season (GS) metrics (start date, end date, and duration) play an important role in controlling C and water fluxes (Wilson and Baldocchi, 2000). In the northern latitudes where boreal forest ecosystems are dominant, their GS is limited by the length of the snow-free season (Baldocchi et al., 2008). With climate change, the GS has been starting earlier, ending later and therefore lengthening since 1950 but with varying decadal and seasonal trends over the northern hemisphere (Tucker et al., 2001; Barichivich et al., 2013).

Many eddy-covariance (EC) studies have focused on the annual and seasonal variations of C exchange due to climatic variability at boreal aspen and conifer sites (Amiro et al., 2006; Baldocchi et al., 2001, 2008; Barr et al., 2004, 2007; Black et al., 2000; Dunn et al., 2007; Kljun et al., 2006). Many EC flux tower studies have only a few years of data to study climate response so often miss multi-year responses, extreme climate events and the role of pre-conditioning of
the ecosystem state (Desai, 2014). To capture droughts or precipitation variability due to *El Nino* and *La Nina*, several years of data may be needed (Krishnan *et al.*, 2006; Wharton and Falk, 2016). Short-term studies also miss long-term trends in the changing climate variables and their impact on long-term fluxes. Short-term studies aren’t long enough to distinguish trends from sampling and measurement error for the annual C balance, since the errors sum to around 20-50 g C m⁻² year⁻¹ (Richardson *et al.*, 2007). Baldocchi *et al.* (2017) found that with records exceeding 20 years scientists should be able to detect trends as small as 3 g C m⁻² year⁻².

The present study focuses on analysis of 22 and 19 years of climate and flux measurements in two southern boreal forest stands, a mature deciduous aspen stand (OA) and a mature coniferous black spruce stand (OBS), respectively. Specifically, I investigated the long-term trends in the non-filtered: (i) annual aclimate variables, including air temperature (*Tₐ*), net radiation (*Rₙ*), photosynthetically active radiation (PAR), vapour pressure deficit (*D*), CO₂ concentration, precipitation (*P*), and volumetric soil water content (*θ*), (ii) annual and GS gross ecosystem production (GEP), ecosystem respiration (*Rₑ*), net ecosystem production (NEP), and evapotranspiration (*E*), and (iii) annual and GS *P - E* and water use efficiency (WUE). I also determined the contribution of GS C and water fluxes to the corresponding annual values, and investigated the impacts of the start date, end date, and length of the GS on NEP, GEP and *E*.

4.2 Materials and Methods

4.2.1 Site Descriptions

OA and OBS are located near the southern edge of the boreal forest in Saskatchewan in the Boreal Plains ecozone. OA is a mature deciduous broadleaf forest located in Prince Albert National Park (53.62889°N, 106.19779°W, WGS-84). OBS is a mature evergreen forest located approximately 100 km NE of Prince Albert, near White Swan Lake (53.98°N, 105.12°W). Both
sites have uniformly aged stands that regenerated after natural fires in 1919 at OA and 1879 at OBS (Barr et al., 2012). OA is dominated by trembling aspen (*Populus tremuloides* Michx.) with a scattered (~10%) balsam poplar (*Populus balsamifera* L.) overstory and a hazelnut (*Corylus cornuta* Marsh.) understory, while OBS consists of black spruce (*Picea mariana*) with a sporadically distributed tamarack (*Larix laricina* Du Roi) overstory and a sparse understory of shrubs such as *Ledum groenlandicum* Retzius and *Vaccinium vitis-idaea* L. The stand heights are 21 m and 14 m respectively and are highly coupled to the atmosphere (decoupling coefficient (Ω) of 0.13 and 0.15, respectively at OA and OBS. The Orthic Gray Luvisol (Typic Cryalf) soil at OA has a forest-floor consisting of an 8-10 cm thick LFH (litter-fermented-humic) layer beneath which is a 30-cm-thick silt loam layer over glacial till (Padbury et al. 1978; Barr et al., 2012). The soil is moderately well drained with high available soil water storage capacity in the root zone, and the water table depth is approximately 3 m (Kljun et al., 2006). The Peaty Orthic Gleysol (Peaty Phase Typic Cryaquept) soil at OBS has a 20-30-cm thick forest-floor comprising hummocky peat (*Sphagnum* spp.) in wet areas and feather mosses (*Hylocomium Splendens*) and lichens (*Cladina* spp.) in drier areas (Anderson et al., 1976; Arain et al., 2002; Gaumont-Guay et al., 2008). This peat is above a waterlogged sandy clay with poor drainage and a shallow water table that ranges between 0 and 1 m below the surface. The terrain is generally level at OA while OBS has a slight slope (< 2°) from north to south. The sites have a uniform fetch of 3 km in all directions and 1.2 km in the prevailing wind directions, respectively, for OA and OBS. Flux footprints (90%-isopleth along the wind direction) under convective conditions were typically 450-550 and 200-300 m and during stable and neutral conditions were 900 and 500 m at OA and OBS, respectively (Kljun et al., 2006). Both the daytime and nighttime flux footprints at each site are significantly within the uniform fetch around the towers.
4.2.2 Climate Measurements

Air temperature was measured at a height of 37 m with temperature/humidity sensors (model HMP45C, Vaisala Oy, Finland) enclosed in aspirated radiation shields (model 076B, Met-One Instruments Inc., Grants Pass, OR). Air temperature was also measured at the height of 36 m with a platinum resistance thermometer (PRT) and a 36-gauge chromel-constantan thermocouple (Omega Engineering Inc., Laval, Quebec), both enclosed in an aspirated radiation shield. Shortwave and longwave radiation were measured with paired pyranometers (model CM11, Kipp & Zonen BV, Delft, The Netherlands) and paired pyrgeometers (model PIR, Eppley Laboratory, Newport, RI, USA) at 36-m (downwelling) and 30-m (upwelling) heights. At the same heights, upwelling and downwelling components of photosynthetically active radiation (PAR) were measured with paired quantum sensors (model LI-190SA, LI-COR Inc., Lincoln, NE). P was measured using both a tipping bucket rain gauge (model TR-525, Texas Electronics Inc., Dallas, TX, USA or model CS700, Campbell Scientific Inc. (CSI), Logan, UT, USA) and a weighing rain gauge (model 3000 with an Alter shield, Belfort Instruments, Baltimore, MD, USA or a model T-200B3, Geonor, Augusta, NJ, USA). At OA the precipitation gauges were located in the center of a natural clearing approximately 50 m northeast of the tower on a raised platform at a height of ~2 m while at OBS the weighing gauge was mounted on top of the instrument hut (height of 3.5 m) to reduce under-catch at high wind speeds. In winter, antifreeze was added to prevent freezing and in summer, motor oil was added to minimize evaporative losses from the weighing rain gauges. Two profiles of soil temperature ($T_s$) were made at six depths (2, 5, 10, 20, 50, 100 cm) with copper-constantan thermocouples. $\theta$ was measured using two profiles of soil water reflectometers (model CS 615, Campbell Scientific Inc.) at the depths
of 2.5, 7.5, 22.5, 45 and 60 cm along with TDR probes (Moisture Point type B, Gabel Corp., Victoria, Canada) at depths of 0-15, 15-30, 30-60, 60-90, and 90-120 cm.

4.2.3 Eddy-Covariance Flux Measurements

Continuous eddy–covariance (EC) flux measurements have been made since 1996 at OA (CA-Oas) and 1999 at OBS (CA-Obs) as part of the Boreal Ecosystem Research and Monitoring Sites (BERMS) program and the FLUXNET Canada Research Network (FCRN)/Canadian Carbon Program (CCP). Starting in 2013, BERMS became one of the 14 Water, Ecosystem, Cryosphere and Climate (WECC) Observatories included in the Changing Cold Regions Network (CCRN). EC measurements of fluxes of water vapor, CO$_2$, and sensible heat were made half hourly at 39 and 27 m above ground for OA and OBS, respectively. The fluxes were measured using a tri-axial sonic anemometer (model R2 (1996-1999) or R3 (1999- present) Gill Instruments Ltd., Lymington, UK) and a closed-path, temperature-controlled infrared gas (CO$_2$/H$_2$O) analyzer (IRGA) (model LI-6262 or LI-7000, LI-COR Inc.). A diaphragm pump (model DOA-V191-AA, Gast Inc., Dayton, OH) pulled air through a heated sampling tube (4 m length; 4 mm inner diameter) at a flow rate of 10 L min$^{-1}$ and 15 L min$^{-1}$ for the LI-6262 and LI-7000 IRGAs, respectively (Krishan et al., 2006; Barr et al., 2007, 2012). Daily calibrations to correct CO$_2$ concentration measurements for zero and span shifts were implemented automatically using CO$_2$ standard gases from the Greenhouse Gases Measurement Laboratory (GGML) of Environment and Climate Change Canada in Downsview, ON, Canada (Krishnan et al., 2006). Heated sample tubes (to prevent condensation) were replaced every 6-12 months to improve the response times in H$_2$O and CO$_2$ sampling that get reduced due to the buildup of dust, pollen and smoke particles on the tubing walls. Half-hourly fluxes were measured at 20 Hz, calculated following Webb et al. (1980), and stored directly on the computers located at the sites.
Further details on the experimental setup, calibrations and calculations of fluxes can be found in Arain et al. (2002), Griffis et al. (2003), Barr et al. (2004), Krishnan et al. (2006; 2008), and Zha et al. (2010).

4.2.4 Data Processing and Quality Control

Daily checks of measurements and calibrations were performed as part of a quality control/assurance routine using Matlab (Version 8.5, The Mathworks, Natick, MA, USA). After being received, the raw data went through three stages of cleaning before being used in calculations. In the first stage faulty measurements were removed, in the second stage those values are replaced by the best available alternative measurements from the other repetitive on-site instruments, and lastly gaps are filled with temporal interpolation or based on diurnal variations. In the third data cleaning stage, final values of $E$, NEP, GEP and $R_e$ were calculated.

To estimate the annual NEP, GEP and $R_e$ I followed the Fluxnet-Canada Research Network (FCRN) procedure outlined in Barr et al. (2004) which I summarize here. I obtain $R_e$ from NEP when GEP is zero such as nighttime and during cold seasons (when both air ($T_a$) and soil ($T_s$) temperatures are $< 0°C$). To fill nighttime gaps and estimate the daytime $R_e$ an empirical relationship for an entire year of half hourly $R_e$ and half hourly near-surface (2-cm) $T_s$, filtered for friction velocity ($u_*$) $< u_*$ threshold of 0.35 m s$^{-1}$ (Barr et al., 2004), was utilized. GEP was then calculated as NEP + $R_e$ (daytime) or zero (nighttime and during the cold-season). Gaps in GEP were then filled with the Michaelis-Menten light response equation, a rectangular hyperbolic relationship between GEP and PAR. The difference between the estimated GEP and $R_e$ was used to fill gaps in NEP. A time-varying parameter was developed from each empirical relationship using a moving temporal window to be able to capture changes caused by other
environmental variables such as $D$ or $\theta$. The respective parameters are the slopes of the linear regression between the estimated and measure values of $R_e$ and GEP.

The total uncertainty in the annual C fluxes were calculated after following three steps: (1) for each half hour flux random error was estimated by adding 20% random error per half hour following Morgenstern et al. (2004); (2) uncertainty from gap-filling was examined by deleting up to 40% of the data annually, with gaps produced by a uniformly discrete random number generator which created 500 randomly selected gaps of lengths ranging from on half hour up to 480 half hours, i.e. 10 days of data; (3) systematic bias generated from the choice of $u_*$ threshold was calculated by altering the threshold by $\pm 20\%$ from the chosen 0.35 m s$^{-1}$ threshold and then recalculating the fluxes to determine the impact to the annual values.

The total random error was calculated as the sum of squares of the errors estimated in stage 1 and 2. The random error for NEP, GEP, $R_e$ and $E$ at OA were $\pm 17$ g C m$^{-2}$ year$^{-1}$, $\pm 20$ g C m$^{-2}$ year$^{-1}$ and $\pm 6$ mm year$^{-1}$, respectively. At OBS the errors for NEP, GEP, $R_e$ and $E$ were $\pm 15$ g C m$^{-2}$ year$^{-1}$, $\pm 17$ g C m$^{-2}$ year$^{-1}$, $\pm 14$ g C m$^{-2}$ year$^{-1}$ and $\pm 7$ mm year$^{-1}$, respectively. The systematic error from step 3 for NEP was $\pm 35$ g C m$^{-2}$ year$^{-1}$, GEP was $\pm 53$ g C m$^{-2}$ year$^{-1}$, $R_e$ was $\pm 88$ g C m$^{-2}$ year$^{-1}$, and $E$ was $\pm 2$ mm year$^{-1}$, at OA. The equivalent systematic errors at OBS were $\pm 18$ g C m$^{-2}$ year$^{-1}$ for NEP, $\pm 30$ g C m$^{-2}$ year$^{-1}$ for GEP, $\pm 48$ g C m$^{-2}$ year$^{-1}$ for $R_e$, and $\pm 1$ mm year$^{-1}$ for $E$. The systematic error was added directly to the random error rather than using the sum-of-squares because the error from choosing a $u_*$ threshold will have a similar direction and magnitude each year, so is therefore not random. The overall estimated uncertainty of the annual NEP, GEP, $R_e$ and $E$ at OA were $\pm 52$ g C m$^{-2}$ year$^{-1}$, $\pm 73$ g C m$^{-2}$ year$^{-1}$, $\pm 108$ g C m$^{-2}$ year$^{-1}$, and $\pm 9$ mm year$^{-1}$, respectively. At OBS the overall estimated uncertainty of the annual NEP, GEP, $R_e$ and $E$ were $\pm 33$ g C m$^{-2}$ year$^{-1}$, $\pm 46$ g C m$^{-2}$
year\(^{-1}\), ± 60 g C m\(^{-2}\) year\(^{-1}\), and ± 8 mm year\(^{-1}\), respectively. These values are comparable to ones presented in Krishnan et al. (2006) who had 12 years of data from these sites.

A similar procedure was used to estimate the uncertainty in annual \(E\). Estimates of sensible and latent heat using a moving window based on Amiro et al. (2006) was used for gap filling \(E\) in step 2. The total random error calculated from the sum of squares of the errors from step 1 and 2 were ± 6 mm year\(^{-1}\) and ± 7 mm year\(^{-1}\) for OA and OBS, respectively. The systematic error from step 3 was ± 2 mm year\(^{-1}\) at OA and ± 1 mm year\(^{-1}\) at OBS. The total estimated uncertainty, the sum of the random and systematic errors, was ± 9 mm year\(^{-1}\) and ± 8 mm year\(^{-1}\) for OA and OBS, respectively.

The GS was defined following Wu et al. (2013) where the GS start and end were the days when the smoothed daily GEP had reached 10% of the annual maximum smoothed GEP. This allowed the GEP threshold to vary between sites and annually rather than using a fixed value (Wu et al., 2012). Daily GEP was smoothed using a local regression using a 1st degree polynomial model and weighted linear least squares that assigns lower weight to outliers in the regression. This method leads to a similar fit as spline smoothing used by Richardson et al. (2010) to find the GS start and end.

4.2.5 Calculated Variables

The stand WUE (g C (kg H\(_2\)O\(^{-1}\)) was calculated as

\[
WUE = \frac{GEP}{E}
\]  

(4.1)

Yearly anomalies in measured variables were calculated using two approaches. If a variable had a significant trend over time the anomalies were calculated as the difference between the observed value and the value predicted from a linear regression fit to the values as defined below,
\[ A_i = x_i - f_{(\text{year},i)} \]  

(4.2)

where \( A_i \) is the anomaly of a variable, \( x_i \) is the observed value from year \( i \), \( f_{(\text{year},i)} \) is the value predicted from the linear regression fit. If a variable did not have a trend, then the anomalies were calculated from the difference between the observed value and the mean value given by

\[ A_i = x_i - X_{\text{mean}} \]  

(4.3)

where \( X_{\text{mean}} \) is the mean value for the entire observation period (Wu et al., 2013). The trends and relationships were determined using the Nelder-Mead simplex (direct search) method to minimize the deviation of the desired M-estimate using ordinary least square fit to the data. The Matlab function `regstats` was used to obtain the diagnostic statistics for the regression such as the \( t \)-statistic.

### 4.3 Results

#### 4.3.1 Seasonal Variation in Climate and Fluxes

Figure 4.1 shows the mean seasonal variation in climate variables for 1996-2017 at OA compared with those for 1999-2017 at OBS. Due to their close proximity most of the climate variables follow the same well-defined seasonal cycle, with a few notable departures. The CO\(_2\) mixing ratio was higher at OBS than at OA throughout the entire year, with a long-term mean annual difference of 5 \( \mu \)mol mol\(^{-1}\), possibly due to higher \( R_e \) at OBS than at OA throughout the year. \( T_s \) at OA was higher for most of the year, except March and April when \( T_s \) means and standard deviations for OA and OBS overlap. Different \( T_s \) values were expected due to different soil types at the two stands. With water logged sandy-clay soil and a high water table, OBS had lower \( T_s \) than the moderately well drained silt loam at OA. The \( T_s \) and \( Q \) at the two sites were so similar that their means were indistinguishable and their standard deviations have only minor deviations from each other. \( D \) at both sites was very similar for the majority of the year but was
higher at OA, compared to OBS, during the spring (April-May) and fall (September-October) as seen by the higher mean and standard deviation. From January to August, the two sites showed matching cumulative $P$ but thereafter OBS started accumulating more than OA such that by the end of the year they had distinctly different $P$ totals. This difference could be due to lower $P$ at OA during 1996-1998 thereby lowering the mean at OA, the slightly differing installations of $P$ gauges at the two sites, and the approximately 80km distance leading to storms impacting one site and not the other. The mean $\theta$ was higher at OA throughout the entire year, with larger differences between the sites occurring in spring (Feb-April).
Figure 4.1 Five-day 24-h averaged CO₂ mixing ratio, 2-cm soil temperature ($T_s$), air temperature ($T_a$), photosynthetically active radiation ($Q$), vapour pressure deficit ($D$), cumulative precipitation ($P$) and average (0-90-cm at OA and 0-60-cm at OBS) soil volumetric water content ($\theta$) from 1996-2017 at Old Aspen (OA) by the red dot-dashed line and 1999-2017 at Old Black Spruce (OBS) by the blue dot-dashed line. Shaded red and blue areas denote ±1σ from the long-term mean at OA and OBS, respectively.
Figure 4.2 shows the mean seasonal progression of the C and water fluxes at OA and OBS. GEP at OBS departed from near zero in April while it didn’t begin until May at OA. The maximum GEP peaked slightly earlier at OA reaching approximately 11 g C m$^{-2}$ d$^{-1}$ at the end of June/start of July while at OBS it peaked in late July/early August with approximately 6 g C m$^{-2}$ d$^{-1}$. The decline in GEP at OA was sharp with the start of leaf senescence, causing a cross over of the mean GEP for the two sites in September, and reaching zero by the end of the month. At OBS, GEP declined slowly, symmetrical to the start up and ending in late October to early November. The standard deviation in GEP was larger at OA than OBS due to interannual differences in phenology directing the annual GEP. Since annual $R_e$ was mostly controlled by annual $T_s$, the former was similar at the two sites since their mean $T_s$ were not very different. Since $T_s$ at OA increased quicker than at OBS, as seen in Figure 4.1, $R_e$ at OA increased faster than at OBS. As was the case for GEP, $R_e$ peaked earlier at OA with approximately 7 g C m$^{-2}$ d$^{-1}$ compared to a peak of less than 6 g C m$^{-2}$ d$^{-1}$ at OBS, but it decreased at the same rate at both sites. The different dynamics in the progression of GEP, but similar progression of $R_e$ at the two sites lead to distinct NEP temporal progressions. The transition of NEP from negative to positive occurred a month earlier at OBS than OA. Peak NEP of approximately 2 g C m$^{-2}$ d$^{-1}$ occurred in mid-May at OBS, when NEP at OA was still increasing. At OA, peak NEP occurred in late June with just over 4 g C m$^{-2}$ d$^{-1}$. At OBS, maximum NEP occurred in May and quickly dropped and remained near zero from July till the end of September when it transitioned back to negative. At OA, after the maximum NEP had been reached, it slowly decreased to zero in September, decreasing to its minimum of approximately -2 g C m$^{-2}$ d$^{-1}$ and slowly became less negative as $R_e$ declined. The seasonal progression of $E$ matched that of GEP at the two sites. $E$ at OBS started earlier as expected because the trees began transpiring and photosynthesizing earlier. Peak $E$ at
both sites occurred in July, following peak $T_a$, with a maximum $E$ of 3.5 mm d$^{-1}$ at OA and just over 2 mm d$^{-1}$ at OBS.

Figure 4.2 Seasonal variation in five-day 24-h averaged (1996-2017 mean for Old Aspen (OA), red dashed line, and 1999-2017 mean for Old Black Spruce (OBS), blue dashed line) (a) gross ecosystem production (GEP), (b) ecosystem respiration ($R_e$), (c) net ecosystem production (NEP), and (d) evapotranspiration ($E$). Shaded red and blue areas denote ±1σ from the long-term mean at OA and OBS, respectively. The shaded area for panel d is not visible because the magnitude of deviation spans a range similar to the thickness of the lines.
4.3.2 Interannual Variation in Growing Season Climate and Fluxes

Figure 4.3 shows annual time series showing the interannual variability in GS mean CO$_2$ mixing ratio, $T_s$, $T_a$, $Q$, $D$, $P$, and average $\theta$ for the 0-90 cm depth for OA (1996-2017) and the 0-60 cm depth for OBS (1999-2017). The CO$_2$ mixing ratio increased significantly at both sites (slope = 1.4 $\mu$mol mol$^{-1}$ y$^{-1}$, $R^2 = 0.46$, $p < 0.001$ at OA and slope = 2.1 $\mu$mol mol$^{-1}$ y$^{-1}$, $R^2 = 0.92$, $p < 0.001$ at OBS). The CI of the slopes from the fits at each site overlap, indicating the two trends were not significantly different from each other. The long-term GS mean at OA was 379 $\mu$mol mol$^{-1}$ while at OBS it was 386 $\mu$mol mol$^{-1}$. There was no significant trend in GS $T_s$ at either site. The long-term GS mean $T_s$ at OA (1996-2017) was 10.6$^\circ$C with yearly anomalies ranging from -0.88 to 1.2$^\circ$C, while at OBS (1999-2017) it was 7.2$^\circ$C with anomalies ranging -0.72 to 0.73$^\circ$C. The maximum $T_s$ occurred in 2006 at OA with 11.9$^\circ$C and in 2012 at OBS with 8.0$^\circ$C. The minimum GS $T_s$ occurred in 2004 at both sites with 9.8 and 6.5$^\circ$C at OA and OBS, respectively. At both sites there was no significant long-term trend in $T_a$. The long-term GS mean $T_a$ at OA was 13.6$^\circ$C and at OBS it was 11.3$^\circ$C. The yearly anomalies in GS $T_a$ ranged from -1.8 to 1.8$^\circ$C at OA and -1.5 to 1.8$^\circ$C at OBS. The warmest GS occurred in 2003 with 15.4$^\circ$C at OA and in 2006 with 13.1$^\circ$C at OBS. At OA the coldest GS with 11.8$^\circ$C was in 2005 while at OBS it occurred in 2000 with 9.8$^\circ$C.

Both sites showed a decreasing trend in GS $Q$ (slope = -2.83 $\mu$mol m$^{-2}$ s$^{-1}$ y$^{-1}$, $R^2 = 0.21$, $p = 0.03$ at OA, slope = -2.01 $\mu$mol m$^{-2}$ s$^{-1}$ y$^{-1}$, $R^2 = 0.27$, $p = 0.02$ at OBS). Long-term GS means were 396 and 382 $\mu$mol m$^{-2}$ s$^{-1}$ at OA (1996-2017) and OBS (1999-2017), respectively. The highest measured GS $Q$ occurred in 2001 at both sites with OA measuring 436 $\mu$mol m$^{-2}$ s$^{-1}$ and
OBS 425 µmol m\(^{-2}\) s\(^{-1}\). The lowest \(Q\) occurred at OBS in 2017 with 336 µmol m\(^{-2}\) s\(^{-1}\) and at OA in 2014 with 365 µmol m\(^{-2}\) s\(^{-1}\).

There were no trends in GS \(D\) at either site, with long-term means of 0.65 and 0.58 kPa and yearly anomalies ranging from -0.14 to 0.23 and -0.15 to 0.29 kPa at OA and OBS, respectively. As expected, the year of maximum GS \(D\) coincided with maximum GS \(T_a\) at each site, with values of 0.89 and 0.87 kPa at OA and OBS, respectively. The minimum GS \(D\) occurred in 2000 at both sites with 0.51 and 0.44 at OA and OBS, respectively. There was a significantly increasing trend at the 90% CI in GS \(P\) (slope = 6.38 mm y\(^{-1}\), \(R^2 = 0.17\), \(p = 0.058\)) at OA, but not at OBS. When looking at the same measurement years as at OBS (1999-2017), this significant trend disappears. I measured a long-term GS mean of 342 and 371 mm with anomalies ranging from -189 to 148 and -169 to 153 mm at OA and OBS, respectively. The lowest GS \(P\) at OA occurred in the first year of the drought with 153 mm while the lowest at OBS occurred in the last year of the drought with 202 mm. The maximum GS \(P\) at OA occurred in 2010 with 490 mm, while it occurred only one year after the drought, in 2004, at OBS, with 524 mm. There was a significantly increasing trend at the 95% confidence interval (CI) in \(\theta\) (slope = 0.0032 m\(^3\) m\(^{-3}\) y\(^{-1}\), \(R^2 = 0.25\), \(p = 0.017\)) at OA, but no trend at OBS. The long-term mean values of \(\theta\) at both sites were very similar, despite their different root zone depths, with 0.33 and 0.30 m\(^3\)m\(^{-3}\) at OA and OBS, respectively. At OBS, the yearly anomalies ranged from -0.05 to 0.04 m\(^3\)m\(^{-3}\). At both sites, \(\theta\) decreased during the 2001-2003 drought with a greater decrease from the mean at OA than at OBS. The lowest \(\theta\) of 0.24 m\(^3\)m\(^{-3}\) at OA occurred in 2002, a year after the lowest \(P\), while the lowest \(\theta\) of 0.24 m\(^3\)m\(^{-3}\) at OBS occurred in the lowest \(P\) year (i.e., 2003).
Figure 4.3 Interannual variation in growing season averaged: CO₂ mixing ratio, 2-cm soil temperature ($T_s$), air temperature ($T_a$), downwelling photosynthetically active radiation ($Q$), vapour pressure deficit ($D$), growing season precipitation ($P$) and average (0-90-cm depth at OA and 0-60-cm depth at OBS) soil volumetric water content ($\theta$) from 1996 to 2017 at Old Aspen (OA) and 1999-2017 at Old Black Spruce (OBS) (all values were obtained from 24-h averages or totals). The gray bar denotes the 2001-2003 drought and the green bar denotes the 2016 forest tent caterpillar (FTC) defoliation at OA. Note: values are different from those in Figure 3.1 because in Figure 3.1 values are for the rain-free periods of the GS averaged over the daytime (PAR > 200 $\mu$mol m$^2$ s$^{-1}$).
Figure 4.4 shows the GS total C and water fluxes for 1996-2017 at OA and for 1999-2017 at OBS. There was a significantly increasing trend (slope = 6.66 g C m\(^{-2}\) y\(^{-1}\), \(R^2 = 0.47\), \(p = 0.001\)) in GS GEP at OBS, but not at OA. The long-term mean GS GEP was 1047 g C m\(^{-2}\) y\(^{-1}\) at OA and 810 g C m\(^{-2}\) y\(^{-1}\) at OBS. The highest GS GEP occurred in 2006 at OA with 1225 g C m\(^{-2}\) y\(^{-1}\) while the highest at OBS occurred in 2016 with 897 g C m\(^{-2}\) y\(^{-1}\). The lowest GS GEP values at 756 g C m\(^{-2}\) y\(^{-1}\) and 683 g C m\(^{-2}\) y\(^{-1}\) at OA and OBS, respectively, occurred in 2004 at both sites, when the stands were still recovering from the drought. Just like GEP, GS \(R_e\) had a significant trend (slope = 7.88 g C m\(^{-2}\) y\(^{-2}\), \(R^2 = 0.59\), \(p < 0.001\)) at OBS but not at OA. The long-term mean GS \(R_e\) at OA was 772 g C m\(^{-2}\) y\(^{-1}\) and at OBS it was 700 g C m\(^{-2}\) y\(^{-1}\). The lowest \(R_e\) of 610 g C m\(^{-2}\) y\(^{-1}\) and 580 g C m\(^{-2}\) y\(^{-1}\) at OA and OBS, respectively, occurred in 2004, coinciding with the lowest GEP. At OA the highest \(R_e\) of 881 g C m\(^{-2}\) y\(^{-1}\) occurred in 2006, the same year as the highest GEP, while the highest \(R_e\) at OBS occurred in 2016 with 798 g C m\(^{-2}\) y\(^{-1}\). Despite no significant trends in GEP or \(R_e\) at OA, there was a significant decreasing trend in NEP at both sites (slope = -8.65 g C m\(^{-2}\) y\(^{-2}\), \(R^2 = 0.30\), \(p =0.008\) at OA and slope = -2.65 g C m\(^{-2}\) y\(^{-2}\), \(R^2 = 0.55\), \(p <0.001\) at OBS). The long-term GS mean NEP at OA was 381 g C m\(^{-2}\) y\(^{-1}\) and at OBS it was 116 g C m\(^{-2}\) y\(^{-1}\). The lowest GS NEP at OA occurred in 2016 with 110 g C m\(^{-2}\) y\(^{-1}\) due to low GS GEP from the FTC infestation while \(R_e\) was slightly below the long-term GS average (Stephens et al. 2018; see Chapter 2). The lowest GS NEP at OBS occurred in 2015 with 89 g C m\(^{-2}\) y\(^{-1}\) due to both the GEP and \(R_e\) in that year being among the lowest on the record. The highest GS NEP (570 g C m\(^{-2}\) y\(^{-1}\)) at OA occurred in 1998 due to the high GEP and the slightly below average \(R_e\) occurring in that year. The highest GS NEP at OBS with 154 g C m\(^{-2}\) y\(^{-1}\) occurred in 2001 due to the combination of the fourth highest GEP and slightly above-average \(R_e\). There was no
significant trend in $GS_E$ at either OA or OBS. The long-term mean $GS_E$ was 317 mm y$^{-1}$ and 261 mm y$^{-1}$ at OA and OBS, respectively. The highest $GS_E$ on record corresponded with the highest $GS_{GEP}$ at OA in 2006 with 400 mm y$^{-1}$ while at OBS it occurred in 2008, a different year from when maximum $GS_{GEP}$ occurred, with 306 mm y$^{-1}$. The lowest $GS_E$, at OA, occurred in the second year of the drought (2002) with 230 mm y$^{-1}$ while at OBS it occurred in 2005, a low GEP year at OBS, with 221 mm y$^{-1}$. 
Figure 4.4 Long-term trends and interannual variation in the growing season values (blue squares for OBS (1997-2017), and red circles for OA (1996-2017)) of a) gross ecosystem production (GEP), b) ecosystem respiration ($R_e$), c) net ecosystem production (NEP) and d) evapotranspiration ($E$). Also shown are the linear regression equations and lines fit to the data where the units of the slopes are g C m$^{-2}$ y$^{-1}$ for the C fluxes and mm y$^{-2}$ for $E$. The gray bar denotes the 2001-2003 drought, and the green bar denotes the 2016 forest tent caterpillar (FTC) defoliation period at OA.
4.3.3 Interannual Variation in Annual Climate and Fluxes

Figure 4.5 shows the same climate traces as Figure 4.3 but on an annual rather than GS scale. Just as for the GS, there were significant increasing trends in annual CO\textsubscript{2} concentration at both sites (slope = 1.6 \(\mu\text{mol mol}^{-1}\text{ y}^{-1}\), \(R^2 = 0.63\), \(p < 0.001\) at OA and slope = 2.2 \(\mu\text{mol mol}^{-1}\text{ y}^{-1}\), \(R^2 = 0.97\), \(p < 0.001\) at OBS), with the slopes and \(R^2\) being greater than for the GS values. The CI of the slopes from the fits at each site overlap, indicating the two trends are not significantly different from each other. The long-term annual mean at OA was 384 \(\mu\text{mol mol}^{-1}\), while at OBS it was 389 \(\mu\text{mol mol}^{-1}\). While there were no trends in GS \(T_s\), annual \(T_s\) significantly increased (slope = 0.040°C y\(^{-1}\), \(R^2 = 0.22\), \(p < 0.04\) at OBS but at the 90% CI (slope = 0.035°C y\(^{-1}\), \(R^2 = 0.15\), \(p < 0.07\)) at OA. Similar to the trends in CO\textsubscript{2}, the CI of the slopes for the trends in \(T_s\) overlapped showing the two trends were not significantly different from each other. The long-term mean annual \(T_s\) at OA was 4.7°C with yearly anomalies ranging from -1.3 to 0.8°C. At OBS, the long-term mean annual \(T_s\) was 3.0°C and the anomalies ranged from -1.1 to 0.8°C. Similar to the GS \(T_a\), there were no trends in annual \(T_a\) at either site. Annual mean \(T_a\) at OA was 2.4°C and at OBS it was 1.6°C, with yearly anomalies ranging from -1.7 to 3.1°C at OA and -1.7 to 1.8°C at OBS. The highest annual \(T_a\) occurred in 2017 at both sites with 5.5°C and 3.4°C while the coldest values occurred in 2014 with 0.7°C and -0.01°C for OA and OBS, respectively.

Unlike the GS, which saw a trend in \(Q\) at both sites, there was no trend in annual \(Q\) at OA but there was a decreasing trend at OBS (slope = -1.4 \(\mu\text{mol m}^{-2}\text{ s}^{-1}\text{ y}^{-1}\), \(R^2 = 0.34\), \(p = 0.008\)). When looking at the same years (1999-2017) at both sites, OA also showed a significant decrease in annual \(Q\) (slope = -1.1 \(\mu\text{mol m}^{-2}\text{ s}^{-1}\text{ y}^{-1}\), \(R^2 = 0.21\), \(p = 0.04\)). The two sites had the same long-term annual mean \(Q\) of 266 \(\mu\text{mol m}^{-2}\text{ s}^{-1}\) with yearly anomalies ranging from -23 to 19 \(\mu\text{mol m}^{-2}\).
s^{-1} at OA and -30 to 24 \mu mol m^{-2} s^{-1} at OBS. Compared to the GS that saw the highest Q in 2006, the highest annual Q occurred in 2001 for both sites with 285 \mu mol m^{-2} s^{-1} and 290 \mu mol m^{-2} s^{-1} at OA and OBS, respectively. The lowest annual Q occurred in the same years as the lowest GS Q, in 2016 at OA with 243 \mu mol m^{-2} s^{-1}, and in 2017 at OBS with 235 \mu mol m^{-2} s^{-1}. There were no trends in annual D at either site, as was the case for the GS values. The long-term mean annual D at OA was 0.38 kPa and 0.36 kPa at OBS, with yearly anomalies of -0.07 to 0.24 kPa at OA and -0.08 to 0.28 kPa at OBS. Unlike GS P, which had a significant trend at the 90% CI at OA, there were no trends in annual P at either site. The long-term mean annual P values were 465 and 482 mm at OA and OBS, respectively. The minimum annual P at OA occurred during the first year of the drought, 2001, with 235 mm while at OBS it occurred in the last year of the drought, 2003, with 289 mm. The maximum annual P occurred in 2010 at OA with 705 mm and in 2004 at OBS with 698 mm. There were no trends in annual \theta at either site. The long-term mean annual \theta were 0.32 and 0.27 m^{3} m^{-3} at OA and OBS, respectively. The maximum annual \theta occurred in 2006 at OA with 0.39 m^{3} m^{-3}, and in 2011 at OBS with 0.29 m^{3} m^{-3}. The minimum annual \theta occurred during the last year of the drought in 2003 at both sites with 0.22 m^{3} m^{-3}.
Figure 4.5 Interannual variation in annual average 24-h averaged: (a) CO₂ mixing ratio, (b) 2-cm soil temperature \((T_s)\), (c) air temperature \((T_a)\), (d) downwelling photosynthetically active radiation \((Q)\), (e) vapor pressure deficit \((D)\), (f) growing season precipitation \((P)\) and (g) average (0-90-cm depth at OA and 0-60-cm depth at OBS) soil volumetric water content \((\theta)\) from 1996 to 2017 at Old Aspen (OA) and 1999-2017 at Old Black Spruce (OBS). The gray bar denotes the 2001-2003 drought and the green bar denotes the 2016 forest tent caterpillar (FTC) defoliation period at OA.
Figure 4.6 shows the interannual variation in annual C and water fluxes for 1996-2017 at OA and for 1999-2017 at OBS. Like the GS GEP, which had a trend at OBS, the annual GEP significantly ($p = 0.02$) increased at OBS but not at OA. The long-term annual mean GEP was $1050 \pm 73$ g C m$^{-2}$ y$^{-1}$ at OA and $809 \pm 47$ g C m$^{-2}$ y$^{-1}$ at OBS. The lowest annual GEP at both sites occurred the year after the drought ended (2004) with $763 \pm 97$ g C m$^{-2}$ y$^{-1}$ and $693 \pm 37$ g C m$^{-2}$ y$^{-1}$ at OA and OBS, respectively. The highest annual GEP occurred in 2006 at OA with $1229 \pm 95$ g C m$^{-2}$ y$^{-1}$, and in 2010 at OBS with $904 \pm 57$ g C m$^{-2}$ y$^{-1}$. Similarly to GEP, annual $R_e$ increased significantly ($p < 0.001$) at OBS but not at OA. The long-term mean $R_e$ was $934 \pm 108$ g C m$^{-2}$ y$^{-1}$ at OA and $774 \pm 62$ g C m$^{-2}$ y$^{-1}$ at OBS. The highest annual $R_e$ at OA occurred in 2015 with $1072 \pm 132$ g C m$^{-2}$ y$^{-1}$ while at OBS it occurred in 2017 with $904 \pm 103$ g C m$^{-2}$ y$^{-1}$. The lowest $R_e$ occurred in 2004 at both sites with $763 \pm 133$ g C m$^{-2}$ y$^{-1}$ and $656 \pm 49$ g C m$^{-2}$ y$^{-1}$ at OA and OBS, respectively. As I would expect from different increasing trends in GEP and $R_e$ at OBS, there was a significant ($p = 0.002$) decreasing trend in NEP. Since $R_e$ at OBS increased faster than GEP, NEP significantly decreased. With no trends in GEP or $R_e$ at OA, there was no trend in NEP. The long-term mean at OA was $115 \pm 52$ g C m$^{-2}$ y$^{-1}$, and $35 \pm 33$ g C m$^{-2}$ y$^{-1}$ at OBS. The highest annual NEP at OBS occurred in 2001 with $82 \pm 30$ g C m$^{-2}$ y$^{-1}$ while the lowest occurred in 2017 with $-28 \pm 42$ g C m$^{-2}$ y$^{-1}$. The highest annual NEP at OA occurred in 2001 with $272 \pm 64$ g C m$^{-2}$ y$^{-1}$ and the lowest occurred in 2016 (FTC attack year) with $-72 \pm 59$ C m$^{-2}$ y$^{-1}$. I observed no trend in annual $E$ at either site. The long-term means were $368 \pm 9$ mm y$^{-1}$ and $289 \pm 8$ mm y$^{-1}$ at OA and OBS, respectively. The highest annual value of $E$ at OA occurred in 2006 with 446 mm y$^{-1}$ and at OBS in 2008 with 332 mm y$^{-1}$. The lowest $E$ occurred at OA in 2003 with 267 mm y$^{-1}$ while it occurred in 2005 at OBS with 252 mm y$^{-1}$. 

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Figure 4.6 Long-term trends and interannual variation in annual a) gross ecosystem production (GEP), b) ecosystem respiration ($R_e$), c) net ecosystem production (NEP) and d) evapotranspiration ($E$) with magnitudes of the uncertainty bars calculated as described in Section 4.4 (red circles represent Old Aspen (OA) for 1996-2017, and blue circles represent Old Black Spruce (OBS) for 1999-2017). Uncertainty bars are present in panel d but are not visible because the magnitude of uncertainty spans a smaller range than the symbols. Also shown are the linear regression equations and lines fit to the data where the units of the slopes are g C m$^{-2}$ y$^{-1}$ for the C fluxes and mm y$^{-1}$ for $E$. The gray bar denotes the 2001-2003 drought and the green bar denotes the 2016 forest tent caterpillar (FTC) defoliation at OA.
4.3.4 **Annual and Growing Season WUE**

Figure 4.7 shows the GS and annual WUE for 1996-2017 at OA and for 1999-2017 at OBS. There was a significantly ($p = 0.02$) increasing trend in GS WUE at OBS, as expected due to the trend in GS GEP and lack of change in $E$. There was no trend in GS WUE at OA. The long-term GS mean WUE was 3.4 g C (kg H$_2$O)$^{-1}$ at OA and 3.1 g C (kg H$_2$O)$^{-1}$ at OBS. The highest GS WUE occurred in 2011 at OA with 4.7 g C (kg H$_2$O)$^{-1}$, while the highest at OBS occurred in 2005 with 3.7 g C (kg H$_2$O)$^{-1}$. The lowest occurred in 2007 at OA with 2.7 g C (kg H$_2$O)$^{-1}$ and in 2008 at OBS with 2.6 g C (kg H$_2$O)$^{-1}$. There was a significantly ($p = 0.05$) decreasing trend in annual WUE at OA but not at OBS. The long-term mean annual values of WUE at OA and OBS were 2.9 g C (kg H$_2$O)$^{-1}$ and 2.6 g C (kg H$_2$O)$^{-1}$, respectively. At OA, the highest annual WUE occurred in 2003 with 3.5 g C (kg H$_2$O)$^{-1}$ while the highest annual WUE at OBS occurred in 2005 with 3.3 g C (kg H$_2$O)$^{-1}$. The lowest annual WUE at each site coincided with the lowest GS WUE, in 2016 at OA with 2.5 g C (kg H$_2$O)$^{-1}$ and in 2008 at OBS with 2.4 g C (kg H$_2$O)$^{-1}$. 
Figure 4.7 Long-term trends and interannual variation in growing season (a), and annual (b) water use efficiency (WUE) from 1996-2017 at Old Aspen (OA) (filled red circles) and 1999-2017 at Old Black Spruce (OBS) (filled blue squares). Also shown are the linear regression equations and lines fit to the data where the units of the slopes and intercepts are g C (kg H₂O)⁻¹ y⁻¹ and g C (kg H₂O)⁻¹, respectively. The gray bar denotes the 2001-2003 drought, and the green bar denotes the 2016 forest tent caterpillar (FTC) defoliation period at OA.
4.3.5 Annual and Growing Season $P - E$

Figure 4.8 shows the values of $P - E$ at the GS and annual scales for OA for 1996-2017 and at OBS for 1999-2017. There were no significant trends in the GS or annual $P - E$ at either site. The long-term GS $P - E$ was 25 mm at OA and 110 mm at OBS. The maximum occurred at both sites in 2004 with 216 mm and 287 mm at OA and OBS, respectively. The minimum occurred at OA in 2001, the first year of the drought, with -170 mm and in 2008 at OBS with -47 mm. The long-term annual $P - E$ at OA was 97 mm and at OBS it was 193 mm. The maximum and minimum annual $P - E$ values at the two sites occurred in the same years as the respective maximum and minimum GS values. The maximum values were 369 mm and 431 mm and the minimum values were -113 mm and 31 mm at OA and OBS, respectively. Lower $E$ at OBS even with slightly lower $P$ resulted in a higher contribution to groundwater (i.e., $P - E$). It was 33% higher on average over the 10 years after the drought period than the pre-drought value. During the drought years the difference was much larger with mostly negative $P - E$ values at OA. Nijseen and Lettenmaier (2002) studied the water balance of White Cull Creek watershed and found the ratio of annual streamflow to precipitation ranged from 12 to 27% for 1994-1996 and Zha et al. (2010) found a slightly increased range of 14 to 37% for 2000-2006.
Figure 4.8 Long-term trends and interannual variation in growing season $P - E$ (a), and annual $P - E$ (b) for 1996-2017 at Old Aspen (OA) (red circles) and 1999-2017 at Old Black Spruce (OBS) (blue squares). Also shown are the linear regression equations and lines fit to the data where the units of the slopes and intercepts are mm y$^{-2}$ and mm y$^{-1}$, respectively. The gray bar denotes the 2001-2003 drought, and the green bar denotes the 2016 forest tent caterpillar (FTC) defoliation period at OA.

4.3.6 Comparison of Growing Season and Annual C and Water Fluxes

Table 4.1 summarizes the average values of GS and annual C and $E$ fluxes over the study period (1996-2017 at OA and 1999-2017 at OBS). It also shows the ratios of GS to annual fluxes. Since the GS was defined as the period with significant ecosystem photosynthesis occurring, the ratio of GS to annual GEP was close to 1.0. The ratios of GS to annual $R_e$ were 0.83 and 0.90 for OA and OBS, respectively. The small proportion of $R_e$ occurring in the non-GS part of the year had a major impact on the distribution of NEP over the year (Figure 4.6c), resulting in GS NEP of 381 g C m$^{-2}$ y$^{-1}$ at OA to drop to 115 g C m$^{-2}$ y$^{-1}$ at the annual scale and GS NEP at OBS of 116 g C m$^{-2}$ y$^{-1}$ to drop to 35 g C m$^{-2}$ y$^{-1}$ at the annual scale. As a result, the
ratio of GS to annual NEP was 3.3 for both sites, i.e., annual NEP was 30% of GS NEP. The ratios of GS to annual $E$ very closely matched those for $R_e$, with values of 0.86 at OA and 0.90 at OBS. These values were significantly higher than ratios of GS to annual $P$, which were 0.73 and 0.77. The ratios of GS $E$ to $P$ for the respective sites were 0.93 and 0.70, while the corresponding ratios for annual values were 0.79 and 0.60. These values show that OA returned a significantly higher proportion of $P$ to the atmosphere as water vapour than OBS, as expected. At both sites, a higher proportion of GS $P$ was lost as $E$ compared to annual $P$. GS WUE at OA (3.4 g C (kg H$_2$O)$^{-1}$) was 9% higher than at OBS (3.1 g C (kg H$_2$O)$^{-1}$) reflecting the 29% higher GEP and 21% higher $E$ at OA than at OBS. Annual $P – E$, a good estimate of site runoff, was 97 and 193 mm at OA and OBS, respectively, which greatly exceeded GS values (25 and 110 mm, respectively). The significantly higher runoff at OBS was mainly the result of its 21% lower annual $E$ than at OA.
Table 4.1 Long-term mean growing season and annual gross ecosystem production (GEP), ecosystem respiration ($R_e$), net ecosystem production (NEP), evapotranspiration ($E$), water use efficiency (WUE), precipitation ($P$) and $P – E$, along with the ratio of the growing season to annual values for 1996-2017 at Old Aspen (OA) and 1999-2017 at Old Black Spruce (OBS).

<table>
<thead>
<tr>
<th>Growing season mean</th>
<th>Annual mean</th>
<th>Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>OA</td>
<td>OBS</td>
<td>OA</td>
</tr>
<tr>
<td>GEP (g C m$^{-2}$ y$^{-1}$)</td>
<td>1047</td>
<td>810</td>
</tr>
<tr>
<td>$R_e$ (g C m$^{-2}$ y$^{-1}$)</td>
<td>772</td>
<td>700</td>
</tr>
<tr>
<td>NEP (g C m$^{-2}$ y$^{-1}$)</td>
<td>381</td>
<td>116</td>
</tr>
<tr>
<td>$E$ (mm y$^{-1}$)</td>
<td>317</td>
<td>261</td>
</tr>
<tr>
<td>WUE (g C (kg H$_2$O)$^{-1}$)</td>
<td>3.4</td>
<td>3.1</td>
</tr>
<tr>
<td>$P$ (mm y$^{-1}$)</td>
<td>342</td>
<td>371</td>
</tr>
<tr>
<td>$P – E$ (mm y$^{-1}$)</td>
<td>25</td>
<td>110</td>
</tr>
</tbody>
</table>

4.3.7 Impact of Growing Season Metrics on C and Water Fluxes

The start, end, and length of the GS are determined by the atmospheric conditions during the year. Thus with interannual variability in climate variables, there is likely to be variability in the GS metrics. At both sites there was an increasing trend in the GS length over the observation period but neither was statistically significant (data not shown). As summarized in Table 4.2, the mean GS length at OA was 140 days with the shortest GS being only 125 days long and the longest being 152 days. The mean GS length at OBS with 194 days was 54 days longer than at OA. The shortest GS length at OBS was 166 days and the longest was 209 days. No observable or significant trend in GS start date occurred at either site. The GS at OA started on average on 14 May with the earliest GS starting on 30 April in 1998, and the latest occurring on 27 May in
2004. Due to the conifer trees at OBS, the GS started much earlier than at OA, with the average start occurring on 14 April 14. The earliest GS at OBS started on 30 March in 2010, and the latest start occurred on 2 May in 2002. There was a positive increase in GS end date, i.e., later termination of GS, but it too was not statistically significant at either site. The average GS end date at OA was 1 October with the earliest end occurring on 22 September in 2010, and the latest on 9 October in 2009. OBS had a later GS end with the average end date occurring on 25 October. The earliest end date at OBS occurred on 15 October in 2010 while the latest was on 1 November in 2009. At OA at the 90% CI, there was a significant relationship (slope = 0.63, $R^2 = 0.15$, $p = 0.08$) between GS end and start date, while this was not observed at OBS.

Table 4.2. The mean, shortest and longest growing season (GS) length, GS start date, and GS end date at Old Aspen (OA) and Old Black Spruce (OBS).

<table>
<thead>
<tr>
<th></th>
<th>OA</th>
<th>OBS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean GS length (days)</td>
<td>140</td>
<td>194</td>
</tr>
<tr>
<td>Mean GS start</td>
<td>May 14</td>
<td>April 14</td>
</tr>
<tr>
<td>Earliest GS start</td>
<td>April 30, 1998</td>
<td>March 30, 2010</td>
</tr>
<tr>
<td>Latest GS start</td>
<td>May 27, 2004</td>
<td>May 2, 2002</td>
</tr>
<tr>
<td>Mean GS end</td>
<td>October 1</td>
<td>October 25</td>
</tr>
<tr>
<td>Earliest GS end</td>
<td>September 22, 2010</td>
<td>October 15, 2010</td>
</tr>
<tr>
<td>Latest GS end</td>
<td>October 9, 2009</td>
<td>November 1, 2009</td>
</tr>
</tbody>
</table>

Figure 4.9 shows the relationship between annual NEP and the GS length, start date and end date at both sites. NEP had a significant relationship with GS length at the 90% CI ($p = 0.06$)
at OA but was not at OBS. The relationship at OA would have been stronger (the magenta line Figure 4.9a, slope = 9.1 g C m$^{-2}$ 365 days$^{-2}$, $R^2 = 0.59$, $p < 0.001$) if the exceptionally large negative NEP values (magenta asterisks in Figure 4.9) from the FTC defoliation (2016) and cold spring (2007) were removed. There was no significant relationship between annual NEP and GS start or end date at either site. If the large negative NEP values are removed then the relationship between NEP and GS start becomes significant (slope= -7.6 g C m$^{-2}$ y$^{-1}$ d$^{-1}$, $R^2 = 0.43$, $p = 0.001$), while removing these points has no impact on the relationship between annual NEP and GS end date. Since NEP is the difference between GEP and $R_e$, I investigated the impacts of GS length, start date and end date on annual GEP also as shown in Figure 4.10. The relationship significance for annual GEP and the GS length was opposite to that for NEP, with the relationship being significant ($p = 0.03$) at OBS and not significant at OA. Unlike NEP that saw no significant relationship with GS start at either site, GEP had a significant relationship with GS start at the 90% CI ($p = 0.07$) at OA but not at OBS. For both sites, there was no significant relationship between GEP and GS end date. Figure 4.11 shows the relationships between annual $E$, and GS length, start date and end date for OA and OBS. There were no significant relationships between annual $E$ and GS length, start date and end date. There was a trend at the 90% CI (slope = 5.3 g C m$^{-2}$ y$^{-1}$ d$^{-1}$, $R^2 = 13$, $p = 0.09$) at OA between GS GEP and GS length and a significant relationship (slope= -7.9 g C m$^{-2}$ y$^{-1}$ d$^{-1}$, $R^2 = 20$, $p = 0.03$) between GS GEP and GS start date but no relationship with GS end date. OBS had a significant trend between GS length (slope = 3.7 g C m$^{-2}$ y$^{-1}$ d$^{-1}$, $R^2 = 26$, $p = 0.02$) and GS GEP, and at the 90% CI there was a significant relationship with GS start date (slope = -3.2 g C m$^{-2}$ y$^{-1}$ d$^{-1}$, $R^2 = 17$, $p = 0.07$) and none with GS end date. Furthermore, no significant relationships between GS $E$, GS NEP, and GS length, start date, or end date were found at OA or OBS (results not shown).
Figure 4.9 Relationships between annual net ecosystem production (NEP) and GS length (a), GS start date (b), and GS end date (c) at Old Aspen (OA, filled red circles and red line) and Old Black Spruce (OBS, filled blue squares and blue line). If the large negative values at OA (magenta asterisks) resulting from the FTC defoliation in 2016 and the exceptionally cold spring in 2007 are removed the relationships are given by the magenta lines. Also shown are the linear regression equations when all points are included. The regression equations with the magenta points excluded are: (a) NEP = 9.1GSL - 1139.2, $R^2 = 0.59$; (b) NEP = -7.6GSS + 1146.8, $R^2 = 0.43$; (c) NEP = 3.0GSE - 684.7, $R^2 = 0.03$. Units of the slopes and intercepts are g C m$^{-2}$ y$^{-1}$ and g C m$^{-2}$ y$^{-1}$, respectively.
Figure 4.10 Relationships between annual gross ecosystem production (GEP) and growing season length (a), growing season start date (b), and growing season end date (c) at Old Aspen (OA, filled red circles and red line) and Old Black Spruce (OBS, filled blue squares and blue line). Also shown are the linear regression equations. Units of the slopes and intercepts are g C m\(^{-2}\) yr\(^{-1}\) d\(^{-1}\) and g C m\(^{-2}\) yr\(^{-1}\), respectively.
Figure 4.11 Relationships between annual evapotranspiration (E) and growing season length (a), growing season start date (b), and growing season end date (c) at Old Aspen (OA, filled red circles and red line) and Old Black Spruce (OBS, filled blue squares and blue line). Also shown are the linear regression equations. Units of slopes and intercepts are mm y$^{-1}$ d$^{-1}$ and mm y$^{-1}$, respectively.
4.4 Discussion

4.4.1 Climate Trends

Over the past three decades, the global averaged atmospheric CO$_2$ concentration has increased at a mean rate of 1.7 ppm y$^{-1}$ (IPPC, 2013). I have seen a similar trend in annual values at both sites, with a slope of 1.6 µmol mol$^{-1}$ at OA and 2.2 µmol mol$^{-1}$ at OBS (Figure 4.5), which are not significantly different from each other because the confidence intervals of the slopes overlap. Research has shown Northern Hemisphere land masses warming annually and for all seasons except winter, which has no significant trend or sometimes a negative trend, since 1987 (Cohen et al., 2012). For Canada, specifically, there has been observed an average warming of 1.4$^\circ$C with a stronger warming trend in the western continental region with an increase of 2.0$^\circ$C from 1950 to 2003 (Lempière et al., 2008). I have not seen a significant trend in warming of the GS (i.e., no increase in $T_a$ or $T_s$) at either site. While at the annual scale, I have seen a significant warming at OBS, and at the 90% CI at OA. The lack of a trend in GS temperature is consistent with research that has shown that from 1950-2010, using homogenized data from 338 climate stations across Canada, there is more warming in winter (2-3$^\circ$C) and spring (1-2$^\circ$C) compared to summer and fall (<1$^\circ$C) (Vincent et al., 2012; Bush et al., 2014). A warming climate can result in changes to the water balance. Despite the warming trend in annual $T_a$, I have seen no significant changes to $D$, $P$ or $\theta$. Unlike the temperature that had clear trends across Canada and in specific regions, trends in $P$ are weaker with only 21% of reference stations measuring significant increases in annual $P$, with it increasing in spring and fall at many sites, especially in western Canada, and showing decreasing winter $P$ (Mekis and Vincent, 2011).
4.4.2 Carbon and Water Fluxes

I have found no long-term trend in GS or annual GEP at OA but have seen an increasing trend in both GS and annual GEP at OBS. Contrary to our results, Keenan et al. (2013) found a significant ($p = 0.02$) decrease in GEP of 2.60% $y^{-1}$ from 1994 to 2003 in the black spruce site (NOBS) in the northern study area (NSA) of BOREAS. Similar to my results, Ohta et al. (2014) found that GEP increased from 2004 to 2007 but then decreased and remained constant from 2008-2011 in a Siberian larch (Larix sibirica) stand. Matching the trends in GEP, I found no trends in GS or annual $R_e$ at OA but found an increasing trend in both annual and GS $R_e$ at OBS. Despite the lack of trends in GEP and $R_e$ at OA, I observed decreasing trends in GS NEP at both sites. At NOBS for 1994 to 2003, Keenan et al. (2013) found a decreasing trend in NEP, but it was not significant. Baldocchi et al. (2017) reviewed FLUXNET sites with 5 or more years of measurements and found that interannual variations in NEP were more sensitive to climate and weather anomalies that drive photosynthesis than $R_e$, such that conditions that increase GEP from one year to another have a smaller (49%) impact in $R_e$. Previous studies (Black et al., 2000; Barr et al., 2004, 2007; Krishnan et al., 2008) showed the main climatic control of interannual variability in NEP at OA and OBS was spring temperature. Warm springs lead to quicker leaf out at OA, increasing absorbed $Q$ and the canopy leaf out duration, thus leading to increased annual GEP while having a small impact on $R_e$ (Chen et al., 1999; Black et al., 2000; Barr et al., 2004; Griffis et al., 2004). Unlike the previous studies that emphasized the importance of spring phenology, using 1996-2010 data from OA, Wu et al. (2012) found that 70 to 80% of interannual variability in annual NEP can be explained by a period they termed the autumn interval, which is the difference between the GEP derived end date and the C uptake derived end date.
During the long-term monitoring record, I was able to capture two disturbance events, the 2001-2003 drought and the 2016 FTC defoliation at OA. The drought caused both $R_e$ and GEP to decrease but the overall impact on NEP varied during the three drought years. The start of the drought had little effect on GEP but decreased $R_e$, leading to an increase in NEP, but as the drought became more severe, GEP decreased significantly (Barr et al., 2007; Krishnan et al., 2008). The drought persisted in western North America from 2000-2004 causing the C sink of this region to decline substantially, with the C sink strength decreasing by 30 to 398 Tg C y$^{-1}$ (Schwalm et al., 2012). The FTC defoliation event in 2016 at OA led to the most negative NEP on record (-72 ± 59 C m$^{-2}$ y$^{-1}$) due to the large decrease in GEP relative to the smaller decrease in $R_e$ (Stephens et al., 2018; see Chapter 2). A meta-analysis of 65 flux sites by Shao et al. (2015) found that biotic factors accounted for 57% of the variability in NEP compared to 43% for climatic factors.

No trends in GS $E$ or annual $E$ were detected at OA and OBS. GS $E$ at OA mostly comes from transpiration, with 5% of it coming from evaporation from the soil surface and about 6% from wet leaves (Blanken and Black, 2004; Krishnan et al., 2006). At 10 out of the 14 FLUXNET sites studied, Keenan et al. (2013) found a decreasing trend in ecosystem $E$. One of the four sites not showing the decreasing trend (for 1994 to 2003) was the northern black spruce site (NOBS) of the BOREAS NSA. Our observation of no trend in $E$ at OBS corresponds to that found at NOBS.

4.4.3 WUE and Water Balance

The response of ecosystem WUE depends on the tradeoff between water loss and C uptake. With increased atmospheric CO$_2$ concentrations across the globe, GEP is increasing, but without a significant increase in $E$, thereby increasing water use efficiency ($\text{WUE} = \text{GEP}/E$)
(Cheng et al., 2017), although this trend is not consistent across all biomes and latitudes (Keenan et al., 2013; Ohta et al., 2014). I found an increasing trend in annual WUE at OA but not at OBS. Keenan et al. (2013), using long-term EC measurements from FLUXNET sites, found an overall significant increase in WUE in temperate and boreal forests in the Northern Hemisphere over the past two decades. They also found there was no significant trend in daytime summer (JJA) WUE at NOBS from 1993-2004. The results of the current analysis agree with these findings since I found no significant trend in GS OA. At OA, the maximum value of WUE occurred in 2003 at the height of the 2001-2003 drought, when GS total $E$ was the fourth lowest on record, consistent with results from earlier studies observing increased WUE with increased drought stress (Krishnan et al., 2006; Baldocchi, 1997). Unlike at OA, maximum WUE at OBS did not occur during the drought but rather in 2014 with above average GS GEP and $E$. Ohta et al. (2014) observed decreasing WUE from 2004-2010 in their Siberian larch stand due to the $E$ increasing more than GEP in the early years and relatively constant $E$ and GEP in the later years. Others (e.g., Dekker et al., 2016; Frank et al., 2015) have found that EC data alone were not able to reliably determine the CO$_2$ concentration sensitivity of WUE because the data records were too short to detect significant changes in CO$_2$ concentration so they relied on longer time series of tree ring or C-isotope data. Cheng et al. (2017), using an analytical WUE model, found annual WUE at 11 sites with 6 years of continuous EC data to increase on average by 14.7 ± 9.0 mg C m$^{-2}$ (mm H$_2$O)$^{-1}$ y$^{-1}$ (0.0147 g C (kg H$_2$O)$^{-1}$ y$^{-1}$), which was consistent with the in situ observed mean trend of 12.6 ± 11.4 mg C m$^{-2}$ (mm H$_2$O)$^{-1}$ y$^{-1}$ (0.0126 g C (kg H$_2$O)$^{-1}$ y$^{-1}$) at the same sites. Both the modelled and observed trends in WUE reported by Cheng et al. (2017) are less than the observed rate of increase in GS WUE at OBS.
4.4.4 Impact of Start, End and Duration of Growing Season on C and Water Fluxes

OA and OBS showed no significant trend in any of the GS metrics, i.e., GS length did not increase and starting or end dates did not occur earlier or later, respectively. Similarly, Dunn et al. (2007) did not observe an increase in GS length at NOBS. Dietrich et al. (2016) found an increase in GS length from 1902 to 2007 at a boreal jack pine stand in Ontario. Barichivich et al. (2013) found a long-term advance in GS start in North America since 1950 but the start of the thermal GS (day when air temperature rises to 5 °C in spring) or photosynthetic GS (day when NDVI reaches a local threshold for maximum green-up rate) has not changed significantly since 1982, while GS end has been delayed between 4 and 6 days since 1982. I found a significant relationship between NEP and GS length at the 90% CI at OA but not at OBS. I found no significant relationships between NEP and GS start or end at either site, but when large negative values of NEP at OA are removed, the relationship between NEP and GS start becoming significant and the relationship with GS length becomes even stronger. This agrees with the results of Dunn et al. (2007) who found no correlation between GS length and net uptake at NOBS. At NOBS, Goulden et al. (1997) found that earlier thaws can decrease C sequestration due to increased $R_e$. Baldocchi et al. (2001) reported that for conifer forests in North America, only latitude and position on a continent were significant in determining seasonal changes in CO$_2$ exchange.

4.5 Conclusions

1) There were increasing trends in GS CO$_2$ concentration and decreasing trends in GS $Q$ at both sites, along with an increasing trend in GS $\theta$ at OA. There were no trends in GS $T_a$, $T_s$ and $D$ at both sites. Annual trends in climate included increasing CO$_2$
concentration, $T_s$ and $T_a$ at both sites and decreasing $Q$ at OBS. At both sites there was no trend in annual $D$.

2) Increasing trends in GS GEP and $R_e$, with a faster increase in $R_e$, led to a significant decrease in GS NEP at OBS. This was also true at the annual scale. A significantly decreasing trend in NEP at OA was the result of a weak decline in GEP being greater than that in $R_e$. No annual trends in C fluxes (GEP, $R_e$ and NEP) were observed at OA.

3) Although no trends in GS or annual $E$ at either site were observed, there was a significant decrease in annual WUE at OA due to the weak decline in GEP, and a significant increase in GS WUE at OBS due to the significant increase in GS GEP. There were no trends in GS or annual $P - E$ at either site since there were no trends in both GS and annual $P$ and $E$.

4) There were no trends in GS start date, end date, and length at either site. Of the three GS metrics, only GS length was important when looking at all the available observations. It was significantly related to GEP at OBS and NEP at OA. There were no significant relationships between $E$ and these metrics at either site.

5) Over the study period, the relatively small proportion of $R_e$ occurring in the non-growing season (17% and 10% at OA and OBS, respectively) resulted in the annual NEP being 30% of the GS values at both sites. GS WUE at OA was 6% higher than at OBS reflecting the 29% higher GEP and 21% higher $E$ at OA than at OBS. Annual $P - E$, which is a good estimate of site runoff, was 97 and 193 mm at OA and OBS, respectively.
Chapter 5: Surface Conductance Modelling Using Two Decades of Eddy-Covariance Measurements in Boreal Black Spruce and Aspen Stands

5.1 Introduction

Boreal forests have a significant effect on water, energy and C budgets of the Northern Hemisphere (Arain et al. 2004; Bonan et al., 2008). For modeling current and future water, energy, and CO₂ exchange between vegetation and the atmosphere, parameterisation of canopy conductance ($G_c$) is vital. A recent study of $E$ from 12 Canadian EC sites found that in five boreal coniferous sites, the stomatal conductance term of the Penman-Monteith equation was the key to determining the actual $E$ (Brümmer et al. 2012). Commonly used stomatal conductance models applied to larger spatial scales are semiempirical, because they are founded on physiological theory but require empirical or mathematical simplifications (Franks et al., 2017).

The first type of stomatal conductance model was a multiplicative function introduced by Jarvis (1976). The model adjusts the reference conductance, a measured, usually maximum, value of canopy conductance ($G_{c_{max}}$), according to changes in the controlling environmental variables e.g., photosynthetically active radiation ($Q$), leaf temperature ($T_o$), vapor pressure deficit ($D$), leaf water potential and ambient CO₂ concentration. Stewart (1988) compared four surface conductance models, and for the Jarvis model replaced leaf water potential with soil water deficit. He defined soil water deficit as the difference between the saturated soil water content and the average soil water content in the top metre of soil. It then became common to use the Jarvis–Stewart approach to estimate $G_c$ using independent multiplicative functions (Stewart, 1988; Kelliher et al., 1995) expressed as follows:

$$G_c = G_{c_{max}} f(LAI) f(Q) f(T_o) f(D) f(\theta) \ldots \; (5.1)$$
where $LAI$ is the leaf area index, $T_a$ is the air temperature at the reference level, and $\theta$ is the volumetric soil water content. Much work has been done to derive and parameterize these functions, e.g., Saugier and Katerji (1991), Kelliher et al. (1995), Dolman et al. (1991), for $Q$. One of the criticisms of multiplicative models is that they assume the impact of environmental variables on $G_c$ are independent and do not consider the influence of leaf physiology (Wang et al., 2009). Multiplicative models also do not consider feedbacks between the conductance and the surface energy balance or the changes internally in the leaf.

At approximately the same time as the introduction of the multiplicative model, progress was being made on understanding the relationship between plant physiology and environmental variables. Among plant physiologists and ecologists it was generally assumed that stomata evolved to provide a way to limit water loss from plants during photosynthesis (Meidner and Mansfield, 1968); however, for many years there was considerable uncertainty about the extent of control stomata could exert (Mansfield, 2004). The firm physical basis of theories of diffusion of CO$_2$ and water vapour through the stomata came from Brown and Escombe (1900) and Penman and Schofield (1951). From the latter work, Gaastra (1959) determined exchange rates of water vapour from leaves under different environmental conditions and was able to identify stomatal and internal resistances. Based on his findings, the first leaf gas exchange models were fashioned as analogues of electrical resistances (Von Caemmerer, 2000). Not until Cowan (1977) and Cowan and Farquhar (1977) proposed the optimization theory, that stomata tend to maximize leaf C gain while minimizing water loss through transpiration, did it become clearly defined. The biochemistry of photosynthetic C assimilation, through electron transport and enzyme kinematics, was integrated in a compatible form with studies of gas exchange in leaves by Hall and Björkman (1975) and Berry and Farquhar (1978). Work by Wong et al. (1979)
demonstrated the capacity of the mesophyll tissue to fix C determined the stomatal aperture, and thus the conductance correlates to the photosynthetic capacity. It is common to use the photosynthesis model of Farquhar et al. (1980) modified by Farquhar and Von Caemmerer (1982) which describes the limiting factors and feedbacks on assimilation rate under various conditions (Farquhar and Sharkey, 1982) or the optimization theory first proposed by Cowan (1977) and Cowan and Farquhar (1977).

With this foundation of work came the empirical Ball-Woodrow-Berry (BWB) model (Ball et al., 1987). The model is based on stomatal conductance being linearly related to the product of leaf net photosynthesis rate and leaf surface relative humidity, and inversely related to CO₂ concentration at the leaf surface, as indicated by the following equation:

$$g_s = kA \frac{h_s}{c_s}$$  \hspace{1cm} (5.2)

where $A$ is the assimilation rate, $h_s$ is the relative humidity at the leaf surface and $c_s$ is the CO₂ mole fraction at the leaf surface (Ball et al., 1987). Some workers argue that rather than $h$, stomatal conductance is driven more by the vapour pressure deficit (Leuning et al., 1995; Monteith, 1995). In their paper, Leuning et al. modified the BWB model to use vapour pressure deficit and two parameters, which made model parameterization more complex. However, this type of stomatal conductance model requires fewer tuning parameters than multiplicative models. This model was initially developed from direct measurements of conductance at the leaf level in a laboratory-controlled environment. Applying it to a canopy becomes complex due to the heterogeneity of canopy structure, leaf physiology and spatial variation in the canopy microclimate. Upscaling from leaf to canopy, models requires simplifications and assumptions that can lead to significant uncertainties.
Despite using similar environmental variables, the two models can produce substantially different values because of the way they parameterize environmental stress factors, specifically soil water deficit (Gash & Shuttleworth, 2007). The relationships that determine the coefficients in each model are highly dependent on parameterizations based on observations. This brings up the issue of varying timescales altering the parameterizations. How these relationships change seasonally, annually, and up to decadal scales is important to understand, and, if possible, include in the models.

In this chapter, I compare the application of the Jarvis-Stewart (JS) and modified Ball-Woodrow-Berry (MBWB) models at OA and OBS. These specific models and variations of these models have been applied at OA and OBS but using only small amounts of data, ranging from days to a couple of years (Wu et al., 2000; Blanken and Black, 2004). Here, I use 22 years of half-hourly measurements (1996-2017) at OA and 19 years (1999-2017) at OBS made in rain-free conditions year-round. Parameterization of these functions become of increasing value as we know that CO$_2$ concentration has risen approximately 52 µmol (mol of dry air)$^{-1}$ from 1996 to 2017 at OA and 43 µmol (mol of dry air)$^{-1}$ from 1999 to 2017 at OBS (Chapter 4). On a global scale the annual average CO$_2$ concentration has risen 1.7 µmol (mol of dry air)$^{-1}$ y$^{-1}$ from 1980 to 2011 (IPCC, 2013) with the rate of increase higher in 2002-2011 than any previous decade since direct measurements began in 1958 and is projected to increase steadily into the future (IPCC, 2013).

5.2 Materials and Methods

5.2.1 Site Description

The OA and OBS sites are located near the southern edge of the boreal forest in Saskatchewan in the Boreal Plains ecozone. OA is a mature deciduous broadleaf forest located in
Prince Albert National Park (53.62889°N, 106.19779°W, WGS-84). OBS is a mature evergreen forest located approximately 100 km NE of Prince Albert, near White Swan Lake (53.98 °N, 105.12°W). Both sites have uniformly aged stands that regenerated after natural fires in 1919 at OA and 1879 at OBS (Barr et al., 2012). OA is dominated by trembling aspen (Populus tremuloides Michx.) with a scattered (~10%) balsam poplar (Populus balsamifera L.) overstory and a hazelnut (Corylus cornuta Marsh.) understory, while OBS consists of black spruce (Picea mariana) with a sporadically distributed tamarack (Larix laricina Du Roi) overstory and a sparse understory of shrubs such as Ledum groenlandicum Retzius and Vaccinium vitisidaea L. The stand heights are 21 m and 14 m respectively and are highly coupled to the atmosphere with decoupling coefficients (Ω) of 0.13 and 0.15, respectively at OA and OBS (Brümmer et al. 2012). The Orthic Gray Luvisol (Typic Cryalf) soil at OA has a forest-floor consisting of an 8-10 cm thick LFH (litter-fermented-humic) layer beneath which is a 30-cm-thick silt loam layer over glacial till (Padbury et al. 1978; Barr et al., 2012). The soil is moderately well drained with high available soil water storage capacity in the root zone, and the water table depth is approximately 3 m (Kljun et al., 2006). The soil at OBS is a Peaty Orthic Gleysol with a 20-30 cm thick forest-floor comprising hummocky peat (Sphagnum spp.) in wet areas and feather mosses (Hylocomium Splendens) and lichens (Cladina spp.) in drier areas (Arain et al., 2002). This peat is above a waterlogged sandy clay with poor drainage and a shallow water table that ranges between 0 and 1 m below the surface. The terrain is generally level at OA while OBS has a slight slope (< 2°) from north to south. The sites have a uniform fetch of 3 km in all directions and 1.2 km in the prevailing wind directions, respectively, for OA and OBS. Flux footprints (90%-isopleth along the dominant wind direction) under convective conditions were typically 450-550 and 200-300 m during stable and 900 and 500 m for neutral conditions at OA and OBS, respectively (Kljun et
Both the daytime and nighttime flux footprints at each site were significantly within the uniform fetch around the towers.

5.2.2 Climate Measurements

Air temperature was measured at a height of 37 m at OA and 25 m at OBS with temperature/humidity sensors (model HMP45C, Vaisala Oy, Finland) enclosed in aspirated radiation shields (model 076B, Met-One Instruments Inc., Grants Pass, OR). Air temperature was also measured at the height of 36 m at OA and 24 m at OBS with a platinum resistance thermometer (PRT) and a 36-gauge chromel-constantan thermocouple (Omega Engineering Inc., Laval, Quebec), both enclosed in aspirated radiation shields. Shortwave and longwave radiation were measured with paired pyranometers (model CM11, Kipp & Zonen BV, Delft, The Netherlands) and paired pyrgeometers (model PIR, Eppley Laboratory, Newport, RI, USA) at 36-m (downwelling) and 30-m (upwelling) heights at OA and 25-m (downwelling) and 20-m (upwelling) heights at OBS. At the same heights, upwelling and downwelling components of photosynthetically active radiation (PAR) were measured with paired quantum sensors (model LI-190SA, LI-COR Inc., Lincoln, NE). Precipitation was measured using both a tipping bucket rain gauge (model TR-525, Texas Electronics Inc., Dallas, TX, USA or model CS700, Campbell Scientific Inc. (CSI), Logan, UT, USA) and a weighing rain gauge (model 3000 with an Alter shield, Belfort Instruments, Baltimore, MD, USA or a model T-200B3, Geonor, Augusta, NJ, USA). At OA, the precipitation gauges were located in the center of a natural clearing approximately 50 m northeast of the tower on a raised platform at a height of ~2 m, while at OBS the weighing gauge was mounted on top of the instrument hut (height of 3.5 m) to reduce under-catch with high wind speeds. In winter, antifreeze was added to prevent freezing and in summer, motor oil was added to minimize evaporative losses from the weighing rain gauges. At
both sites, two profiles of soil temperature ($T_s$) at six depths (2, 5, 10, 20, 50, and 100 cm) were measured with copper-constantan thermocouples. At OA, $\theta$ was measured using two profiles of soil water reflectometers (model CS 615, Campbell Scientific Inc.) at the depths of 2.5, 7.5, 22.5, 45 and 60 cm along with TDR probes (Moisture Point type B, Gabel Corp., Victoria, Canada) at depths of 0-15, 15-30, 30-60, 60-90, and 90-120 cm. At OBS, $\theta$ was measured using two profiles of soil water reflectometers (model CS 615, Campbell Scientific Inc.) at the depths of 2.5, 7.5, 22.5, 45 and 60 cm.

5.2.3 Eddy-Covariance Flux Measurements

Eddy-covariance (EC) measurements of fluxes of water vapour, CO$_2$, and sensible heat were made half hourly at 39 and 27 m above ground for OA and OBS, respectively. The fluxes were measured using tri-axial sonic anemometers (model R2 (1996-1999) or R3 (1999- present) Gill Instruments Ltd., Lymington, UK) and closed-path, temperature-controlled infrared gas (CO$_2$/H$_2$O) analyzers (model LI-6262 or LI-7000, LI-COR Inc.). A diaphragm pump (model DOA-V191-AA, Gast Inc., Dayton, OH) pulled air through a heated sampling tube (4 m length; 4 mm inner diameter) at a flow rate of 10 L min$^{-1}$ for the LI-6262 and 15 L min$^{-1}$ for the LI-7000 (Krishan et al., 2006; Barr et al., 2007, 2012). Calibrations to correct CO$_2$ concentration measurements for zero and span shifts were implemented daily and automatically using CO$_2$ standard gases from the Greenhouse Gases Measurement Laboratory (GGML) of Environment and Climate Change Canada in Downsview, ON, Canada (Krishnan et al., 2006). Heated sample tubes were replaced every 6-12 months to improve the response times in H$_2$O and CO$_2$ sampling that become reduced due to buildup of dust, pollen, smoke particles or condensation in the tubing. Half-hourly fluxes were measured at 20 Hz, calculated following Webb et al. (1980), and stored directly on the computers located at the sites. Further details on the experimental setup,
calibrations and calculations of fluxes can be found in Arain et al. (2002), Griffis et al. (2003), Barr et al. (2004), Krishnan et al. (2006; 2008), and Zha et al. (2010).

5.2.4 **Data Processing and Quality Control**

Daily checks of measurements and calibrations were performed as part of a quality control/assurance routine using Matlab (Version 8.5, The Mathworks, Natick, MA, USA). After being received the raw data went through three stages of cleaning before being used in calculations. In the first stage, faulty measurements were removed; in the second those values were replaced by the best available alternative measurement from the other repetitive on-site instruments, and lastly gaps are filled with temporal interpolation or based on diurnal variations. In the final stage the gross ecosystem production (GEP) was calculated.

The total uncertainty in the annual fluxes was calculated after following three steps: (1) for each half hour flux random error was estimated by adding 20% random error per half hour following Morgenstern et al. (2004); (2) uncertainty from gap-filling was examined by deleting up to 40% of the data annually, with gaps produced by a uniformly discrete random number generator which created 500 randomly selected gaps of lengths ranging from on half hour up to 480 half hours, i.e. 10 days of data; and (3) systematic bias generated from the choice of $u^*$ threshold was calculated by altering the threshold by $\pm$ 20% from the chosen 0.35 m s$^{-1}$ threshold and then recalculating the fluxes to determine the impact to the annual values.

Estimates of sensible ($H$) and latent heat ($\lambda E$) fluxes using a moving window based on Amiro et al. (2006) were used for gap filling $E$ in step 2. For $H$ and growing season daytime $\lambda E$, a regression was developed with net radiation ($R_n$) – soil heat flux ($G$) based on a 240 half-hour moving window moved by 48 half-hour increments. Non-growing season ($T_a$ and $T_s < 0^\circ C$) daytime $\lambda E$ half hours were gap-filled using the average value from the previous and following 5
days. The total random error calculated from the sum of squares of the errors from step 1 and 2 were ± 6 mm year\(^{-1}\) and ± 7 mm year\(^{-1}\) for OA and OBS, respectively. The systematic error from step 3 was ± 2 mm year\(^{-1}\) at OA and ± 1 mm year\(^{-1}\) at OBS. The total estimated uncertainty, the sum of the random and systematic errors, was ± 9 mm year\(^{-1}\) and ± 8 mm year\(^{-1}\) for OA and OBS, respectively.

Data were filtered to obtain rain-free periods to calculate daytime growing season values for model parameterization but then models were applied year-round for rain-free conditions. To determine rain free periods, rain events (precipitation >0.1 mm) and the next 24 hours were removed. Then data were filtered for days with sufficient light (photon flux density > 200 \(\mu\)mol m\(^{-2}\) s\(^{-1}\)) (Blanken and Black, 2004; Krishnan \textit{et al.}, 2006). This was necessary to restrict to the periods of physiological controls of water vapour fluxes, i.e. to those dominated by transpiration. The growing season was defined following Wu \textit{et al.} (2013) where the growing season start and end were the days when the smoothed daily GEP had reached 10\% of the annual maximum smoothed GEP. This allowed the GEP threshold to vary between sites and annually rather than using a fixed value (Wu \textit{et al.} 2012). Daily GEP was smoothed using a local regression using a 1st degree polynomial model and weighted linear least squares that assigns lower weight to outliers in the regression. This method leads to a similar fit as spline smoothing used by Richardson \textit{et al.} (2010) to find the GS start and end.

5.2.5 Calculation of Canopy Conductance

By rearranging (or inverting) the Penman-Monteith (P-M) equation, the following expression for calculating half hourly \(G_c\) (m s\(^{-1}\)) (Jarvis and McNaughton, 1986) is obtained

\[
\frac{1}{G_c} = \frac{\rho C_p D}{\gamma A E} + \frac{1}{G_a} \left[ \frac{s}{\gamma (\lambda E)} - 1 \right] - 1
\]

(5.3)
where $\lambda$ is the latent heat of vaporization (J kg$^{-1}$), $A$ is the available energy flux (W m$^{-2}$) ($= R_n - G$), $\rho$ is the air density (kg m$^{-3}$), $c_p$ is the specific heat of air (J kg$^{-1}$ K$^{-1}$), $s$ is the slope of the saturation water vapour pressure versus air temperature curve (kPa °C$^{-1}$), $\gamma$ is the psychrometric constant (kPa °C$^{-1}$), $D$ is the vapour pressure deficit (kPa) and $G_a$ is the aerodynamic conductance (m s$^{-1}$) for sensible heat and water vapour transfer. $G_a$ is given by:

$$\frac{1}{G_a} = \frac{u}{u^*} + \frac{1}{ku_s}(2 + \psi_m - \psi_h)$$  \hspace{1cm} (5.4)

where $u$ is the wind speed (m s$^{-1}$), $u^*$ is the friction velocity (m s$^{-1}$), $k$ is the von Karman constant ($= 0.4$) and $\psi_m$ and $\psi_h$ are the integral diabatic correction factors for momentum and sensible heat transfer, respectively. A coefficient of 2 is the value of $kB^{-1}$ (where $B$ is the sub-layer Stanton number) recommended for all vegetated surfaces by Garratt (1978) and Hicks et al. (2018).

5.2.6 Jarvis-Stewart Conductance Model

After obtaining the measured $G_c$ values, from the P-M equation, the modeling of $G_c$ began with the Jarvis-Stewart model. $G_c$ was modeled using Eq 5.1, with some of the multiplicative coefficients of the controlling variables currently set to the optimum value of 1. For both sites, the $\theta$ coefficients were set to the optimum, with this being the case for the $T_a$ function as well at OA. The value of $G_{c_{max}}$ used for OA was 32.6 mm s$^{-1}$ (Wu et al., 2000) and 9 mm s$^{-1}$ at OBS (Arain et al., 2003). These values were confirmed as appropriate values from a review of the data used in this analysis. These are similar to values used at other deciduous broadleaf sites (37 mm s$^{-1}$ Matsumoto et al. (2008)) and conifer sites (16 mm s$^{-1}$ Matsumoto et al. (2008)). Using Eq 8.12 from Pearcy et al. (1989) to convert conductances from cm s$^{-1}$ to
molar units, when pressure and temperature are known, provides the conversion: $1 \text{ mm s}^{-1} \approx 41 \text{ mmol m}^{-2} \text{s}^{-1}$.

For the $G_c$ response to $D$ the exponential equation being utilized comes from Wu et al. (2000):

$$f(D) = \exp(-k_1 D)$$  \hspace{1cm} (5.5)

where $k_1$ is a fitting parameter, $D$ (kPa) is $D$ at the surface and is calculated as $D = \frac{\gamma \frac{LE}{\rho c_p G_c}}{}$ (Blanken et al., 1997). The photosynthetically active radiation function is based on a Michaelis-Menten (i.e., rectangular-hyperbolic) function:

$$f(Q) = \frac{Q_p}{Q_p + K_q}$$ \hspace{1cm} (5.6)

where $K_q$ is the value of $Q$ at which the $G_c$ is half its maximum value. The influence of air temperature is described using a beta function as presented in Stewart (1988). The function contains three temperatures: the maximum and minimum temperatures ($T_{max}$ and $T_{min}$) when $f(T_a) = 0$ and the optimal temperature ($T_{opt}$) where $G_c$ is at a maximum:

$$f(T_a) = \frac{(T-T_{min})(T_{max}-T)^\beta}{(T_{opt}-T_{min})(T_{max}-T_{opt})^\beta}$$ \hspace{1cm} (5.7)

where $\beta$ is given by $(T_{max} - T_{opt})/(T_{opt} - T_{min})$. The function to capture the influence of soil moisture was that of Matsumoto et al. (2008)

$$f(\theta) = \frac{(\theta-\theta_{min})(\theta_{max}-\theta_{min}+k_2)}{(\theta_{max}-\theta_{min})(\theta-\theta_{min}+k_2)}$$ \hspace{1cm} (5.8)

where $\theta_{min}$ and $\theta_{max}$ are the minimum and maximum observed $\theta$ values, respectively, and $k_2$ is a fitting parameter. The impact of changing LAI is considered at OA following Wu et al. (2000):

$$f(\Lambda) = \frac{\Lambda}{\Lambda_{max}}$$ \hspace{1cm} (5.9)

where $\Lambda$ (leaf area index) is calculated using the relationship between $\Lambda$ and the ratio of $Q$ to shortwave irradiance derived for OA by Barr et al. (2004). $\Lambda_{max}$ is the maximum $\Lambda$ observed.
value from the rlowess smoothed calculated $\Lambda$. Among the parameters in Eqs (5.5)-(5.9), $k_1, K_q$ and $T_{opt}$ are obtained by optimization using non-linear least squares analysis on the growing season (GS) data using a Matlab (Version 7.5, The Mathworks, Natick, MA, USA) program.

5.2.7 Modified BWB Conductance Model

The second model tested is a modified version of the Ball-Woodrow-Berry (BWB) model. The BWB model for stomatal conductance (Eq 5.2) applied to the canopy scale, as presented by Sellers et al. (1996) becomes

$$G_c = m_1 \frac{A_0}{c_0} h_0 + b_4$$

(5.10)

where $A_0$ is the rate of net CO$_2$ assimilation (µmol m$^{-2}$ s$^{-1}$), $h_0$ is the relative humidity at the leaf surface (unitless ratio), $c_0$ is the mole fraction of CO$_2$ at the surface calculated from $c_0 = c_a - (A_0/G_a)$ (µmol mol$^{-1}$), $m_1$ (mmol mol$^{-1}$) and $b_4$ (mmol m$^{-2}$ s$^{-1}$) are the slope and intercept, respectively, obtained from the linear regression analysis of measured $G_c$ against the BWB index ($A_0 h_0/c_0$). The zero subscript refers to the reference surface for the big-leaf model approach. The traditional BWB model was not tested since Wu et al. (2000) reported a higher explanation of the variance in $G_c$ at OA and another conifer site with the Modified BWB (MBWB) than the traditional model. The modified model from Lloyd (1991) replaces the relative humidity at the surface with the reciprocal of $\Delta e_0$, the saturation deficit at the surface (expressed as a mole fraction), and is written as:

$$G_c = m_2 \frac{A_0}{\Delta e_0 c_0} + b_4$$

(5.11)

In this analysis gross ecosystem productivity (GEP) is used as a proxy for $A_0$. 


5.2.8 Model Calibration and Validation

Model calibrations and validations were performed using a Monte Carlo simulation by using a random number generator to choose approximately half of the data (11 years at OA and 9 years at OBS) to obtain the coefficients in the calibration stage and test the coefficients on the remaining data for the validation stage (11 years of data for OA and 9 years for OBS as in Figure 5.4). This process was repeated 500 times at each site, for each model. The coefficients from the best fit, determined by the combination of the highest slope, lowest intercept, highest $R^2$ and lowest RMSE value of the measured vs. modeled comparison, were selected and used to test the model for individual years (grey lines in Figure 5.4).

To test for the impact of the hysteretic response of $G_c$ to climate variables, the models were run splitting the data into morning (before 12 pm) and afternoon (after 12 pm) to obtain a set of coefficients for each period.

5.3 Results

5.3.1 Model Parameterization

Aspen is known for its stomatal response to $D$ (Baldocchi et al., 2014). Just as Blanken et al. (1997) found in 1994, I found that the exponentially decreasing response of $G_c$ to $D$ has a tendency to overestimate $G_c$ at lower $D$ and underestimate $G_c$ at higher $D$ at OA (Figure 5.1a,b). The $D$ modifier derived by Wu et al. (2000) is similar to the one derived by Baldocchi et al. (2014) in that both cause $G_c$ to be halved as $D$ rises from 0.5 to 2.5 kPa. The fitted parameter $k_1$ from Eq. 5.5 was found to be lower than -0.645 found by Wu et al. (2000) for OA. The data for studying the relationship between $G_c$ and $Q$ were divided into two periods: before noon and afternoon to capture the variability in the response to changing light conditions. The $K_q$ obtained for each of the periods is higher than 430 reported by Wu et al. (2000) for OA. The discrepancies
may be due to the limited data set (only 154 days during 1994 and 27 days during 1996) in Wu et al. (2000), compared to the decade of data used in this analysis that encompass a larger range of climatic variability including the three-year drought. Eq 5.7 was set to the optimality ($f(T_a) = 1$) because the effect of temperature was negligible, due the strong correlation between $D$ and $T_a$ (Wu et al. 2000). Using 12 Canadian flux sites, including OA and OBS, Brümmer et al. (2012) found SWC did not strongly control $G_c$ on a monthly or annual bases at the forest sites. They also found mean annual and GS daytime rain-free $G_c$ were controlled by $D$ and $R_n$. A linear relationship between $G_c$ and $\Lambda$ was used because Blanken et al. (1997) showed this relationship to be valid for dry-canopy conductance at OA. $\Lambda_{max}$ in Eq. 5.9 was calculated from the observations and varied from year to year for individual year model testing, unlike Wu et al. (2000) who had a $\Lambda_{max}$ set at 2.3 m$^2$ m$^{-2}$ for OA during their model testing period. In boreal, cool- and warm-temperate locations in Siberia and Japan, Matsumoto et al. (2008) used different $f(Q)$ and $f(D)$ functions to test the JS model at deciduous broadleaf and evergreen conifer forests. Rayment et al. (2000) modelled stomatal conductances and compared them to individual shoot, whole branches and the whole ecosystem conductance measurements at OBS; finding that the MBWB model accounted for more variation than the JS model but neither accounted for more than 41% of the variation. Their JS model included a Michaelis-Menten function and beta temperature function as used here, but their humidity response was a linear decrease in conductance with increasing $D$. 
Figure 5.1 Empirical relationship between measured (i.e., inversion of P-M equation) rain-free $G_c$ and $D$ (a,b) and between $G_c$ and $Q$ (c,d) for the Old Aspen (OA) and Old Black Spruce (OBS) stands for 11 years and 9 years, respectively. A mean $G_c$ was calculated for binned $D$ values in 0.25 kPa intervals (morning (red) $n=15$ and afternoon (green) $n=12$ for OA and $n=20$ for OBS). A mean $G_c$ was calculated for $Q$ values binned in 200 µmol m$^{-2}$ s$^{-1}$ intervals (morning $n=10$ and afternoon $n=9$ for OA and $n=10$ for OBS). Vertical lines represent ± one standard deviation from the mean. Also shown are the equations for $G_c/G_{c_{max}}$. 

$G_c/G_{c_{max}} = \exp (-0.46D) \quad R^2 = 0.93$

$G_c/G_{c_{max}} = \exp (-0.40D) \quad R^2 = 0.56$

$G_c/G_{c_{max}} = Q/(Q + 178.89) \quad R^2 = 0.48$

$G_c/G_{c_{max}} = Q/(Q + 385.84) \quad R^2 = 0.83$

$G_c/G_{c_{max}} = Q/(Q + 5.21) \quad R^2 = 0.38$
The parameters needed to run the MBWB model were obtained by linear regression of measured $G_c$ (mmol m\(^{-2}\) s\(^{-1}\)) on the MBWB index ($\mu$mol m\(^{-2}\) s\(^{-1}\)/(kPa mol CO\(_2\) (mol air)\(^{-1}\)). At OA, the linear regression fit to the data was $G_c = 0.028$ MBWB + 157.44 mmol m\(^{-2}\) s\(^{-1}\) with $R^2 = 0.88$ (Figure 5.2a). Wu et al. (2000) obtained a linear regression of $G_c = 0.038$ MBWB + 142.9 mmol m\(^{-2}\) s\(^{-1}\) at OA using 154 days of data from 19 April-19 September 1994. Some of the difference in the slope and intercept in this study compared to theirs could be due to 1) their MBWB indices were calculated by subtracting the measured EC CO\(_2\) flux at 39-m height from that at the 4-m height (to obtain aspen canopy conductance characteristics), which was not done here since there was no measurement at 4-m height for the entire measurement period used in this analysis, 2) their mean $G_c$ values were calculated at binned MBWB index values of 750 $\mu$mol m\(^{-2}\) s\(^{-1}\)/(kPa mol CO\(_2\) (mol air)\(^{-1}\)) intervals, whereas I used a fixed number of samples per bin (i.e., 500), and despite this difference I have 3 times as many samples ($n = 61$ for OA and $n = 69$ for OBS) in our plots as in their Figure 4. Blanken and Black (2004) found the relationship between aspen $G_c$ and the MBWB index to be $G_c = 0.035$ MBWB + 135.6 mmol m\(^{-2}\) s\(^{-1}\) at OA using half-hourly data from 1 June - 15 September 1994 ($n = 1717$). The difference from the results in this analysis could be due to 1) mine being the total canopy conductance including the hazelnut understory while theirs is only the aspen $G_c$, and 2) their mean $G_c$ values were calculated using MBWB index bin intervals of 750 $\mu$mol m\(^{-2}\) s\(^{-1}\)/(kPa mol CO\(_2\) (mol air)\(^{-1}\)). At OBS, the linear regression was $G_c = 0.031$ MBWB + 96.05 500 mmol m\(^{-2}\) s\(^{-1}\) with $R^2 = 0.94$ (Figure 5.2b). The parameters needed to run this model at both sites are presented in Table 5.1.
Figure 5.2 Empirical relationship between measured rain-free $G_c$ and the Modified Ball-Woodrow-Berry index ($MBWB = A_0/\Delta e_0 c_0$) (symbols defined in text) for a) Old Aspen (OA) and b) Old Black Spruce (OBS) stands for 11 and 9 years, respectively. Mean $G_c$ values were calculated for binned MBWB index values at 500 point intervals ($n= 61$ for OA and $n= 69$ for OBS). Vertical lines represent ± one standard deviation from the mean.

Table 5.1 Fitted parameter values for the Jarvis-Steward (JS) and the Modified Ball-Woodrow-Berry (MBWB) models at Old Aspen (OA) (morning and afternoon for JS) and at Old Black Spruce (OBS).

<table>
<thead>
<tr>
<th>Site</th>
<th>$k_1$</th>
<th>$K_q$ (µmol m$^{-2}$ s$^{-1}$)</th>
<th>$G_{\text{max}}$ mmol m$^{-2}$ s$^{-1}$</th>
<th>$m_2^*$ mmol m$^{-2}$ s$^{-1}$</th>
<th>$b_4$ mmol m$^{-2}$ s$^{-1}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>OA morning</td>
<td>-0.46</td>
<td>385.84</td>
<td>32.6</td>
<td>1340</td>
<td>0.028</td>
</tr>
<tr>
<td>OA afternoon</td>
<td>-0.40</td>
<td>178.89</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>OBS</td>
<td>-0.43</td>
<td>5.21</td>
<td>9</td>
<td>370</td>
<td>0.031</td>
</tr>
</tbody>
</table>

* The units of $m_2$ are mmol m$^{-2}$ s$^{-1}$/µmol m$^{-2}$ s$^{-1}$/(kPa mol CO$_2$ (mol air)$^{-1}$)
5.3.2 Model Performance at the Half-Hour Scale

The JS and MBWB models were run to find half-hourly values of $G_c$ from the measured environmental variables at OA and OBS. Figure 5.3 compares the calculated and measured diurnal $G_c$ values ensemble-averaged from 1996-2017 for OA and 1999-2017 for OBS for the months of May to September. MBWB estimated $G_c$ values were converted to mm s$^{-1}$ for direct comparison with JS model estimates and measurements. At OA, the highest $G_c$ is reached shortly after sunrise and decreases steadily through the rest of the day as $D$ increases and $Q$ decreases with sunset (Blanken and Black, 2004). In May at OA, the values of the modelled $G_c$ from the MBWB were significantly larger than the measured, especially in the later part of the day (18-22h CST) when the modelled values were 2 times greater than the measured. The JS values matched the measured values fairly closely, except for the delayed and slower rise in $G_c$ in the mornings, which became greater than the measured at 7h and slightly elevated until 11h. This feature of a delayed and slower rise in the JS modelled $G_c$ was present across all months at OA.

Using a simple JS approach based on $D_0$ and $Q$, Blanken and Black (2004) found that the diurnal pattern of the measured $G_c$ was represented well in the modelled $G_c$ but the model tended to overestimate $G_c$ when $D_0$ was low. For the MBWB modelled $G_c$, they found an overestimation of $G_c$ in the early morning with a tendency to underestimate the mid-day $G_c$. Wu et al. (2000) found that the models underestimated $G_c$ in May, but for the full-leaf period (June to August), the models agreed well with the measured values with JS model values being larger than both the MBWB and BWB models. During the full-leaf period, I observed that the JS model obtained the highest peak $G_c$ in each month at OA but then decreased, causing the measured $G_c$ to have larger values during mid-day in July (13.96 mm s$^{-1}$ at 12.5h) and August (13.58 mm s$^{-1}$ at 12h). This mid-day dip was also visible in the MBWB $G_c$ but on a smaller scale than the JS model. The
MBWB $G_c$ had a delayed and more rapid shut down in the evening in all months, going from 5 to 0 mm s\(^{-1}\) in just a half hour while the measured $G_c$ dropped by only about 0.5 mm s\(^{-1}\). These results are contrary to Wu \textit{et al.} (2000) who did not observe a mid-day dip using either model at OA. They attributed this to a lack of soil water stress in 1994 and 1996, along with the high drought tolerance of aspen (Blanken, 1997).

For May at OBS, I saw an opposite pattern in the models compared to OA, with the JS calculated $G_c$ values being significantly larger (up to 1.5 times greater) than the measured values, and the MBWB tracking the measured values closely throughout the day, but with some very large $G_c$ values occurring in the evening (e.g., 3.29 mm s\(^{-1}\) MBWB vs 1.72 mm s\(^{-1}\) measured at 21.5h). In June and July, both models have $G_c$ increasing too quickly in the morning, getting close to the maximum value but dipping during the mid-day and closing the stomata quickly later in the day rather than a gradual closing as seen in the measured values. In August and September, the two models closely match the measured $G_c$ morning increase but slightly fall short of the maximum measured $G_c$. The mid-day dip is minimal in the models during September leading to closely matched $G_c$ values until late afternoon (18h) when the models and measurements diverge, with the measured $G_c$ decreasing moderately over a longer time period than the modelled values.

Using a sunlit and shaded leaf canopy photosynthesis model of Wang and Leuning (1998) coupled with CLASS, Arain \textit{et al.} (2002) found that the BWB model performed better than the JS model, with the JS model producing large $G_c$ in early morning at OA and OBS. They also observed the rapid decrease in $G_c$ after midday with the simulated $G_c$ decreasing at times when the measured values did not. Ju \textit{et al.} (2006) found the BWB model underestimated $G_c$ during mid-day at OA leading to underestimated $\lambda E$. At old growth evergreen conifer and
deciduous broadleaf sites, Matsumoto et al. (2008) found large $G_c$ values from morning to mid-day that slowly decreased until nighttime, with mean half-hourly $G_c$ values of 5.5-7 mm s$^{-1}$ at the evergreen conifer sites and 20 mm s$^{-1}$ at the deciduous broadleaf sites. Their evergreen conifer $G_c$ values are in close agreement with those for OBS, while their deciduous broadleaf $G_c$ values are approximately 5 mm s$^{-1}$ larger than those observed at OA during June, July, and August.
Figure 5.3. Diurnal progression of monthly ensemble half-hourly Central Standard Time (CST) measured rain-free $G_c$ (black circles), Jarvis-Stewart (JS) modelled $G_c$ (blue squares), and Modified Ball-Woodrow-Berry (MBWB) modelled $G_c$ (red stars) at OA (left column (a-e) May-Sept for 1996:2017) and OBS (right column (f-j) May-Sept for 1999:2017).
At OA, the two models performed similarly, with the JS model explaining 38% ($R^2 = 0.38$) of the variance in the half-hourly measured values of $G_c$ and the MBWB explaining 36% ($R^2 = 0.36$) (Figure 5.4). Wu et al. (2000) reported similar findings at OA with the JS and MBWB models explaining 33% and 31% of the variances, and RMSEs of 3.88 and 4.56, respectively, for 2681 half-hours. With the modified CLASS model, Arain et al. (2002) found the model explained 41% of the variance (correlation coefficient, $r = 0.64$, RMSE = 4.95 mm s$^{-1}$, $n=3612$) of half-hourly $G_c$ values for the 1999 growing season at OA. The model performances were not as good at OBS as they were at OA. At OBS, the JS explained only 19% of the variance ($R^2 = 0.19$, RMSE = 5.42 mm s$^{-1}$, $n=31,660$) and the MBWB explained 27% of the variance ($R^2 = 0.27$, RMSE = 4.97 mm s$^{-1}$, $n=31,660$). The Arain et al. (2002) model explained 34% of the 1999 growing season variance at OBS ($r=0.58$, RMSE = 3.81 mm s$^{-1}$, $n=3431$). The equations for the model performance for each individual year (the grey lines in Figure 5.4) at OA and OBS are given in Table C1 and C2 in the appendices section. The slopes and $R^2$ values for the JS model for individual years varied, respectively, from 0.55 to 1.30 and 0.33 to 0.51 for $G_c$ and from 0.89 to 1.44 and 0.59 to 0.87 for $\lambda E$ for OA, and from 0.38 to 0.67 and 0.11 to 0.24 for $G_c$ and from 0.94 to 1.25 and 0.34 to 0.60 for $\lambda E$ for OBS. The slopes and $R^2$ values for the BWB model for individual years varied, respectively, from 0.76 to 1.29 and 0.24 to 0.49 for $G_c$ and from 0.55 to 1.59 and 0.39 to 0.80 for $\lambda E$ for OA, and from 0.51 to 1.42 and 0.16 to 0.43 for $G_c$ and from 0.76 to 1.06 and 0.55 to 0.72 for $\lambda E$ for OBS. With the JS model, Matsumoto et al. (2008) reported the relationship between the observed and predicted $G_c$ had an RMSE of 1.5 mm s$^{-1}$ at the deciduous broadleaf site. Unfortunately, they did not run the model at the evergreen conifer site. They reported a high correlation coefficient ($r = 0.88$) and significance ($P < 0.01$) between the
predicted and actual $G_c$, but do not report slopes and only report that deviations from the 1:1 line were relatively large at both sites.

Figure 5.4 Measured rain-free half-hourly growing season $G_c$ vs. modelled Jarvis-Stewart (JS) and modelled modified Ball-Woodrow-Berry (MBWB) $G_c$ at Old Aspen (OA) ($n = 33,699$ for 11 years) and Old Black Spruce (OBS) ($n = 31,660$ for 9 years). The black line is the 1:1 line, the blue and red lines are the regression for 11 years at OA and 9 years at OBS, respectively, with the equations given in the plots, and the grey lines are the regression lines for all the individual years tested at each site (1996:2017 at OA and 1999:2017 at OBS).

5.3.3 Model Performance at the Daily Scale

At OA in May, the MBWB modelled $G_c$ was higher than the measured $G_c$ by 2 times on average the entire month, but as large as 3.4 times on the 6 May (Figure 5.5). Starting in June, the persistent difference decreased starting on 6 June such that by 14 June the MBWB modelled
$G_c$ tracked the measured $G_c$ values till the end of the growing season around 24 September. In May, the JS modelled $G_c$ started out near zero (0.34 mm s$^{-1}$), increasing to closely match the measured values from the 10 to 20 May, when it crossed over the measured $G_c$ and quickly increased to a maximum of 9.09 mm s$^{-1}$ on the 30 June, which was 2.1 times greater than the measured $G_c$ of 4.37 mm s$^{-1}$. From June to mid-September, the JS modelled values were significantly greater than the measured $G_c$, often with a difference of 3 to 4 mm s$^{-1}$. At OBS in May, the two models produced daily values that were greater than the measured $G_c$ with the JS model values being significantly higher, often twice the measured values. For June-September the two models had similar magnitude values as the measured $G_c$; however, the MBWB model on average performed better matching the peaks and drops in the measured $G_c$. 
Figure 5.5 Daily ensemble averaged measured rain-free $G_c$ (black circles), Jarvis-Stewart (JS) modelled $G_c$ (blue squares), and Modified Ball-Woodrow-Berry (MBWB) modelled $G_c$ (red stars) at OA (left column (a-e) May-Sept for 1996:2017) and OBS (right column (f-j) May-Sept for 1999:2017).
At the daily scale, the two models showed better performance (higher $R^2$ and lower RMSE) compared to at the half-hourly scale at OA, but at OBS, the MBWB performed better while the JS performance worsened (Figure 5.6). One reason for the improved performance of the MBWB model can be explained by decreased sample size, as decreasing $n$ improves fits, similar to binning, by decreasing the residuals/errors.

Figure 5.6 Measured rain-free growing season daily $G_c$ vs. modelled Jarvis-Stewart (J-S) and modelled modified Ball-Woodrow-Berry (MBWB) $G_c$ at Old Aspen (OA) ($n = 1203$ for 11 years) and Old Black Spruce (OBS) ($n = 1795$ for 9 years). The black line is the 1:1 line, the blue lines and red lines are the regression lines for 11 years at OA and 9 years at OBS, with the equations given in the plots, and the grey lines are the regression lines for all the individual years tested at each site (1996:2017 at OA and 1999:2017 at OBS).
5.3.4 Model Performance at the Seasonal Scale

Figure 5.7 shows the mean seasonal variation in climate variables for 1996-2017 at OA compared with those for OBS for 1999-2017. Due to the close proximity of the two sites, most of the climate variables follow the same well-defined seasonal cycle with a few notable departures. The CO$_2$ mixing ratio was higher at OBS than OA throughout the entire year, with a long-term mean annual difference of 5 μmol mol$^{-1}$. $T_s$ at OA was higher for most of the year, except during March and April when their means and standard deviations overlap. With water logged sandy-clay soil and a high water table, OBS had lower $T_s$ than the moderately well drained silt loam at OA. $T_a$ and $Q$ at the two sites were so similar that their means were indistinguishable and their standard deviations have only minor deviations from each other. $D$ at both sites was very similar for most of the year but was higher at OA during spring (April-May) and fall (September-October) as seen by the higher mean and standard deviation compared to OBS. The two sites showed relatively matching cumulative $P$ throughout the year such that the $P$ totals are nearly identical by the end of the year (see Table 4.1). The small difference from June to September could be due to lower $P$ in 1996-1998 lowering the mean at OA, and the slightly differing installations of $P$ gauges at the two sites. Also, the distance of approximately 80 km between the sites could cause one site to experience a storm that misses the other. The mean $θ$ was higher at OA throughout the entire year, with a larger difference between the sites occurring in spring (Feb-April).
Figure 5.7 Five-day 24-h averaged CO$_2$ mixing ratio, 2-cm soil temperature ($T_s$), air temperature ($T_a$), photosynthetically active radiation ($Q$), vapour pressure deficit ($D$), cumulative precipitation ($P$) and average (0-90-cm at OA and 0-60-cm at OBS) soil volumetric water content ($\theta$) from 1996:2017 at Old Aspen (OA) by the red dot-dashed line and 1999:2017 at Old Black Spruce (OBS) by the blue dot-dashed line. Shaded red and blue areas denote ±1σ from the long-term mean at OA and OBS, respectively. This figure is the same as Fig. 4.1.
Figure 5.8 shows the seasonal ensemble-average measured and modelled dry foliage $G_c$ and $E$, at OA and OBS. The ensemble-average measured $G_c$ at OA started off relatively high at 6.35 mm s$^{-1}$ and decreased slowly to 2.27 mm s$^{-1}$ on 11 May when it abruptly began to climb steadily till the maximum of 10.68 mm s$^{-1}$ was reached on 15 July. In mid-September, the measured $G_c$ begins declining to the end of season minimum of 3.89 mm s$^{-1}$ on 28 September, and began to climb again reaching up to 7.89 mm s$^{-1}$ at the end of December. The standard deviation of the measured $G_c$ was 5.73 mm s$^{-1}$ with the maximum deviation occurring in December at 12.44 mm s$^{-1}$ and the minimum deviation of 1.95 mm s$^{-1}$ occurring in early May (11 May). The ensemble-average JS $G_c$ values at OA remained near zero till the start of May (1 May 0.48 mm s$^{-1}$) and quickly increased to 9 mm s$^{-1}$ by the end of the month. The JS $G_c$ stayed above 9 mm s$^{-1}$ between early June and mid-September, reaching a maximum of 12.57 mm s$^{-1}$ on 14 August, and quickly decreased back to near zero where it remained for the rest of the year. The standard deviation of the ensemble-average JS $G_c$ was small (average of 0.10 mm s$^{-1}$) from Jan-April, increased greatly during the growing season with an average of 5.34 mm s$^{-1}$ for May-Sept, and decreased back down to 0.45 mm s$^{-1}$ for Sept-Dec. The MBWB ensemble-average $G_c$ fell in between the ensemble-measured and JS modelled $G_c$ during the winter. The MBWB $G_c$ started at 2.82 mm s$^{-1}$ and slowly climbed, becoming greater than the measured $G_c$ from March through May, until it matched the measured $G_c$ on 20 June at 9.19 mm s$^{-1}$. During the peak growing season period, the MBWB $G_c$ closely matched the measured $G_c$ with a maximum difference of 1.69 mm s$^{-1}$ on 20 July. From 13 September until 3 October, MBWB $G_c$ was greater than measured $G_c$ but then continued to decrease steadily ending at 2.78 mm s$^{-1}$ in December.

For OBS, the JS and MBWB modelled $G_c$ very closely matched the measured $G_c$ from 10 June through 18 October. Similar to the pattern observed at OA, the measured $G_c$ started high at
5.64 mm s\(^{-1}\) then slowly decreased to a minimum of 2.92 mm s\(^{-1}\) on 1 April when it began to increase again. From the end of May through October, the measured \(G_c\) hovered around 4 to 6 mm s\(^{-1}\). In early November, the measured \(G_c\) increased and became noisy till the end of December. The measured \(G_c\) standard deviation was large (4.14 mm s\(^{-1}\)) in the shoulder seasons (Jan-Mar and Oct-Dec) and smaller (1.94 mm s\(^{-1}\)) in the summer. The JS \(G_c\) at OBS, like the measured \(G_c\), began high at 3.72 mm s\(^{-1}\) and climbed to its maximum of 6.57 mm s\(^{-1}\) on 25 February when it slowly began declining to match the measured \(G_c\) from June to late October. When the measured \(G_c\) started increasing in November the JS \(G_c\) slowly decreased till the end of December, ending slightly higher than the start at 4.24 mm s\(^{-1}\). Similar to the measured \(G_c\) standard deviation, the JS \(G_c\) standard deviation was larger in the shoulder season at approximately 2.48 mm s\(^{-1}\) and decreased during the growing season with an average of 1.86 mm s\(^{-1}\). Distinctly, the MBWB \(G_c\) started low at 1.84 mm s\(^{-1}\) and slowly climbed matching the measured from 26 April till 13 October when it quickly dropped ending near the starting value.

The standard deviation of the MBWB \(G_c\) was small (0.55 mm s\(^{-1}\)) at the start of the year (Jan-Mar) then grew larger during the growing season up to 2.56 mm s\(^{-1}\) and decreased to a similar value by the end of the year (Nov-Dec). As expected, \(G_c\) at OA was much higher than OBS during the middle of the growing season but OBS \(G_c\) was higher than at OA during early spring and late fall due to the extended growing season in conifers compared to deciduous trees (Arain \textit{et al.}, 2003).

From January to April, the measured \(E\) at OA remained low, not increasing above 0.5 mm day\(^{-1}\) until 16 April when it started increasing slowly till 11 May, after which it quickly increased. The maximum of 5.18 mm day\(^{-1}\) was reached on 10 July and remained near this value till 30 July, and from here \(E\) steadily dropped throughout August and September returning to
below 0.5 mm day\(^{-1}\) on 13 October. Due to the zero \(G_c\) value until the start of May from the JS model, the JS modelled \(E\) also remained zero until the start of May when it quickly rose, crossing over the measured \(G_c\) on 11 May. After this crossover, the JS modelled \(E\) continued to be on average 0.84 mm day\(^{-1}\) higher than the measured \(E\), until they crossover again on 23 Sept at 1.78 mm day\(^{-1}\). MBWB modelled \(G_c\) was too large from March to mid-June, leading to MBWB modelled \(E\) being overestimated during those months, with the largest difference occurring on 11 May when measured \(E\) was 0.94 mm day\(^{-1}\) while MBWB modelled \(E\) was 2.95 mm day\(^{-1}\). From mid-June to the start of September, MBWB modelled \(E\) closely matched the measured \(E\). Since the difference between MBWB modelled and measured \(G_c\) was significantly smaller in the senescence period, MBWB modelled \(E\) during this period was on average less than 1 mm day\(^{-1}\) greater than measured \(E\).

At OBS, the JS and MBWB models performed better in matching the seasonal progression of measured \(E\). The JS modelled \(G_c\) was much larger than the measured \(G_c\) especially during March to May, which translated to a modelled \(E\) on average 1.1 mm day\(^{-1}\) larger for the same period. The maximum JS modelled \(E\) of 4.3 mm day\(^{-1}\) occurred on 30 June and was 0.84 mm day\(^{-1}\) greater than the measure \(E\) that day. Through the peak summer months (June, July, and August), the JS modelled \(E\) was on average 0.59 mm day\(^{-1}\) greater than the measured \(E\), with this decreasing to only 0.32 mm day\(^{-1}\) for September-December. The MBWB modelled \(E\) matched the measured \(E\) from January through the beginning of March, when the MBWB modelled \(E\) rose more rapidly, such that from mid-March to 30 May, the modelled \(E\) was on average 0.36 mm day\(^{-1}\) greater than the measured \(E\). During the peak summer months, the MBWB modelled \(E\) was only 0.28 mm day\(^{-1}\) greater than the measured \(E\), with the difference decreasing to 0.07 mm day\(^{-1}\) for September-December.
Over a 5-day period (13 to 17 August 1994), Wu et al. (2000) found the cumulative evaporation totals obtained from the JS and MBWB were respectively 8% and 21% less than the measured values. At the monthly scale, Arain et al. (2002) found that the modified BWB CLASS model tended to overestimate $E$ in spring and underestimate it in July and August at OA, especially in the warmer years, but had an overall variance explanation of 90% ($\text{RMSE} = 0.54 \text{ mm day}^{-1}, n=50$). Their model performed better at OBS than OA with an explained variance of 94% ($\text{RMSE} = 0.22 \text{ mm day}^{-1}, n=20$). They also found that the model overestimated $E$ at OA between snowmelt and leaf emergence and towards the end of the growing season. Similar to my measured $E$, Arain et al. (2003) reported maximum daily $E$ of 3.0-3.5 mm day$^{-1}$ in the summer and 0.1-0.2 mm day$^{-1}$ in winter with higher winter $E$ due to snow sublimation and evaporation during warmer weather. For July to August, Matsumoto et al. (2008) observed average $E$ values of 1.4-1.8 mm day$^{-1}$ with maximum values of 2.9-3.3 mm day$^{-1}$ at a boreal forest in eastern Siberia.
Figure 5.8 Mean annual five-day averaged measured rain-free $G_c$, Jarvis-Stewart (JS) modelled $G_c$, and Modified Ball-Woodrow-Berry (MBWB) modelled $G_c$ at OA for 1996:2017 (a) and OBS for 1999:2017 (b) and mean annual five-day averaged rain-free $E$ at OA for 1996:2017 (c) and at OBS for 1999:2017(d).

5.3.5 Model Performance at Growing Season and Annual Scales

Figure 5.9 shows the interannual variability in annual mean CO$_2$ mixing ratio, $T_s$, $T_a$, $Q$, $D$, $P$, and average $\theta$ for the 0-90 cm depth for OA (1996-2017) and the 0-60 cm depth for OBS (1999-2017). Annual mean CO$_2$ mixing ratio increased by 47 $\mu$mol mol$^{-1}$ at OA and 44 $\mu$mol
mol$^{-1}$ at OBS from 1999 to 2017. The long-term annual mean at OA was 384 µmol mol$^{-1}$ for 1996 to 2017, while at OBS it was 389 µmol mol$^{-1}$ for 1999 to 2017. The long-term mean annual $T_s$ at OA was 4.7°C with yearly anomalies ranging from -1.3 to 0.8°C. At OBS the long-term mean annual $T_s$ was 3.0°C and the anomalies ranged from -1.1 to 0.8°C. Annual mean $T_a$ was 2.4 °C at OA and 1.6°C at OBS with yearly anomalies ranging from -1.7 to 3.1°C and -1.7 to 1.8 °C, respectively. The highest annual $T_a$ occurred in 2017 at both sites with 5.5 °C and 3.4 °C while the coldest values occurred in 2014 with 0.7°C and -0.01°C for OA and OBS, respectively. The two sites had the same long-term annual mean $Q$ of 266 µmol m$^{-2}$s$^{-1}$ with anomalies ranging from -23 to 19 µmol m$^{-2}$s$^{-1}$ at OA and -30 to 24 µmol m$^{-2}$s$^{-1}$ at OBS. The highest annual $Q$ occurred in 2001 for both sites with 285 µmol m$^{-2}$s$^{-1}$ and 290 µmol m$^{-2}$s$^{-1}$ at OA and OBS, respectively. The lowest annual $Q$ occurred in the same years as the lowest GS $Q$, in 2016 at OA with 243 µmol m$^{-2}$s$^{-1}$ and in 2017 at OBS with 235 µmol m$^{-2}$s$^{-1}$. The long-term mean annual $D$ was 0.38 kPa at OA and 0.36 kPa at OBS with anomalies of -0.07 to 0.24 kPa and -0.08 to 0.28 kPa, respectively. The long-term mean annual $P$ values were 465 and 482 mm at OA and OBS, respectively. The minimum annual $P$ at OA occurred during the first year of the drought, 2001, with 235 mm while at OBS it occurred in the last year of the drought, 2003, with 289 mm. The maximum annual $P$ occurred in 2010 at OA with 705 mm and in 2004 at OBS with 698 mm. The long-term mean annual $\theta$ were 0.32 and 0.27 m$^3$m$^{-3}$ at OA and OBS, respectively. The maximum annual $\theta$ occurred in 2006 at OA with 0.39 m$^3$m$^{-3}$ and in 2011 at OBS with 0.29 m$^3$m$^{-3}$. The minimum annual $\theta$ occurred during the last year of the drought in 2003 at both sites with 0.22 m$^3$ m$^{-3}$.
Figure 5.9 Interannual variation in annual averaged: CO₂ mixing ratio, 2-cm soil temperature ($T_s$), air temperature ($T_a$), downwelling photosynthetically active radiation ($Q$), vapour pressure deficit ($D$), growing season precipitation ($P$) and average (0-90-cm depth at OA and 0-60-cm depth at OBS) soil volumetric water content ($\theta$) from 1996 to 2017 at Old Aspen (OA) and 1999:2017 at Old Black Spruce (OBS). The gray bar denotes the 2001:2003 drought, and the brown bar denotes the 2016 forest tent caterpillar (FTC) defoliation period at OA. This figure is the same as Fig. 4.5).
Figure 5.10 shows the interannual variation in growing season average $G_c$ and $E$ for 1996-2017 at OA and for 1999-2017 at OBS. At OA, the JS and MBWB modelled GS $G_c$ were both greater than the measured GS $G_c$ for most of the observation period. The MBWB modelled GS $G_c$ was on average 0.76 mm s$^{-1}$ larger than the measured GS $G_c$, with a minimum difference of 4.5x10$^{-2}$ mm s$^{-1}$ in 2009 and a maximum difference of 2.94 mm s$^{-1}$ in 2003, the last year of the drought. The JS modelled GS $G_c$ was on average 1.77 mm s$^{-1}$ larger than the measured $G_c$, but achieved better agreement after 2008 with a minimum difference of 1.3x10$^{-2}$ mm s$^{-1}$ occurring in 2010. The maximum difference between the JS modelled GS $G_c$ and measured GS $G_c$ was 5.79 mm s$^{-1}$ in 2001. At OBS the MBWB modelled GS $G_c$ matched the interannual variation in measured GS $G_c$ quite well. The mean difference was 0.31 mm s$^{-1}$, with a minimum difference of 4.7x10$^{-2}$ mm s$^{-1}$ occurring in 2017, and a maximum difference of 0.79 mm s$^{-1}$ occurring in 2009. Similar to OA, the JS modelled GS $G_c$ at OBS was too large compared to the measured GS $G_c$, but the model performance didn’t improve after 2008. The JS modelled GS $G_c$ was on average 0.84 mm s$^{-1}$ greater than the measured $G_c$, with a minimum difference of 8.4$^{-2}$ mm s$^{-1}$ in 2012, and a maximum difference of 1.92 mm s$^{-1}$ in 2015.

The model results for GS $E$ matched those of $G_c$ at OA. The MBWB modelled GS $E$ results were similar to the GS $G_c$ results with the modelled value being greater than the measured, on average 40.77 mm y$^{-1}$. A minimum difference of 4.31 mm y$^{-1}$ occurred in 1996 while the maximum difference of 157.74 mm y$^{-1}$ occurred in 2003. Just as the JS modelled GS $G_c$ matched the measured values post 2008, the JS modelled GS $E$ also closely matched the measured GS $E$. Due to the JS modelled $E$ values being significantly larger than the measured values pre-2008, the mean difference was 7% larger than for MBWB at 43.82 mm y$^{-1}$. Matching the $G_c$ results, the maximum difference of 154.63 mm y$^{-1}$ occurred in 2001, while the minimum
difference of 0.21 mm $y^{-1}$ occurred in 2012. At OBS, the MBWB modelled GS $E$ did not match the measured $E$ as well as the modelled $G_c$ did. The MBWB modelled GS $E$ was on average 31.52 mm $y^{-1}$ greater than the measured GS $E$, with the minimum difference of 3.21 mm $y^{-1}$ occurring in 2000 and the maximum difference of 78.44 mm $y^{-1}$ occurred in 2013. The larger difference between the JS modelled GS $G_c$ and measured $G_c$ carried through to the $E$ results, with the JS modelled GS $E$ being on average 60.25 mm $y^{-1}$ larger than the measured $E$. The minimum difference of 15.37 mm $y^{-1}$ occurred in 2009, while the maximum difference of 125.27 mm $y^{-1}$ occurred in 2013.
Figure 5.10 Interannual variation in growing season measured rain-free $G_c$ and $E$ (black circles), year round Jarvis-Stewart (JS) modelled $G_c$ (a) and $E$ (blue squares) (c), and Modified Ball-Woodrow-Berry (MBWB) modelled $G_c$ (b) and $E$ (red stars) (d) at Old Aspen (OA) 1996:2017 and Old Black Spruce (OBS) 1999:2017, respectively.

Figure 5.11 takes the results presented in Figure 5.10 and presents them as one to one, model vs. measured plots. The MBWB model performed better (higher $R^2$ and lower RMSE) than the JS model at both sites in replicating the GS $G_c$ over the years. The two models performed more similarly in replicating the GS $E$ over the years. At OA, the JS model performed
slightly better than the MBWB in capturing the variation in GS $E$, while at OBS the MBWB slightly outperformed the JS model (Figure 5.11c,d).

Figure 5.11 Measured rain-free growing season mean $G_c$ and $E$ vs. modelled Jarvis-Stewart (JS) and modelled modified Ball-Woodrow-Berry (MBWB) $G_c$ and $E$ at Old Aspen (OA) and Old Black Spruce (OBS). The black line is the 1:1 line, the blue lines are JS regression lines and red lines are the MBWB regression lines for 1996:2017 at OA and 1999:2017 at OBS, with the equations given in the plots.

Figure 5.12 shows the interannual variation in annual $G_c$ and $E$ for 1996-2017 at OA and for 1999-2017 at OBS. At OA for most of the observation period the measured $G_c$ was higher.
than the $G_c$ from both models. The annual MBWB modelled $G_c$ is slightly lower than the measured $G_c$, on average 0.66 mm s$^{-1}$ larger with a maximum difference of 1.94 mm s$^{-1}$ occurring in 1996 and a minimum difference of 1.5x10$^{-3}$ mm s$^{-1}$ in 2008. The annual JS modelled $G_c$ was slightly lower than the measured $G_c$ pre-drought, on average 0.33 mm s$^{-1}$ higher, but after 2001 it became significantly lower, on average 2.36 mm s$^{-1}$ smaller. The maximum difference between JS modelled and measured $G_c$ of 3.76 mm s$^{-1}$ occurred in 2010 and the minimum 0.43 mm s$^{-1}$ occurred in 1998. At OBS, the model results reversed with the JS modelled $G_c$ on average being greater than the measured $G_c$ and the MBWB modelled $G_c$ the smallest of the three. The MBWB modelled $G_c$ was on average 1.54 mm s$^{-1}$ smaller than the measured $G_c$, with a minimum difference of 0.63 mm s$^{-1}$ in 2016 and a maximum difference of 2.29 mm s$^{-1}$ occurring in 2002.

The JS modelled $G_c$ was larger than the measured $G_c$, with an average difference of 0.59 mm s$^{-1}$, with a large difference during the drought years although the maximum difference of 1.89 mm s$^{-1}$ occurred in 2015, with the minimum difference of 4.7x10$^{-2}$ mm s$^{-1}$ in 2009.

Despite the MBWB model $G_c$ matching the measured $G_c$, seen at OA, the MBWB modelled $E$ was significantly larger than the measured $E$. The minimum difference between the MBWB modelled $E$ and measured $E$ was 1.32 mm y$^{-1}$ in 1996 with a maximum difference of 201.33 mm y$^{-1}$ occurring in 2003, and an average difference of 68.44 mm y$^{-1}$ for the entire period. The JS modelled $E$ was higher than the measured $E$ from 1997 to 2003 after which it quite closely matched the pattern and values of the measured $E$. The minimum difference between the JS modelled $E$ and measured $E$ occurred in 2008 with only 0.17 mm y$^{-1}$ while the maximum difference was 131.70 mm y$^{-1}$ in 2001, and the overall mean difference was 35.25 mm y$^{-1}$. Similar to the $G_c$ comparison at OBS, the JS modelled $E$ was higher than the measured $E$, but with a greater relative difference than the $G_c$ results. The mean difference between the JS
modelled $E$ and measure $E$ was 74.65 mm with a minimum difference of 25.23 mm $y^{-1}$ and a maximum difference of 143.89 mm $y^{-1}$ with these occurring in 2017 and 2013, respectively. While the MBWB modelled $G_c$ was significantly lower than the measured $G_c$, it resulted in modelled $E$ matching fairly well the pattern and values of the measured $E$. This better performance is illustrated by a mean difference of 30.39 mm $y^{-1}$, a minimum difference of 4.94 mm $y^{-1}$ occurring in 2017 and a maximum difference of 77.93 mm $y^{-1}$ in 2013. In the last year of the drought (2003), Krishnan et al. (2008) found that $G_c$ at OBS declined by 50% but that $E$ was relatively unaffected because $D$ was almost twice as large.
Figure 5.12 Interannual variation in annual mean measured rain-free $G_c$ and $E$ (black circles), year round Jarvis-Stewart (JS) modelled $G_c$ (a) and $E$ (blue squares) (c), and Modified Ball-Woodrow-Berry (MBWB) modelled $G_c$ (b) and $E$ (red stars) (d) at Old Aspen (OA) 1996:2017 and Old Black Spruce (OBS) 1999:2017, respectively.

To compare the model performances at the annual scale to that of the growing season, the results were again plotted as one to ones, of the model vs. measured values for each model at both sites (Figure 5.13). The results at the annual scale matched the pattern observed at the GS scale. The MBWB model better than the JS model in capturing the annual variation in $G_c$ at both
sites. The JS model performed better than the MBWB in capturing the annual \( E \) at OA, while the MBWB model performed better than the JS model in depicting the variation of annual \( E \) at OBS.

**Figure 5.13** Measured rain-free annual mean \( G_c \) and \( E \) vs. modelled Jarvis-Stewart (JS) and modelled modified Ball-Woodrow-Berry (MBWB) \( G_c \) and \( E \) at Old Aspen (OA) and Old Black Spruce (OBS). The black line is the 1:1 line, the blue lines are JS regression lines and red lines are the MBWB regression lines for 1996:2017 at OA and 1999:2017 at OBS, with the equations given in the plots.
5.4 Conclusions

1) At OA, at the half-hourly scale, the two models performed similarly but each model had its unique problems not being able to reproduce the measured $G_c$ values. Diurnally, both models reached their maximum $G_c$ values before the measured $G_c$ values. The JS model showed a delayed rise in $G_c$, while the MBWB matched the early morning rise but remained elevated in the evening when the measured $G_c$ was steadily decreasing. The model performance improved when the relationships were parameterized for am and pm to capture $G_c$ responses to climate.

2) At OBS, at the half-hourly scale, the MBWB model performed slightly better than the JS model. Both models showed a dip in $G_c$ during mid-day, then increased before a rapid decline in $G_c$ in the late evening, which was not observed in the measured $G_c$, leading to overestimated $G_c$ values for several hours.

3) At the daily scale, the performances of the two models improved relative to the hourly scale at OA but at OBS, only the MBWB model improved, while the JS model performance worsened. At both sites, the MBWB model had better agreement with measured $G_c$ by being able to capture more of the variability in the measured values.

4) At the seasonal scale, both models were unable to capture the pattern of measured $G_c$ in the shoulder seasons, which is expected due to the parameterizations containing only GS data. At OA, the JS model resulted in significantly greater $G_c$ than the measured $G_c$ during the GS, while the MBWB modelled $G_c$ was too low in July and August but matched the GS increase and decline quite well. At OBS, both models matched the measured $G_c$ quite well from June-September, with the MBWB model showing a slightly better agreement with the trend in $G_c$ over the full GS.
5) At the GS scale, the MBWB model performed better than the JS model in capturing the interannual variability in GS $G_c$ at both sites. For modelling $E$, the JS model performed better than the MBWB model at OA, while the MBWB model performed better at OBS.

6) At the annual scale, the MBWB model performed better in capturing the interannual variability in $G_c$ at OA, with the two models performing similarly in explaining the variability in $E$. At OBS, the MBWB model performed better than the JS model in capturing the interannual variability in the measured $G_c$, and this pattern maintained when modelling $E$, with the MBWB model performing slightly better than the JS model.

7) Both model performances worsened when stepping from the GS scale to the annual scale.

8) These results show that utilizing one set of parameter values to capture variation of $G_c$ from half-hourly to annual scales across nearly two decades of changing climate, does not yield the best results, which could possibly be achieved through parameter sets for distinct time scales or climate regimes (drought years vs wet years).
Chapter 6: Conclusions

In this thesis, I examined 22 and 19 years of climate and EC flux measurements in two southern boreal forest stands, a mature deciduous aspen stand (OA) and a mature coniferous black spruce stand (OBS), to determine the impact of climatic variation and disturbance on the C and water fluxes, and the efficacy of two commonly used conductance models to reproduce $G_c$ and $E$ over the measurement period. Few studies have been able to use eddy covariance measurements to study insect defoliation events (Cook et al., 2008; Clark et al., 2010) and many lack data records comparable in length to that of OA. Hence, the FTC defoliation event that occurred at OA provided a unique opportunity to study the impact of FTC defoliation on the C and water dynamics of a stand with a long-term pre-disturbance data record. The FTC defoliation event studied in Chapter 2, led to 2016 NEP and GEP values being largely reduced, while $R_e$ was slightly reduced; and all three fluxes recovered to normal levels by the end of the growing season. This reduction in NEP led to the most negative annual NEP ($-72 \text{ g C m}^{-2} \text{ y}^{-1}$) observed at OA from 1996-2017, which would have been even more negative had the stand not had a quick recovery and re-leafed before the end of the GS. The FTC infestation had a smaller impact on $E$, with observed $E$ during the 4-week defoliation period being one half to two thirds of simulated $E$ (without the defoliation) leading to a minimal effect on annual $E$. The C fluxes simulated without the defoliation event occurring showed that the OA stand would have been a C sink in 2016, similar to most years since 1996. Remote sensing indices along with tower-based fluxes and indices helped quantify the intensity and extent of the defoliation event at this site. With these measurements along with flux modelling, I showed that insect-caused defoliation events can have large short-term impacts on the water and C fluxes, leading to a large decrease in annual net C uptake. This loss of C uptake was greater than the decreased C uptake caused by a three-year
drought experienced at OA from 2001-2003. Unlike after the drought when it took the stand over a year to recover near normal C and water fluxes, after the defoliation in 2017 GEP and $E$ returned to near the long-term mean values, while $R_c$ remained depressed, leading to a higher than average NEP. With climate change, we are likely to see increased disturbance events due to fire and insects leading to a shift of the forest to a younger age class, which will alter C dynamics (Volney & Fleming, 2000; Bonan et al., 2008). Old-growth forests, under ideal climatic conditions, have the potential to sequester C at high rates (>300 g C m$^{-2}$ y$^{-1}$) similar to younger forests, but in non-ideal conditions, C sequestration capabilities decrease rapidly (Wharton et al., 2016; Luyssaert et al., 2008). Due to their potential to cause large perturbations from mean C and water fluxes, impacts of insect infestations will be important to include in models for scientists to be able to more accurately predict ecosystem-atmosphere exchange and future climate.

To study canopy conductances scientists often limit the data to periods where the conductance measurements are known to be more robust. Common conditions are for rain-free daytime growing season values, such as the filtering used for data in Chapter 3. I used filtering in order to study the environmental controls of $G_c$ and compare them to the controls of $E$. I found that the environmental controls of $G_c$ and $E$ were both time scale dependent, similar to Otha et al. (2008) and Yoshida et al. (2010). At the growing season scale, $\theta$ was the strongest control on $E$ at both sites, while at the monthly scale it was $T_a$. The controls of $G_c$ were distinct between the sites at the monthly scale with $T_a$ having the highest relationship with $G_c$ at OA, while at OBS it was $Q$. At the growing season scale, the strongest control on $G_c$ was $D$ for both sites. Under my specific filtering for this chapter, the sites showed no significant trend in the long-term climate and fluxes.
Expanding the long-term trend analysis to non-filtered growing season and annual data in Chapter 4, I observed trends in the climate and fluxes not detected in Chapter 3. There were increasing trends in GS CO₂ concentration and decreasing trends in GS Q at both sites, along with an increasing trend in θ at OA. There were no trends in GS Tₐ, Tₛ and D at both sites. At the annual scale, there were trends of increasing CO₂ concentration, Tₛ and Tₐ at both sites and decreasing Q at OBS. At both sites, there were no trends in D. Increasing trends in GS GEP and Re, with a faster increase in Re, led to a significant decrease in GS NEP at OBS. This was also true at the annual scale. A significantly decreasing trend in NEP at OA was the result of a decline in GEP being greater than that in Re. No annual trends in C fluxes (GEP, Re and NEP) were observed at OA. Although no trends in GS or annual E at either site were observed, there was a significant decrease in annual WUE at OA due to a small decline in GEP, and a significant increase in GS WUE at OBS due to the significant increase in GS GEP. There were no trends in GS or annual P – E at either site since there were no trends in both GS and annual P and E. Over the study period, the relatively small proportion of Re occurring in the non-growing season (17% and 10% at OA and OBS, respectively) resulted in the annual NEP being 30% of the GS values at both sites. GS WUE at OA was 6% higher than at OBS reflecting the 22% higher GEP and 18% higher E at OA than at OBS. Annual P – E, which is a good estimate of site runoff, was on average 97 and 193 mm at OA and OBS, respectively. There were no trends in GS length, start date or end date at either site. Of the three GS metrics, only GS length was important when analyzing all the available observations. It was significantly related to GEP at OBS and NEP at OA. There were no significant relationships between E and these metrics at either site. Identifying trends in climate variables and their ability to create trends in C fluxes is important to capture and monitor as climate variables alter with global climate change.
To model $G_c$ and hence $E$, scientists commonly use a short time series of data to obtain model parameters. If the year or years used to obtain the model parameters are missing climatic variability experienced by a site, such as larger or less than average precipitation, will they be capable of capturing the variability observed in long-term $G_c$ and $E$? In Chapter 5, I attempted to answer this question by using the long-term data record at OA and OBS to randomly sample half of the data set to obtain the best fit model parameters from rain-free daytime growing season values, tested on year-round data. The Jarvis-Stewart (JS) model and Modified Ball Woodrow Berry (MBWB) model results varied across time scales and were distinct for each site. At the half-hourly scale, the two models performed similarly at OA while at OBS, the MBWB model performed better than the JS model, but at both sites the two models had unique problems in explaining the variability in the measured $G_c$ values. Increasing the time scale to daily, I observed both model performances improved at OA but only the MBWB model improved at OBS, with the MBWB model showing better agreement with the measured $G_c$ at both sites. Advancing to the seasonal scale, both models were not successful in capturing the pattern of the measured $G_c$ in the shoulder seasons due to the lack of parameterization outside of the GS values, with both models performing quite well at OBS and the MBWB model performing a little better than the JS model during the GS at OA. The models performed better when restricting the analysis to the GS scale. The MBWB model performed better than the JS model in capturing the variation in GS $G_c$ at both sites ($\text{MBWB } R^2 = 0.69$ and $R^2 = 0.82$ compared to $\text{JS } R^2 = 0.15$ and $R^2 = 0.04$ at OA and OBS, respectively). The model results diverged when modelling GS $E$, with the JS model performing better at OA and the MBWB model performing better at OBS. As expected, the model performances decreased when stepping up to the annual scale. At the annual scale, the MBWB model performed better than the JS model for capturing the variation in annual
$G_c$ at both sites ($\text{MBWB } R^2 = 0.54$ and $R^2 = 0.66$ compared to $\text{JS } R^2 = 0.27$ and $R^2 = 0.03$ at OA and OBS, respectively). To model $E$, the JS model performed slightly better ($\text{JS } R^2 = 0.60$) than the MBWB ($R^2 = 0.48$) at OA, while at OBS the MBWB performed slightly better ($R^2 = 0.53$) than the JS model ($R^2 = 0.46$). Bernier et al. (2006) found that increasing the time scale for analysis led to the linearization of canopy conductance responses to environmental variables; making some variables that were critical at finer scales non-significant at coarser time scales.

Models of canopy gas exchange have been successful because they are mathematically simple and agree with direct measurements of $G_c$ under many conditions, but the mathematical structures don’t translate directly to the regulatory mechanism they try to model, limiting their usefulness for predicting canopy functions under future climates (Buckley et al., 2003). Accurately modeling these processes to past and current climate is vital for predicting our future climate.

6.1 Limitations of the Research

Due to the popularity of using EC to measure trace gas fluxes, illustrated by over 900 active and historical flux sites worldwide (Chu et al., 2017), there have been an increasing number of review papers and books discussing the issues with this technique and the significance of measurements (Moncrieff et al., 1996; Aubinet et al., 2000; Kruijt et al., 2004; Loescher et al., 2006; Foken 2008; Baldocchi et al., 2008; Wang and Dickinson, 2012; Aubinet et al., 2012; Mauder et al., 2013). Known limitations of EC data include: the uncertainty in fluxes, energy balance closure (EBC) issues, flux footprints, flux partitioning. I briefly discuss these issues here and give more in-depth discussion of each issue in Appendix D. For the data presented and discussed in this thesis, I have provided annual uncertainty estimates for all the C and water fluxes, which need to be taken into account when making assessment of any diurnal, seasonal,
and interannual variability, and long-term trends and while using data to validate models. While at many sites EBC can be a major issue, Barr et al. (2006) found relatively high EBC at OA and OBS for 2000-2004 with EC $H + LE$ underestimating $R_n - G$ by 11% and 15%, respectively. I found a mean EBC for the long-term record (1996-2017) at OA of 82% (±7%) and a long-term (1999-2017) mean EBC of 77% (±9%) at OBS. There are many different ways scientists have chosen to partion EC measured C and water fluxes, and each comes with their own set of assumptions and problems. While I have not attempted to partition $E$ into its component fluxes, NEE has been partitioned using a relationship between nighttime NEE and the 2-cm depth soil temperature, therefore ignoring daytime light inhibition of $R_e$.

6.2 Future Work

Ideally, the trend analysis would be repeated when the data set reaches 30 years in length because the longer the time series the easier it is to distinguish trends from random noise (Baldocchi et al., 2017). As atmospheric CO$_2$ concentration continues to rise, stomatal conductance may decrease in response, which is expected to reduce $E$, along with a rise in VPD, and therefore will likely reinforce warming (Bonan et al., 2008). Thus, is it important to continue flux measurements into the future, especially $E$ measurement, which have been under-reported in the past (Baldocchi, 2019). To date, no decrease in $E$ has been observed at either site but changing GEP has led to a decrease in annual WUE at OA and an increase in GS WUE at OBS. How these stands respond to the increasing CO$_2$ concentration and projected warming will be important to monitor since they are a key part of the global forest C sink, which may not be sustained in the future with increasing drought- and disturbance- related impacts (Charney et al. 2016) that I have shown in this thesis to have a large impact on the C and water fluxes at OA and OBS.
As I and other scientists have observed, the driving variables of $G_c$ and $E$ varied with scale, and the two model performances also varied with scale at the two sites, such that a scaling phenomenon likely occurs when determining $G_c$ and its various responses to environmental drivers, meaning that different parameter sets might need to be used in models with different time steps (Bernier et al., 2006). One way of testing this would be to derive model parameters at each scale, daily, seasonal/GS, and annual, and compare the results with those obtained by scaling up the half-hourly model results presented in Chapter 5. As previously mentioned, these models are often parameterized for rain-free periods of the growing season. To improve the model’s performance, it might be useful to parameterize the model for periods including when foliage is wet. At OBS after rain when the canopy is wet, evaporation of intercepted rainfall dominates the ET water flux and needle conductance can be considered to present an insignificant limitation to water vapour flux (Rayment et al., 2000). Currently, $E$ is not partitioned into transpiration and evaporation, meaning I was unable to separate the model periods when evaporation dominates over the transpiration.

Many EC studies, and thus modelling studies, focus on a few years of data to identify climate responses and are likely to miss multi-year responses, and have low probability of capturing extreme climate events (Desai, 2014). In this study, a long-term record of nearly two decades at each site provided an opportunity to identify climate responses including extreme events such as the three-year drought and the 2016 insect infestation. To parameterize the JS and MBWB models, I used half of each site’s data record, but it would be beneficial to study the minimum number of years of data necessary to obtain reliable parameters. Along with the minimum number of years’ data needed, it would be interesting to see whether one or more of the drought or above-average precipitation years are required to be in the calibration years in
order to capture such extreme climate events. Model parameterization and performance could be improved by the use of artificial neural networks as shown by Alemohammad et al. (2017) and Saylan et al. (2019).

Some researchers have stated that a comprehensive model, i.e., a soil-plant-atmosphere continuum (SPAC) model, is necessary to describe the water vapour and CO₂ exchange (Tuzet et al., 2003, Leuning et al., 2004). Both Tuzet et al. (2003) and Zhang et al. (2014) showed the hysteresis in response of E to climate variables, particularly D and soil moisture, and the need for SPAC models to be able to capture this phenomenon. Accounting for the liquid resistances between the soil and foliage may improve the simulation of the canopy conductance and therefore E, which will be important to capture any changes in E with climate change. However, some researchers believe that model validation does not exist; rather we can only attempt to falsify a model with data, which is complicated by the uncertainty in the model parameters, structure and EC data itself (Baldocchi, 2008).

Few EC sites in the world have continuous EC measurement records as long as those from OA and OBS. This record has allowed me to conduct trend and relationship analyses on over two decades of flux measurements in this thesis from two sites, which are currently types of analyses that are limited to a few sites. Baldocchi et al. (2017) reported that of 59 sites flux sites with 5 or more years of data, only 5 had more than 15 years; and the longest contained 18 years. Maintaining these long-term flux sites is of the utmost importance if we want to be able to monitor flux trends and responses to present and future climate. It is therefore unfortunate that such an important site, OA, has been decommissioned due to lack of funding to properly maintain the site. Losing a long-term flux site which monitored one of the dominant tree types in
the Canadian boreal forest is a true loss because of the large impact that the boreal forest has on global C and water balances.
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Appendices

Appendix A  Photographs of the Measurement Sites and Eddy-Covariance Instrumentation

This appendix shows photographs of the Old Aspen and Old Black Spruce sites where EC-measurements were made. The photographs were taken by members of the Biometeorology and Soil Physics Group and technicians hired by the group.

Figure A.1 View of the Old Aspen forest from the scaffold tower in summer 2013.
Figure A.2 View of the Old Aspen forest from the scaffold tower in the winter of March 2011.
Figure A3. Photograph of the 37-m tall tower at OA as seen from the ground.
Figure A.4 Photograph of the eddy-covariance (EC) system at the 39-m height at OA, showing a three-dimensional ultrasonic anemometer (model R3 (1999-present) Gill Instruments Ltd., Lymington, UK), a sample tube that connects to a closed-path, temperature-controlled infrared gas (CO₂/H₂O) analyzer (IRGA) (model LI-6262 or LI-7000, LI-COR Inc.), and 36-gauge chromel-constantan thermocouples.
Figure A.5 View of the Old Black Spruce forest from the scaffold tower in summer 2013.
Figure A.6 View of the Old Black Spruce forest from the scaffold tower in the winter of October 2013.
Figure A.7 Photograph of the 25-m tall tower at OBS with the eddy-covariance (EC) system, radiometer boom, and air temperatures in aspirated fans, as seen from the ground.
Figure A.8 Photograph of the eddy-covariance (EC) system at the 27-m height at OBS, showing a three-dimensional ultrasonic anemometer (model R3 (1999-present) Gill Instruments Ltd., Lymington, UK), a sample tube that connects to a closed-path, temperature-controlled infrared gas (CO₂/H₂O) analyzer (IRGA) (model LI-6262 or LI-7000, LI-COR Inc.), and 36-gauge chromel-constantan thermocouples.
Appendix B  Monthly Relationships Between Climate and \( E \) and \( G_c \)

This appendix shows the individual growing season monthly (May, June, July, August, and September) relationships between climate variables and \( E \) and \( G_c \) at OA and OBS.

Table B1. Relationships between growing-season monthly (May, June, July, August and September) mean evapotranspiration \( E \) (mm d\(^{-1}\)) and respective air temperature (\( T_a \), °C), vapour pressure deficit (\( D \), kPa), net radiation (\( R_n \), W m\(^{-2}\)), downwelling photosynthetically active radiation (\( Q \), µmol m\(^{-2}\)s\(^{-1}\)), total growing season precipitation (\( P \), mm), integrated (90 cm at OA and 60 cm at OBS) soil volumetric water content (\( \theta \), m\(^3\) m\(^{-3}\)) at Old Aspen (OA) and Old Black Spruce (OBS).

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<td>( p )</td>
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Table B2. Relationships between growing-season monthly (May, June, July, August and September) mean canopy conductance \( (G_c) \) (mm s\(^{-1}\)) and respective air temperature \( (T_a) \), vapour pressure deficit \( (D) \), net radiation \( (R_n) \), downwelling photosynthetically active radiation \( (Q) \), total growing season precipitation \( (P) \), integrated (90 cm at OA and 60 cm at OBS) soil volumetric water content \( (\theta) \) at Old Aspen (OA) and Old Black Spruce (OBS).

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Appendix C  Individual Year Model Versus Measured Results

This appendix has tables showing the half-hourly Jarvis-Stewart and Modified Ball-Woodrow-Berry model fits for individual years (1999-2017) at OA and (1999-2017) at OBS.

Table C1. Relationships between half-hourly Jarvis-Stewart (JS) and Modified Ball-Woodrow-Berry (MBWB) modelled versus measured $G_c$ (mm s$^{-1}$) and $\lambda E$ (W m$^{-2}$) for OA from 1996-2017 (See Figure 5.4).

<table>
<thead>
<tr>
<th>Year</th>
<th>Jarvis-Stewart</th>
<th>Modified Ball-Woodrow-Berry</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$G_{c,\text{meas}} = 1.01 G_{c,\text{mod}} + 0.01, R^2 = 0.51$</td>
<td>$G_{c,\text{meas}} = 1.21 G_{c,\text{mod}} - 1.06, R^2 = 0.33$</td>
</tr>
<tr>
<td></td>
<td>$\lambda E_{\text{meas}} = 1.24 \lambda E_{\text{mod}} - 20.54, R^2 = 0.86$</td>
<td>$\lambda E_{\text{meas}} = 1.16 \lambda E_{\text{mod}} - 23.25, R^2 = 0.72$</td>
</tr>
<tr>
<td>1996</td>
<td>$G_{c,\text{meas}} = 0.87 G_{c,\text{mod}} + 1.21, R^2 = 0.40$</td>
<td>$G_{c,\text{meas}} = 1.18 G_{c,\text{mod}} - 1.80, R^2 = 0.34$</td>
</tr>
<tr>
<td></td>
<td>$\lambda E_{\text{meas}} = 1.21 \lambda E_{\text{mod}} - 25.26, R^2 = 0.66$</td>
<td>$\lambda E_{\text{meas}} = 1.16 \lambda E_{\text{mod}} - 33.69, R^2 = 0.73$</td>
</tr>
<tr>
<td>1997</td>
<td>$G_{c,\text{meas}} = 0.64 G_{c,\text{mod}} + 1.20, R^2 = 0.33$</td>
<td>$G_{c,\text{meas}} = 1.02 G_{c,\text{mod}} - 1.47, R^2 = 0.26$</td>
</tr>
<tr>
<td></td>
<td>$\lambda E_{\text{meas}} = 1.12 \lambda E_{\text{mod}} - 34.31, R^2 = 0.80$</td>
<td>$\lambda E_{\text{meas}} = 1.09 \lambda E_{\text{mod}} - 34.82, R^2 = 0.70$</td>
</tr>
<tr>
<td>1998</td>
<td>$G_{c,\text{meas}} = 0.76 G_{c,\text{mod}} + 0.96, R^2 = 0.38$</td>
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<td>$\lambda E_{\text{meas}} = 1.11 \lambda E_{\text{mod}} - 26.39, R^2 = 0.85$</td>
<td>$\lambda E_{\text{meas}} = 1.18 \lambda E_{\text{mod}} - 26.54, R^2 = 0.76$</td>
</tr>
<tr>
<td>1999</td>
<td>$G_{c,\text{meas}} = 0.76 G_{c,\text{mod}} + 0.61, R^2 = 0.42$</td>
<td>$G_{c,\text{meas}} = 1.11 G_{c,\text{mod}} - 1.76, R^2 = 0.41$</td>
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<tr>
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<td>$\lambda E_{\text{meas}} = 1.05 \lambda E_{\text{mod}} - 22.22, R^2 = 0.84$</td>
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</tr>
<tr>
<td>2000</td>
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<td>$\lambda E_{\text{meas}} = 0.95 \lambda E_{\text{mod}} - 23.60, R^2 = 0.79$</td>
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<tr>
<td>2001</td>
<td>$G_{c,\text{meas}} = 0.77 G_{c,\text{mod}} + 1.00, R^2 = 0.33$</td>
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<td>$\lambda E_{\text{meas}} = 0.89 \lambda E_{\text{mod}} + 1.91, R^2 = 0.61$</td>
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</tr>
<tr>
<td>Year</td>
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<td>λEmeas</td>
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<td>--------</td>
</tr>
<tr>
<td>2003</td>
<td>0.55Gcmod + 0.95, R² = 0.34</td>
<td>0.96λEmod - 10.82, R² = 0.59</td>
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<tr>
<td>2005</td>
<td>0.82Gcmod + 1.15, R² = 0.39</td>
<td>1.24λEmod - 26.44, R² = 0.86</td>
</tr>
<tr>
<td>2007</td>
<td>0.89Gcmod + 1.39, R² = 0.34</td>
<td>1.26λEmod - 21.69, R² = 0.78</td>
</tr>
<tr>
<td>2009</td>
<td>1.06Gcmod + 1.09, R² = 0.39</td>
<td>1.41λEmod - 21.10, R² = 0.80</td>
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<tr>
<td>2011</td>
<td>0.90Gcmod + 1.27, R² = 0.37</td>
<td>1.28λEmod - 13.74, R² = 0.77</td>
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<tr>
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<td>1.30Gcmod + 0.86, R² = 0.37</td>
<td>1.43λEmod - 19.43, R² = 0.85</td>
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<tr>
<td>2004</td>
<td>0.85Gcmod - 0.52, R² = 0.30</td>
<td>1.03λEmod - 15.62, R² = 0.73</td>
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<tr>
<td>2006</td>
<td>0.94Gcmod - 0.30, R² = 0.29</td>
<td>1.14λEmod - 31.38, R² = 0.77</td>
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<tr>
<td>2008</td>
<td>1.15Gcmod - 2.10, R² = 0.30</td>
<td>1.14λEmod - 35.78, R² = 0.77</td>
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<tr>
<td>2010</td>
<td>0.94Gcmod - 0.61, R² = 0.25</td>
<td>1.10λEmod - 26.85, R² = 0.74</td>
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<tr>
<td>2012</td>
<td>1.24Gcmod - 2.67, R² = 0.28</td>
<td>1.18λEmod - 38.62, R² = 0.75</td>
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</table>
Table C2. Relationships between daily Jarvis-Stewart (JS) and Modified Ball-Woodrow-Berry (MBWB) modelled versus measured $G_c$ (mm s$^{-1}$) and $\lambda E$ (W m$^{-2}$) for OBS from 1999-2017 (See Figure 5.6).

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<td>$G_{c\text{meas}} = 0.60G_{c\text{mod}} - 0.01, R^2 = 0.24$</td>
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<td>$\lambda E_{\text{meas}} = 1.15\lambda E_{\text{mod}} + 11.25, R^2 = 0.60$</td>
<td>$\lambda E_{\text{meas}} = 0.94\lambda E_{\text{mod}} - 3.07, R^2 = 0.72$</td>
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<tr>
<td>2000</td>
<td>$G_{c\text{meas}} = 0.59G_{c\text{mod}} - 0.00, R^2 = 0.21$</td>
<td>$G_{c\text{meas}} = 0.92G_{c\text{mod}} + 0.36, R^2 = 0.36$</td>
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<td>$\lambda E_{\text{meas}} = 1.16\lambda E_{\text{mod}} + 9.21, R^2 = 0.55$</td>
<td>$\lambda E_{\text{meas}} = 0.98\lambda E_{\text{mod}} - 6.47, R^2 = 0.66$</td>
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<td>2001</td>
<td>$G_{c\text{meas}} = 0.50G_{c\text{mod}} - 0.00 R^2 = 0.21$</td>
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<td>$G_{c\text{meas}} = 0.47G_{c\text{mod}} - 0.00, R^2 = 0.20$</td>
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<td>-----------------</td>
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<td>1.04( \lambda E_{\text{mod}} ) + 3.11</td>
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<td>( \lambda E_{\text{meas}} ) = 1.01( \lambda E_{\text{mod}} ) - 2.64</td>
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<td>2016</td>
<td>( G_{\text{meas}} ) = 0.67( G_{\text{mod}} ) - 0.00</td>
<td>0.82( G_{\text{mod}} ) + 1.41</td>
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<td>( \lambda E_{\text{meas}} ) = 01.25( \lambda E_{\text{mod}} ) + 0.21</td>
<td>0.76( \lambda E_{\text{mod}} ) - 0.05</td>
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<td>2017</td>
<td>( G_{\text{meas}} ) = 0.46( G_{\text{mod}} ) + 0.00</td>
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<td>( \lambda E_{\text{meas}} ) = 1.08( \lambda E_{\text{mod}} ) + 1.50</td>
<td>0.77( \lambda E_{\text{mod}} ) - 6.96</td>
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</table>
Appendix D  EC Measurement Issues

This appendix discusses in detail the known issues/problems with EC measurements.

D.1  Uncertainty in EC Fluxes

Total uncertainty in EC measurements comprises two types of error, systematic and random. Systematic (or bias) errors occur due to invalid assumptions and methodological challenges, instrumentation calibration and data processing, while random errors are due to heterogeneity of the vegetation/stands affecting flux footprints, errors due to instrumentation and to the stochastic nature of turbulence (Baldocchi et al., 2008; Richardson et al., 2012). When calculating fluxes, if the assumptions of a homogenous and flat surrounding, stationary transport processes, sufficient turbulent transport and vertical fluxes being the only significant mechanism of transport are not met, errors in the fluxes will result (Baldocchi et al., 1998; Foken and Wichura, 1996; Massman and Lee, 2002). These assumptions are violated in patchy landscapes, landscapes where the instrumentation sees different types of vegetation coming from different wind sectors, or in complex topography where advection leads to a non-zero flux divergence (Lee 1998; Finnigan et al., 2003). Advection can occur even in flat terrain where the canopy source-sink strength is not homogenous (Finnigan, 2008). The systematic errors from unmet assumptions can be reduced through careful site selection and sensor setup (Munger et al., 2012), and by applying the appropriate corrections, such as coordinate rotations (Baldocchi et al., 1998; Lee, 1998; Paw U et al., 2000; Foken et al., 2012).

All meteorological measurements require quality assurance and control procedures, with this being especially important for computed flux covariances (Foken and Wichura, 1996; Aubinet et al., 2000; Foken et al., 2004, 2012; Loescher et al., 2006). Most quality assurance
procedures rely on the friction velocity ($u^*$) threshold filter for poor turbulent mixing periods, first proposed by Goulden et al. (1996) (Aubinet et al., 2000; Falge et al., 2001; Papale et al., 2006, Aubinet et al., 2012). These procedures leave the best-measured data but many gaps are introduced, with on average of 35%, due to system failures and data rejections (Falge et al., 2001) or anywhere from 20-60% rejected by various applied quality filters (Papale et al., 2006). For OA and OBS, annual EC flux data rejection was generally less than 20% with most of this being due to low nighttime $u^*$. Gap-filling is required to produce a continuous data set to calculate daily to annual totals. Common gap-filling methods include using the mean diurnal variation (Falge et al., 2001), non-linear equations which express semi-empirical relationships (Hollinger et al., 2004; Barr et al., 2004; Richardson et al., 2006), neural-networks (Papale and Valentini, 2003; Braswell et al., 2005) and process-based models (Gove and Hollinger, 2006).

D.2 Energy Balance Closure Issues

Another commonly used metric to assess the quality of a flux data set is the achieved energy balance closure, also called the closure fraction or closure ratio $R = (H + LE)/(R_n - G)$ (Wang and Dickinson, 2012). Many sites and flux network summaries report that energy balance closure is underestimated by 10-30% (Aubinet et al., 2000; Wilson et al., 2002; Oncley et al., 2007; Beer et al., 2010). There is no clear cause for the energy imbalance, with several likely reasons summarized and ways to deal with them discussed (Foken, 2008; Foken et al., 2012; Gerken et al., 2018). Some researchers have achieved energy balance closure of >90% when bole/canopy energy storage due to photosynthesis and respiration are measured properly (Lindroth et al., 2010) and when including the rate of change in biomass temperature, by equating it with the rate of change of the air temperature within the canopy (Meyers and Hollinger, 2004). Recent studies have found that use of a longer averaging period up to several
hours (Sakai et al., 2001; Finnigan et al., 2003; Mauder and Foken, 2006) or using spatially averaged fluxes (Kanda et al., 2004; Steinfelt et al., 2007) could improve energy balance closure. Foken et al. (2012) have concluded that the energy balance closure issue is not a problem with the EC method but the heterogenous terrain and its impact on the turbulent exchange. They recommend that sensible and latent heat fluxes be corrected assuming that the Bowen-ratio is correct and not correcting the CO$_2$ fluxes. Similarly, Baldocchi et al. (2008) does not recommend correcting CO$_2$ flux measurements for energy balance closure.

D.3 Flux Footprints

To obtain the best EC measurements, a flux tower should be located in a homogeneous forest (same stand height, tree species or even distribution of different species) in flat terrain such that the source area of the measurements is well within the extent of the homogenous surface (Rannik et al., 2012). It is not always possible to attain these ideal conditions, such as in patchy landscapes or when the measurement system sees different vegetation types with changing wind sectors. To interpret seasonal or annual fluxes under such conditions, footprint models are required (Baldocchi et al., 2008). Any inhomogeneity modifies the turbulence and thus the footprint, which is the contribution to a flux measurement point from the fraction of the surface area that is an effective source or sink (Leclerc and Thurtell, 1990; Kljun et al., 2002). Chen et al. (2012) combined a footprint model, remotely sensed vegetation indices, semivariogram and window size analyses to characterize the source of the EC fluxes of the 12 main Canadian Carbon Program sites including OA and OBS. They produced maps overlaying the annual cumulative flux contours on Normalized Difference Vegetation Index (NDVI) maps at a 30-m resolution for each area (6 × 6 km) centred on individual flux towers. They showed that the annual 90% contour flux footprint areas for OA and OBS were 3.2 km$^2$ and 3.8 km$^2$.\hfill 219
respectively, with the former representing a combination of dense and open broadleaf forest and the latter dense and open coniferous forest with some herb and shrub wetland.

D.4 Flux Partitioning Issues

Using these C and water flux data, scientists want to understand ecosystem processes contributing to fluxes, but this is not straight forward with EC, which measures the net exchange of mass and energy. The net ecosystem exchange of CO₂ (NEE) or net ecosystem production (NEP = −NEE) is the difference between two fluxes, CO₂ uptake by photosynthesis, gross ecosystem production (GEP), and CO₂ released by ecosystem respiration (Re) (i.e., NEP = GEP − Re). Thus, it is necessary to use flux partitioning algorithms to split NEE into GEP and Re. As the use of EC grew, the benefits of and issues with various flux partitioning algorithms have been discussed (Reichstein et al., 2005, 2012; Moffat et al., 2007; Desai et al., 2008; Lasslop et al., 2010).

A common partitioning method is based on the idea that only Re occurs at night while GEP is almost zero, such is the case in C₃ and C₄ photosynthetically dominated ecosystems, but the challenge is extrapolating nighttime Re measurements to daytime and calculating GEP (Reichstein et al., 2012). The problem with this method is that at nighttime turbulence is often suppressed and the assumptions necessary to use EC are often violated, so much of the data gets filtered out and must be modelled to gap-fill (Aubinet et al. 2010; Rebmann et al. 2010). Re is often modelled using: a single temperature dependent equation, using either air or soil temperature (Van Dijk and Dolman, 2004; Richardson et al., 2006), a Q₁₀ equation, also using temperature as a dominant driver (Ryan, 1991), an Arrhenius equation (Lloyd and Taylor, 1994; Falge et al., 2001), or exponential temperature-based models (Desai et al., 2005). However,
while these models are mostly driven by temperature, $R_e$ also depends on water and nutrient content (Palmroth et al., 2005; Jarvis et al., 2007; Carbone et al., 2008).

Another method uses fits a model to daytime NEE observations to take into account the response of GEP and $R_e$ to climate variables such as solar or photosynthetically active radiation and VPD (Falge et al., 2001; Lasslop et al., 2010). This approach accounts for the effect of light inhibition of $R_e$. The response of NEE to radiation is often modelled with a rectangular hyperbola (Wofsy et al., 1993) or a non-rectangular hyperbola which often fits measured data better than the rectangular hyperbola (Gilmanov et al., 2003). Other less common techniques used to partition fluxes are: using high frequency data rather than half hourly (Thomas et al., 2008; Scanlon and Kustas, 2010), using stable isotopes (Bowling et al., 2001; Dawson et al., 2002; Ogee et al., 2004; Zhang et al., 2006), upscaling chamber measurements (Bolstad et al., 2004; Ohkubo et al., 2007; Subke et al., 2009; Wang et al., 2010).

C flux partitioning has been the main focus of flux partitioning, but similar to the issue of partitioning CO$_2$ fluxes, EC measures the total flux of water above a canopy, i.e., evapotranspiration (ET), which must be partitioned into its components to study the processes contributing to H$_2$O fluxes. ET is the sum of the transpiration from plants, evaporation of intercepted water and evaporation from the soil surface. As with the C fluxes, it is common to split the data into periods when transpiration and interception are near zero, such as when there are no leaves in a deciduous forest. Evaporation from the soil is often modelled as a function of radiation (Stoy et al., 2006; Dawson et al., 2007; Fisher et al., 2007) or VPD (Oishi et al., 2008). A common method used is partitioning EC measured ET by upscaling sapflux measurements (Köstner et al., 1998; Sauer et al., 2007). As with CO$_2$ flux partitioning, using stable isotope to partition evaporation and transpiration is also utilized (Wang and Yakir, 2000; Albertson et al.,
Evaporation from canopy interception can be estimated by measuring $P$ with two rain gauges, one measuring total rainfall and the other measuring the rainfall under the vegetation, with interception being the difference between the two gauges (Bréda et al., 2006; Herbst et al., 2008). Although $E$ can be derived from latent heat flux observations, transpiration or the ratio of transpiration to evaporation cannot be measured directly, thus Zhou et al. (2016) proposed a novel method using the apparent underlying WUE (observed WUE which is affected by soil evaporation) and the potential underlying WUE (coupled carbon-water relationship applied under steady state conditions in a uniform ecosystem), to estimate transpiration at the ecosystem scale. Similarly, Nelson et al. (2016) created the Transpiration Estimation Algorithm, which uses both GPP and $E$ to estimate temporal patterns of WUE, from which $T$ is calculated.