INTERANNUAL VARIABILITY OF CARBON DIOXIDE (CO₂) AND METHANE (CH₄) FLUXES IN A TEMPERATE BOG OVER A 5-YEAR PERIOD

by

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

Interannual Variability of Carbon Dioxide (CO₂) and Methane (CH₄) Fluxes in a Temperate Bog over a 5-Year Period

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Abstract

Peatland rewetting, which is a management effort to restore water levels in previously drained peatlands, is important for re-establishing the role of peatlands as carbon (C) sinks. Since rewetted peatlands often have a highly variable response to year-to-year changes in climatic conditions and to functional changes, long term studies of C fluxes are needed in these ecosystems. Here, we evaluated the impact of climate variability and functional change on the interannual variability of CO₂ and CH₄ fluxes at Burns Bog, a rewetted temperate bog in Canada, based on five years of continuous eddy-covariance measurements. We found that the study site alternated between being an annual-scale net CO₂ sink and source, ranging from -32.6 ± 21.5 (± 95% CI) to 11.9 ± 15.1 g CO₂-C m⁻² year⁻¹, respectively, while consistently being a CH₄ source, ranging from 11.6 ± 0.7 to 18.0 ± 1.6 g CH₄-C m⁻² year⁻¹. On a five-year average, CH₄ emissions (13.7 ± 2.5 g CH₄-C m⁻² year⁻¹; ± SD across years) completely offset the CO₂ sink (-12.3 ± 20.4 g CO₂-C m⁻² year⁻¹; ± SD across years) on a carbon equivalent basis, resulting in the site losing an average of 1.3 ± 23.9 g C m⁻² year⁻¹ (± SD across years). This finding indicates that excluding CH₄ fluxes from the net ecosystem C budget results in a significant overestimation of the net C uptake at this peatland site. The bog was the greatest annual CO₂ source in the year with a dry and warm summer, emphasizing the importance of temperature and water table depth at the bog. Regardless of the GHG metrics (i.e., global warming potential or sustained global warming potential) used in calculating the annual CO₂-eq GHG balance, the bog consistently had a positive radiative balance during each year of the study period. Despite mainly acting as a GHG source, the rewetted bog will likely have cooling effect on climate over long timescales compared to drained bogs that are large CO₂ sources.
Lay Summary

Peatlands are known to store a large amount of carbon due to their ability to take up carbon dioxide (CO₂) from the atmosphere. However, simultaneously, peatlands release a significant amount of methane (CH₄), which is more effective at trapping heat in the atmosphere than CO₂. This study investigates how climatic and biotic factors influence the year-to-year variability in CO₂ and CH₄ exchange over five years in a rewetted peatland in Canada. We found that warmer and drier summers resulted in the peatland emitting more carbon into the atmosphere. Although the bog mainly acted as a greenhouse gas source over the five years, rewetting effort will likely have a cooling effect on climate over long timescales compared to drained bogs. This research can help inform policy makers about the future impacts of climate change on peatlands and how to improve peatland management for climate change mitigation and adaptation.
Preface

The eddy covariance (EC) tower was built by Andreas Christen, Rick Ketler, Nick Lee, and Zoran Nesic. The EC system and the meteorological sensors maintenance throughout the five years were performed by Rick Ketler, Zoran Nesic, Mark Johnson, Nick Lee, Brenda D’acunha, Laura Morillas, Johannes Exler, Yeonuk Kim, Sarah Russel, Marion Nyberg, Tzu-Yi Lu, June Skeeter, and myself.

The code for high frequency flux processing, methane gap-filling, and water table depth correction was provided by Sara Knox and Marion Nyberg, Yeonuk Kim, and Johannes Exler, respectively. Flux data processing were conducted by Brenda D’acunha, Laura Morillas, Yeonuk Kim, Sara Knox, Marion Nyberg, and myself. Portions of the data wrangling and calculation were modified from the code provided by Marion Nyberg. Analysis of the five-year data was primarily done by myself.

Ancillary weather data was collected from “Delta-Burns Bog” weather station (Environment Canada and Climate Change), and from “UBC Totem Field” weather station (UBC Land and Food Systems).
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<th>Description</th>
<th>Unit</th>
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<tbody>
<tr>
<td>AIC</td>
<td>Akaike information criterion</td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>Carbon</td>
<td></td>
</tr>
<tr>
<td>CH$_4$</td>
<td>Methane</td>
<td></td>
</tr>
<tr>
<td>CI</td>
<td>Confidence interval</td>
<td></td>
</tr>
<tr>
<td>CO$_2$</td>
<td>Carbon dioxide</td>
<td></td>
</tr>
<tr>
<td>DOC</td>
<td>Dissolved organic carbon</td>
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</tr>
<tr>
<td>EC</td>
<td>Eddy covariance</td>
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</tr>
<tr>
<td>ET</td>
<td>Evapotranspiration</td>
<td>mm</td>
</tr>
<tr>
<td>f$_{GPP}$</td>
<td>Relative influence of GPP on interannual variability in NEE</td>
<td></td>
</tr>
<tr>
<td>f$_{RECO}$</td>
<td>Relative influence of R$_{eco}$ on interannual variability in NEE</td>
<td></td>
</tr>
<tr>
<td>GHG</td>
<td>Greenhouse gas</td>
<td></td>
</tr>
<tr>
<td>GPP</td>
<td>Gross primary production</td>
<td>g CO$_2$-C m$^{-2}$ time$^{-1}$</td>
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<tr>
<td>GS</td>
<td>Growing season</td>
<td></td>
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<tr>
<td>Gs</td>
<td>Surface conductance</td>
<td>m s$^{-1}$</td>
</tr>
<tr>
<td>GWP</td>
<td>Global warming potential</td>
<td></td>
</tr>
<tr>
<td>H</td>
<td>Sensible heat flux</td>
<td></td>
</tr>
<tr>
<td>HOS</td>
<td>Homogeneity of slopes</td>
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<tr>
<td>Abbreviation</td>
<td>Description</td>
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<tr>
<td>--------------</td>
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<tr>
<td>LAI</td>
<td>Leaf area index</td>
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<tr>
<td>LE</td>
<td>Latent heat flux</td>
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<tr>
<td>LUE or $\alpha$</td>
<td>Light use efficiency $\mu$mol CO$_2$ ($\mu$mol photon)$^{-1}$</td>
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<td>LUT</td>
<td>Look-up table</td>
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<tr>
<td>MDC</td>
<td>Mean diurnal course</td>
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<td>Marginal distribution sampling</td>
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<tr>
<td>MLR</td>
<td>Multiple linear regression</td>
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<td>Net ecosystem carbon balance g C m$^{-2}$ time$^{-1}$</td>
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<td>Net ecosystem exchange g CO$_2$-C m$^{-2}$ time$^{-1}$</td>
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<tr>
<td>NGS</td>
<td>Non-growing season</td>
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<tr>
<td>Pa</td>
<td>Atmospheric pressure kPa</td>
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<td>Photosynthetically active radiation mol m$^{-2}$ time$^{-1}$</td>
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<td>Light-saturated photosynthetic capacity $\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$</td>
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<td>PPFD</td>
<td>Photosynthetic photon flux density $\mu$mol m$^{-2}$ s$^{-1}$</td>
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<tr>
<td>Q10</td>
<td>Temperature sensitivity</td>
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<td>Temperature sensitivity of methane flux</td>
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<td>Temperature sensitivity of ecosystem respiration</td>
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<tr>
<td>$R_a$</td>
<td>Autotrophic respiration</td>
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<td>$R_{\text{eco}}$</td>
<td>Ecosystem respiration g CO$_2$-C m$^{-2}$ time$^{-1}$</td>
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<tr>
<td>$R_g$</td>
<td>Incoming shortwave radiation (global radiation) on a horizontal surface</td>
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</tr>
<tr>
<td>RH</td>
<td>Relative humidity %</td>
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<tr>
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<tr>
<td>--------</td>
<td>--------------------------------------------------</td>
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</tr>
<tr>
<td>Rh</td>
<td>Heterotrophic respiration</td>
<td></td>
</tr>
<tr>
<td>SD or $\sigma$</td>
<td>Standard deviation</td>
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</tr>
<tr>
<td>SGWP</td>
<td>Sustained global warming potential</td>
<td></td>
</tr>
<tr>
<td>SSE</td>
<td>sum of squares error</td>
<td></td>
</tr>
<tr>
<td>SSR</td>
<td>sum of squares of functional changes</td>
<td></td>
</tr>
<tr>
<td>SSic</td>
<td>sum of squares of interannual climatic variability</td>
<td></td>
</tr>
<tr>
<td>SSsc</td>
<td>sum of squares of the seasonal climatic variability</td>
<td></td>
</tr>
<tr>
<td>SSRt</td>
<td>sum of squares of the interannual climatic variability</td>
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<tr>
<td>T_a</td>
<td>Air temperature</td>
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<tr>
<td>T_s,10cm</td>
<td>Soil temperature at 10 cm depth</td>
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<td>T_s,50cm</td>
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<td>T_s,5cm</td>
<td>Soil temperature at 5 cm depth</td>
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<td>u*</td>
<td>Friction velocity</td>
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<td>VPD</td>
<td>Vapour pressure deficit</td>
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<td>WTD</td>
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Dedication

This thesis is dedicated to my dear husband who believes in me and inspires me everyday, my grandma (1929-2021) and my family back in Indonesia who had always been supportive of my education, and Annie Wong who makes Vancouver feels like a second home.
Chapter 1: Introduction

Peatland ecosystems are known to play a critical role in the global C cycle. Most intact peatlands are CO₂ sinks, collectively sequestering around ~1 Pg C y⁻¹ globally (Frolking et al., 2011). Simultaneously, peatlands are also CH₄ sources, which can influence the overall net C sink status of the bog. Additionally, as a potent greenhouse gas (GHG), CH₄ has a global warming potential 80, 27, and 7 times that of CO₂ on a time scale of 20, 100, and 500 years, respectively (Forster et al. 2021). Thus, including CH₄ fluxes in the net C budget and the net GHG budget of peatlands is necessary (Limpens et al., 2008).

To date, many studies have focused on investigating the short-term carbon balance of peatlands, while only a few have conducted long-term measurements of both CO₂ and CH₄ fluxes (Koehler et al., 2011; Rinne et al., 2018; Roulet et al., 2007). While 1-year studies found that most intact peatlands are C sinks, longer-term studies show that the magnitude of C uptake varies considerably from year-to-year (Drollinger et al., 2019; Rinne et al., 2018; Ueyama et al., 2020). Some long-term studies have also reported that peatlands could alternate between being C sinks and C sources within a few years depending on environmental conditions (Roulet et al., 2007; Strachan et al., 2016). For drained and restored peatlands, their responses to a changing climate are even less understood as there are not as many long-term ecosystem scale C flux studies available compared to their undisturbed counterparts (Holl et al., 2020; Nugent et al., 2018; Swenson et al., 2018; Wilson et al., 2016).
This large interannual variability raises the question of whether short-term studies are adequate in characterizing the C balance of peatlands (Baldocchi et al., 2018). Conducting more long-term C fluxes measurements is necessary to improve our understanding of the stability of peatlands and their response to disturbances and a changing climate, especially since drivers of CO$_2$ and CH$_4$ fluxes vary at different timescales (Wang et al., 2018).

1.1 CO$_2$ and CH$_4$ Exchange in Peatlands

Major pathways of CO$_2$ uptake and release in peatlands are through photosynthesis and respiration, respectively (Mitsch & Gosselink, 2015). Photosynthesis is a light-induced process where CO$_2$ from the atmosphere is taken up by plants and converted into carbohydrates (Vasander & Kettunen, 2006). The total CO$_2$ uptake from photosynthesis is commonly referred to as gross primary productivity (GPP). The carbon product from photosynthesis is used by the plant to add biomass for building plant structures (i.e., stems, roots, and leaves). Plants also respire back some of the CO$_2$ to the atmosphere in a process called autotrophic respiration (R$_a$).

At the same time, organic matter from dead plant matter, litter, and root exudates are decomposed into simpler carbon compounds by aerobic microorganisms in a process called heterotrophic respiration (R$_h$) (Kang & Jang, 2016). The end product of heterotrophic respiration is CO$_2$ that is released back to the atmosphere (Vasander & Kettunen, 2006). Ecosystem respiration (R$_{eco}$) represents the sum of heterotrophic and autotrophic respiration. The net atmospheric CO$_2$ budget of peatland ecosystems, or net ecosystem exchange (NEE), is the difference between R$_{eco}$ and GPP. Negative NEE values indicate that the peatland is a net CO$_2$ sink, taking up more CO$_2$ than it releases back to the atmosphere (Luyssaert et al., 2007).
In peatlands, saturated soil condition limit oxygen availability, resulting in slow decomposition rates (Wieder, 2006). As a result, partially decomposed organic matter accumulates as thick layers of peat, storing carbon in the ecosystem (Wieder, 2006). However, in this anaerobic soil layer, CH$_4$ production can occur (Vasander & Kettunen, 2006). The exchange of CH$_4$ between the surface and the atmosphere depends on the rates of production, transport, and consumption of methane within the soil profile (Bridgham et al., 2013; Dean et al., 2018).

CH$_4$ production is a result of the decomposition of organic compounds under anaerobic condition (Kang & Jang, 2016). In waterlogged soils, anaerobic bacteria promote hydrolysis and fermentation of complex organic matter to produce organic acids, hydrogen and other compounds (Kang & Jang, 2016). These compounds are then metabolized by a type of Archaea called methanogens to produce methane in a process called methanogenesis (Segers, 1998). Methanogenesis can happen through two pathways, acetotrophic and hydrogenotrophic methanogenesis (Whalen, 2005). Acetotrophic methanogens use acetate for substrates, while hydrogenotrophic methanogens convert CH$_4$ from CO$_2$ and H$_2$ (Lai, 2009).

After CH$_4$ is produced in the deeper anoxic layer of the soil, it moves upwards through the soil. Oxygen concentrations can be higher near the surface if the soil is unsaturated, which provides the ideal environment for aerobic methanotrophic bacteria. Here, methanotrophs oxidize methane into CO$_2$ in a process called CH$_4$ consumption. In some anaerobic conditions (e.g., flooded peatland soils), CH$_4$ consumption can also occur with the help of methanotrophic Archaea (Dean et al., 2018).
The rest of the unoxidized \( \text{CH}_4 \) is transported to the atmosphere by diffusion, ebullition, and plant-mediated transport. Diffusion, which is a result of \( \text{CH}_4 \) concentration gradients on the surface (i.e., between soil or water and air) and below the surface (within the soil and water), is known as a primary pathway of \( \text{CH}_4 \) release from bare soil or water (Dušek et al., 2020). The second \( \text{CH}_4 \) transport mechanism is the spontaneous release of \( \text{CH}_4 \) through gas bubbles in a process called ebullition (Lai, 2009). Gas bubbles form when the \( \text{CH}_4 \) gas in the water reaches supersaturation and its partial pressure exceeds the hydrostatic pressure. This condition usually occurs during warm periods or during fluctuations in atmospheric pressure and is more significant in shallow flooded environments (Schütz et al., 1991; T. Tokida et al., 2007). In peatlands with vegetation adapted to a flooded environment, \( \text{CH}_4 \) gas in the water is taken up by the plant roots and transported upwards by the aerenchyma system through different pathways and rates depending on the plant functional types (Villa et al., 2020). Convective (bulk) through-flow is driven by pressure differences between the plant shoots and the roots and is usually rapid (Armstrong & Armstrong, 1991; Sorrell & Boon, 1994). In contrast, molecular diffusion, which is induced by concentration gradients, usually occurs at a much lower rate (Schütz et al., 1991). \( \text{CH}_4 \) then exits the plant through stomata, micropores of leaf sheaths, lenticels of the bark, and degrading plant structures (Nouchi et al., 1990; Schröder, 1989).

1.2 Drivers of \( \text{CO}_2 \) Fluxes in Peatland

Solar radiation at wavelengths of 0.4-0.7 \( \mu \text{m} \), or photosynthetically active radiation (PAR in \( \text{W m}^{-2} \)) or photosynthetic photon flux density (PPFD in \( \text{mol m}^{-2} \text{ s}^{-1} \)), is one of the primary controls of productivity in peatlands (Bubier et al., 1998; Frolking et al., 1998). Despite other site-specific
environmental factors, high PAR in the growing season is associated with higher plant growth across a broad geographical range (Frolking et al., 1998; Loisel et al., 2012). As described by Frolking et al. (1998), the relationship between GPP and PPFD across a range of peatland ecosystems is hyperbolic, with productivity saturating at a given light level depending on the peatland type (e.g., fen productivity saturates at higher PAR than bog productivity). At the seasonal timescale, studies have observed a hysteretic relationship between GPP and PAR, as indicated by the delayed peak of GPP compared to PAR over the growing season (Helfter et al., 2015; Walker et al., 2017). This finding suggests that peatland productivity efficiency (the increase in GPP per increase of PAR) may follow an exponential rate in the early growing season and a logarithmic decline in the late growing season (Helfter et al., 2015).

Besides controlling photosynthesis, solar irradiance directly affects air and peat temperature, which in turn control metabolic processes, i.e., respiration and plant growth (Bubier et al., 1998). Generally, peat temperature influence on R_{eco} is most evident near the surface, as the aerobic zone of the peat layer is often restricted within 10 to 30 cm of the peat surface (Acosta et al., 2017; Bubier et al., 1998; Lafleur et al., 2005). At the seasonal scale, Kross et al. (2014) found that the annual peak of R_{eco} lagged behind the annual peaks of GPP and air temperature by 3 to 4 weeks. Since GPP is more directly related to PAR and air temperature, the lag between GPP and R_{eco} is most likely caused by the delay between soil and surface warming (Bubier et al., 1998; Vasander & Kettunen, 2006).

Water table depth (WTD) also affects CO₂ fluxes, with the intensity of responses varying across sites. By controlling the thickness of the aerobic zone of the soil, WTD has a strong influence on
$R_{eco}$, and can explain up to 20% of the variability in respiration across boreal peatlands (Bubier et al., 1998). Lower WTD has also been observed to be associated with enhanced respiration with a time lag of up to 5 days due to gradual increase in heterotrophic respiration (Bubier et al., 1998; Helfter et al., 2015). A decline in WTD can also induce water stress in plants, which results in a decrease of GPP (Helfter et al., 2015).

Nutrient availability also influences carbon exchange in peatlands. Bubier et al. (1998) and Frolking et al. (1998) found that the range of NEE and $R_{eco}$ varied across peatlands with different trophic status, with higher NEE (i.e., less negative) and $R_{eco}$ observed in rich fens, followed by poor fens, and bogs. In terms of nutrient availability, bogs are generally poor because their sole nutrient input source is precipitation, in contrast to fens that receive their nutrient input from groundwater and run-off (Bubier et al., 1998; Frolking et al., 2011). At 5-10 year timescale, peatlands respond to nitrogen addition through shifts in vegetation composition, in which the dominant moss is replaced by vascular plants (Bubier et al., 2007; Juutinen et al., 2010). Since vascular plants decompose faster than moss, nutrient addition is expected to promote higher CO$_2$ release (Mao et al., 2018; Turetsky, 2003), although long-term studies are needed to confirm these results (Bubier et al., 2007; Juutinen et al., 2010).

Besides having different rates of decomposition, vegetation types influence CO$_2$ exchange through other mechanisms. Productivity varies among plant types, with mosses exhibiting a much lower rate of photosynthesis than vascular vegetation (Frolking, 1997; Korrensalo et al., 2016). Thus, the abundance of a particular vegetation cover has a strong effect on NEE (Yuan et
al., 2014). Limpens et al. (2008) also highlighted the importance of vegetation in determining the peat structure, which controls oxygen diffusion into the peat.

1.3 Drivers of CH$_4$ Fluxes in Peatland

Water table depth (WTD) drives CH$_4$ fluxes by determining the vertical profile of the soil’s oxygen concentration (Whalen, 2005). In the anoxic saturated layer, CH$_4$ is produced by methanogens, while in the overlying unsaturated (i.e. oxic) layer, CH$_4$ is oxidized. Lower water levels, which means a shallower CH$_4$ production layer and thicker CH$_4$ oxidation layer, are generally associated with lower CH$_4$ fluxes (Lai, 2009; Pelletier et al., 2007; Whalen, 2005). Furthermore, with a deeper WTD below the rooting zone of vascular plants, plant-mediated CH$_4$ transport cannot proceed and CH$_4$ production is limited by the lack of labile C substrate (Goodrich, Campbell, Roulet, et al., 2015). However, there are some cases where a deeper WTD resulted in a larger CH$_4$ emission (Kettunen et al., 1996). For example, Turetsky et al. (2014) found that the maximum CH$_4$ flux occurred when water levels were generally below the soil surface, with an optimum WTD of -23.8 cm for bogs and -0.1 to 9.7 cm for fens. At higher WTD (i.e., closer to the surface), as observed during rainfall and flooding events, CH$_4$ fluxes can also be suppressed (Kettunen et al., 1996). Heavy rainfall and flooding can reduce CH$_4$ production by increasing O$_2$ in moving water and limiting diffusion of CH$_4$ through standing water (Turetsky et al., 2014). The control of WTD on CH$_4$ fluxes was further complicated by the lagged response of CH$_4$ fluxes following a change in WTD (e.g. Laine et al., 2007; Moore & Dalva, 1993; Moore & Roulet, 1993; Turner et al., 2021). As WTD increases (e.g. post rainfall), CH$_4$ fluxes can increase again, peaking at a lag of ~10 days (Goodrich, Campbell, Roulet, et al., 2015; Kettunen et al., 1996; Wang et al., 2018).
Peat temperature is also a significant driver of CH$_4$ flux in peatland (Goodrich, Campbell, Roulet, et al., 2015; Hommeltenberg et al., 2014; Turetsky et al., 2014; Wang et al., 2018). Peat temperature controls CH$_4$ fluxes by influencing metabolic processes, e.g., methanogenesis and methanotrophy (Dušek et al., 2020). Generally, methanogenesis is most efficient at temperatures ranging from 20 to 40˚C and has lowest efficiency when temperatures are less than 5˚C (Whalen, 2005). Due to its relationship with methanogenesis, temperature sensitivity is often strongest at depth (e.g., 50 cm) as it is often continuously anoxic (Kettunen et al., 1996; Ueyama et al., 2020; Wang et al., 2018).

In most peatlands, the interaction between WTD and peat temperature is a dominant control on CH$_4$ fluxes. WTD plays a more critical part in tropical peatlands where temperature is not a limiting factor and varies minimally throughout the year (Dušek et al., 2020; Knox et al., 2021). Conversely, temperature is often a significant controlling factor at sites where WTD is less variable throughout the year (Dušek et al., 2020; Goodrich et al., 2015; Knox et al., 2021). Wang et al. (2018) found that WTD correlates to CH$_4$ emission only when peat temperature at 50 cm was above 7-9˚C, indicating that CH$_4$ is more dependent on temperature than water levels under cold conditions. In another study, Ueyama et al. (2020) found that temperature-limited CH$_4$ production regulates CH$_4$ fluxes more in the early growing season, while CH$_4$ transport dominates later in the late growing season, suggesting that which is the stronger driver may vary during the year.
Besides water level and temperature, vegetation also plays a key role in influencing CH$_4$ fluxes in peatlands. Vegetation controls CH$_4$ flux by supplying organic substrates for CH$_4$ production, such as root exudates and plant litter (Bridgham et al., 2013; Dean et al., 2018; Williams & Yavitt, 2009). Different plant species produce different substrate qualities depending on their degradability. For example, litter with higher lignin composition is harder to decompose, thus slowing the substrate utilization rate for CH$_4$ production (Limpens et al., 2008; Williams & Yavitt, 2009).

One way to indirectly assess substrate availability is through primary productivity. Studies have demonstrated a strong correlation between CH$_4$ flux and CO$_2$ exchange (Whalen, 2005). Rinne et al. (2018) observed a hysteretic relationship between monthly GPP and monthly CH$_4$ flux, with CH$_4$ flux lagging behind at 5 to 20 days. Wang et al. (2018) also found a similar behavior between CH$_4$ fluxes and CO$_2$ exchange, where daily CH$_4$ fluxes lagged 30 to 40 days behind the peak in net CO$_2$ uptake. These lags between CH$_4$ fluxes and CO$_2$ exchange suggest that methanogens use organic substrates that take time to decompose (Ueyama et al., 2020).

Besides supplying substrate for CH$_4$ production, vegetation also influences CH$_4$ fluxes by facilitating gas transport directly through vegetation and indirectly by influencing peat composition. Plant species determine the peat structure produced. In turn, peat layer porosity and hydraulic conductivity control redox reactions, gas diffusion, and ebullition (Limpens et al., 2008; Rezanezhad et al., 2016). Additionally, increasing aerenchymatous vegetation cover like sedge and graminoid is known to enhance CH$_4$ release to the atmosphere by facilitating plant-mediated transport (Lai, 2009; Limpens et al., 2008). A linear relationship between leaf area
index (LAI) and CH$_4$ flux further demonstrates the direct importance of vascular vegetation on peatland CH$_4$ exchange (Ueyama et al., 2020).

1.4 Interannual Variability in Peatland Carbon Exchange

1.4.1 CO$_2$ Fluxes

One of the most widely studied drivers of CO$_2$ interannual variability is WTD fluctuations as represented by the severity, timing, and duration of growing season drought and flooding events (Aslan-Sungur et al., 2016; Lund et al., 2012). Summer drought increases CO$_2$ source strength by enhancing $R_{eco}$ and suppressing GPP (Helfter et al., 2015; Lafleur et al., 2003; Lund et al., 2012; McVeigh et al., 2014; Mikhaylov et al., 2019). Similarly, flooding can also decrease net CO$_2$ uptake by inhibiting GPP through water stress in plants (Aslan-Sungur et al., 2016). Whether it is $R_{eco}$ or GPP that plays a more significant role in driving interannual variability of NEE depends on the peatlands’ vegetation composition. In general, GPP of moss-dominated peatlands appears more sensitive to WTD changes than that of peatlands dominated by vascular vegetation because roots of vascular vegetation can reach deeper soil layer even during droughts (Drollinger et al., 2019; Helfter et al., 2015; Lafleur et al., 2003).

Despite the evident relationship, WTD can have a limited impact on NEE interannual variability. Pugh et al. (2018) found that WTD’s effect on $R_{eco}$ and GPP canceled each other, making annual peat? temperature the best factor explaining interannual variability in NEE. In another case, Strachan et al. (2016) detected that during low variability of WTD, NEE variability is more sensitive to temperature changes. These differences may be caused by site-specific peat structures and characteristics (Lafleur et al., 2005).
A number of studies have also investigated how functional changes affect interannual variability of CO₂ exchange in peatlands (McVeigh et al., 2014; Teklemariam et al., 2010). Here, functional changes are defined as indirect factors that drive photosynthesis and respiration over time, such as vegetation composition and microbial composition shift (Hui et al., 2003). However, McVeigh et al. (2014) and Teklemariam et al. (2010) concluded that functional changes can only explain a small portion of the interannual variability of NEE (5.3% to 13.7%).

1.4.2 CH₄ Fluxes

Generally, site-specific climatic and carbon input fluctuations best explain interannual variability of CH₄ fluxes. For example, low water table depth during summer droughts is known to reduce total annual CH₄ fluxes (Drollinger et al., 2019; Goodrich, Campbell, Roulet, et al., 2015). The timing of the drought also matters because the low temperature in autumn right after the drought ends can slow the CH₄ flux recovery (Goodrich, Campbell, Roulet, et al., 2015). In another study, Rinne et al. (2018) found a correlation between the growing season GPP and CH₄ flux, suggesting that carbon input drives interannual variability of CH₄ emission.

Records of short-term disturbance events in CH₄ interannual variability studies are scarce, however, Ueyama et al. (2020) observed two typhoon events driving high episodic CH₄ fluxes three times higher than weekly means in Bibai Mire, Japan. However, its contribution to the interannual variability of CH₄ flux was not significant.
1.5 Net Carbon Balance

The net ecosystem carbon balance (NECB) of peatlands combines the carbon exchanged through both CO₂ and CH₄ fluxes, along with lateral fluxes of carbon, including dissolved organic carbon (DOC) and particulate carbon (PC) (Chapin et al., 2006; Koehler et al., 2011; Nilsson et al., 2008; Roulet et al., 2007). Although many studies have found that the interannual variability of the NECB is driven more by NEE (Rinne et al., 2018; Ueyama et al., 2020), NECB studies have demonstrated that including CH₄ flux in the measurement is crucial to avoid overestimating the net C sink strength of peatlands (Roulet et al., 2007). CH₄ fluxes was reported to contribute between 5% and 17% of NECB (Nilsson et al., 2008; Nugent et al., 2018) and turn peatland from a net C sink to a C source (Koehler et al., 2011). In addition to CH₄ fluxes, DOC is considered important, contributing to more than 6% of peatlands NECB (Nugent et al., 2018; Roulet et al., 2007). However, continuous measurements of DOC are often difficult to conduct for long term studies. From here onwards, the term net C balance (i.e., leaving out “ecosystem” from NECB) will be used to describe the sum of CH₄ flux and NEE only.

1.6 Greenhouse Gas (GHG) Balance

To calculate the net GHG balance, some studies use a global warming potential (GWP) (Drollinger et al., 2019; Ueyama et al., 2020) or sustained GWP (Drollinger et al., 2019; Neubauer & Megonigal, 2015) as weighting matrices to calculate CO₂-equivalent of CH₄ fluxes. GWP (in g CO₂-eq m⁻²) is a matrix that describes the radiative effect of a GHG relative to CO₂ over a time scale (Houghton et al., 1990). Assuming a 100-year time horizon, Drollinger et al. (2019) and Ueyama et al. (2020) found that their bog sites switched from exerting a warming effect to a cooling effect throughout their 3 and 4 years of study, respectively. While Drollinger
et al. (2019) proposed that summer drought caused interannual variability in the GHG balance. Ueyama et al. (2020) observed no anomalous environmental conditions during the study period.

1.7 Research Objectives

This research aims to analyze interannual variability in C fluxes of a restored peatland ecosystem. Here, we conducted long-term measurements of ecosystem scale net CO₂ and CH₄ fluxes at Burns Bog, a restored temperate ombrotrophic bog in Canada, 9 years after rewetting. The bog’s unique morphology, vegetation diversity, and chemistry contribute to its significance in the region. The specific research questions for this study are:

1. What is the annual net carbon budget and GHG balance of Burns Bog and how does it vary across years?

2. What are the drivers of interannual variability in CO₂ and CH₄ fluxes of the bog?
Chapter 2: Methods

2.1 Study Site

This research is carried out in Burns Bog, an ombrotrophic bog located in Delta, British Columbia, Canada. According to the Köppen regional climate classification, Burns Bog is classified as Csb (warm-summer Mediterranean climate). Between 1981-2010, the annual mean air temperature was 10.6 ± 0.6 °C and the annual precipitation was 1262.4 mm with only 2% falling as snow based on the nearest weather station data (9.13 km from the site). The mean monthly temperature is usually above 16°C throughout summer, with July being the warmest and driest month (Environment Canada, 2020).

Historically, disturbance in the area was caused by agricultural activities beginning in the late 1800s, peat harvesting from the 1940s to the mid 1980s, and encroachment for urban/industrial development. As a result, the peat surface, hydrology, and the bog’s original vegetation communities have been greatly impacted. By 2000, Burns Bog had lost approximately 40% of its original area and 1-2 m of its original 4-5 m peat thickness (Hebda et al., 2000; Rigg & Richardson, 1938). In an effort to protect the remaining 2,042 ha of the area, the Burns Bog Conservancy Area (BBECA) was established in 2004. Beginning in 2007, ditch blocking was done to raise the water table and restore the bog’s ecological integrity (Whitfield et al., 2006).

In June 2015, an eddy covariance (EC) tower was installed in Burns Bog (49.1293 N, -122.9849 E; registered as CA-DBB on AmeriFlux Network) (Figure 2.1). The area within the flux footprint is composed of Triggs soil from the soil subgroup Mesic Fibrisol, which mainly
consists of decomposed peat with extremely low pH ranging from 3-4. The vegetation cover is characterized by stands of white beak-rush (*Rhynchospora alba*) growing above a *Sphagnum* carpet (mainly *Sphagnum tenellum*) (Figure 2.2). Other vegetation found in the area includes bog cranberry (*Oxycoccus palustris*), round-leaved sundew (*Drosera rotundifolia*), tawny cotton-grass (*Eriophorum virginicum*), and skunk cabbage (*Lysichiton americanus*) (Hebda et al., 2000).

**Figure 2.1** Eddy covariance (EC) tower location in Burns Bog Ecological Conservancy Area (BBECA)
Figure 2.2 Eddy covariance (EC) tower setup and the vegetation cover within the flux footprint at CA-DBB in Burns Bog

2.2 Eddy Covariance and Meteorological Measurement

Long-term EC measurements have been carried out since 20 June 2015 on a south-facing tower at the 1.8-m height. In this study, the EC method is used to measure vertical fluxes of CO$_2$ and CH$_4$ based on the covariance of high frequency measurements of vertical wind speed and CO$_2$ and CH$_4$ concentrations, respectively (Burba & Anderson, 2008). Three orthogonal wind components ($u$, $v$, and $w$) and sonic temperature were measured using a three-dimensional sonic anemometer (CSAT-3, Campbell Scientific Inc. (CSI) Logan, UT, USA, 20 Hz). CO$_2$ and H$_2$O molar densities and mixing ratios were measured using an enclosed-path infrared gas analyzer LI-7200 and CH$_4$ molar densities were measured with an open-path gas analyzer LI-7700 (both LI-COR Inc. Lincoln, NE, USA, 20 Hz). The EC instruments were equipped with an analyzer interface unit (LI-7550, LI-COR Inc.) and a SmartFlux (LI-COR Inc.) system to enable real-time on-site processing.
Meteorological variables were measured continuously throughout the study period. Incoming and outgoing shortwave and longwave radiation were measured at 4.25 m height using a net radiometer that consists of upward and downward-facing pyranometers and pyrgeometers (CNR1, Kipp and Zonen, Holland). Incoming and reflected photosynthetically active radiation (PAR) were measured at the 1.8-m height using a pair of quantum sensors (LI-190, LI-COR, USA). Air temperature ($T_a$) and relative humidity (RH) were measured at the 2-m height (HMP-35 A, Vaisala Oyj, Vantaa, Finland) and precipitation was measured 10 m from the EC tower with a tipping bucket rain gauge (TR-525M, Texas Electronics, Dallas, TX, USA). Soil thermocouples were mounted 5 m from the tower to measure soil temperatures at the 5-, 10-, and 50-cm depths each ($T_{s,5cm}$, $T_{s,10cm}$, $T_{s,50cm}$). Soil water content (SWC) was measured to a depth of 30 cm within 5 m of the tower (CS616, CSI, Logan, UT, USA). For the water table depth (WTD) measurement, a pressure transducer was installed on 28 July 2015 and was later replaced with a new sensor in summer 2017 (both CS400, CSI). Manual WTD measurements were also conducted once a month from 2018 for calibration purposes. Meteorological measurements were recorded every second and averaged over 30-min periods.

The sensors are powered by solar panels, but due to limited solar radiation during long cloudy periods in the winter, there are some gaps in the raw flux and micrometeorological data. Other causes of missing data related to data exclusion in response to a fire that occurred in the bog in summer 2016, additional instrument failures throughout the study period, and filtered data due to conditions not meeting the EC assumptions. Gaps in the $T_a$, RH, and wind speed measurements were filled using data from Environment and Climate Change Canada’s Delta Burns Bog.
weather station, located 1.32 km from the site. Incoming shortwave radiation \( (R_g) \) and precipitation data were gap-filled using modelled values based on the relationship between the on-site measurement and data from UBC Totem Field weather station, approximately 23 km northwest of the site.

2.3 Flux Data Processing

Raw flux data measured at 20 Hz were processed in EddyPro (LI-COR Inc., US) with an averaging time of 30 minutes. Statistical tests for raw data screening were conducted to remove spikes, data outside plausible limits, skewness and kurtosis (Vickers & Mahrt, 1997). To correct the sonic anemometer tilt relative to the streamline, the double rotation method was applied (Wilczak et al., 2001). For calculating the turbulent fluctuations, block average was used, in which the mean values were removed from the scalar timeseries data. Covariance maximization was then used to compensate for time lags arising from sensor separation (Fan et al., 1990). Other corrections applied to the data include the WPL correction to compensate for the effects of air density changes during the averaging period (Webb et al., 1980) and spectral corrections for low-pass and high-pass filtering (Moncrieff et al., 2004).

The half-hourly fluxes output from EddyPro were further filtered to exclude low quality records and measurements under conditions in which EC assumptions were not fulfilled. The half-hourly fluxes were marked with quality flags following a standard developed by Foken et al. (2004), and records flagged as “2” were discarded. Gas analyzer diagnostic flags were also used to discard errors that were typically caused by heavy precipitation and snowfall. Fluxes with spikes
in the mean densities, variances, and covariances were removed, along with records from wind
direction coming from outside the flux footprint (S. C. Lee et al., 2021; Nyberg, 2021).
Next, the REddyProc package in R was used for friction velocity ($u_*$) filtering, gap-filling, and
partitioning the net CO$_2$ flux to get continuous NEE, GPP, and $R_{\text{eco}}$ records for the whole study
period (Wutzler et al., 2018). $u_*$ filtering was done to exclude underestimated fluxes recorded
during periods with low turbulent mixing. To determine the $u_*$ threshold for the filter, the
moving point method was used (Papale et al., 2006; Reichstein et al., 2005). After data quality
check and filtering, the percentage of valid half-hourly fluxes are given in Table 2.1

Gaps in NEE were filled using the marginal distribution sampling (MDS) approach. In MDS, the
look-up table (LUT) approach was used when $R_g$, $T_{\text{air}}$, and VPD for the gap period were
available. LUT calculated the gap values based on the average values of binned flux in similar
$R_g$, $T_{\text{a}}$, and VPD conditions. In cases where no meteorological variables were available, the mean
diurnal course (MDC) approach was used to fill the gaps. MDC estimates the missing fluxes
based on the average NEE of the adjacent days (Falge et al., 2001). Long gaps (>60 days) that
were not filled by MDS were then filled using a random forest algorithm using VPD, $u_*$, $T_{\text{a}}$,
WTD, PAR, $R_g$, and day of year as predictors (Kim et al., 2020). After gap-filling, NEE was
partitioned into its two components (i.e., GPP and $R_{\text{eco}}$) using the nighttime partitioning
approach. Using this method, daytime $R_{\text{eco}}$ was estimated using daytime $T_{\text{a}}$ based on the
relationship between $T_{\text{a}}$ and $R_{\text{eco}}$ during nighttime ($R_g < 10 \text{ Wm}^{-2}$), and GPP was calculated as
$R_{\text{eco}} - \text{NEE}$ (Reichstein et al., 2005).
Due to limitations of the MDS approach for CH$_4$ gap-filling (i.e., different biophysical variables input and the more episodic and non-linear nature of CH$_4$ fluxes), gaps in CH$_4$ flux were estimated by a random forest algorithm (Kim et al., 2020) using the Caret package in R (Kuhn, 2008). Following Kim et al. (2020) and Knox et al. (2016), we used biophysical variables (i.e., $u^*$, NEE, LE, H, Rs, $T_a$, $T_s$, $T_s$, $T_s$ 5cm, $T_s$ 10cm, $T_s$ 50cm, RH, VPD, WTD) and additional fuzzy variables (i.e., day of year, and sine and cosine wave as a function of time) as inputs.

Table 2.1 Proportion of available half-hourly non-gapfilled flux data for each measurement period

<table>
<thead>
<tr>
<th>Period</th>
<th>Season</th>
<th>Available CO$_2$ flux (%)</th>
<th>Available CH$_4$ flux (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2016-2017</td>
<td>non-growing season</td>
<td>14</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td>growing season</td>
<td>38</td>
<td>34</td>
</tr>
<tr>
<td>2017-2018</td>
<td>non-growing season</td>
<td>22</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>growing season</td>
<td>55</td>
<td>50</td>
</tr>
<tr>
<td>2018-2019</td>
<td>non-growing season</td>
<td>21</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td>growing season</td>
<td>65</td>
<td>60</td>
</tr>
<tr>
<td>2019-2020</td>
<td>non-growing season</td>
<td>27</td>
<td>19</td>
</tr>
<tr>
<td></td>
<td>growing season</td>
<td>60</td>
<td>48</td>
</tr>
<tr>
<td>2020-2021</td>
<td>non-growing season</td>
<td>37</td>
<td>32</td>
</tr>
<tr>
<td></td>
<td>growing season</td>
<td>60</td>
<td>55</td>
</tr>
</tbody>
</table>
2.4 Uncertainty Analysis

Half-hourly random errors in NEE were calculated using the REddyProc package in R (Wutzler et al., 2018). Aggregation was then done by calculating the standard deviation of the annual and seasonal means. To take autocorrelation into account, the aggregated standard deviation was calculated following Zieba and Ramza (2011),

\[
s(\bar{x}) = \sqrt{s^2(\bar{x})} = \sqrt{\frac{s^2}{n_{eff}}}
\]

(2.1)

\[
s^2 = \frac{n_{eff}}{n(n_{eff} - 1)} \sum_{i=1}^{n} \sigma_i^2
\]

(2.2)

where \(\bar{x}\) is the annual or seasonal means of gap-filled NEE, \(s(\bar{x})\) is standard deviation of the mean \(\bar{x}\), \(s^2(\bar{x})\) is the variance of the mean \(\bar{x}\), \(\sigma_i\) is the standard deviation of the \(i^{th}\) half-hourly NEE calculated in REddyProc (column NEE_fsd), and \(n_{eff}\) is the effective number of observations. To get the random errors of annual and seasonal sums, the standard deviation of the means was multiplied by the number of days in the period.

Systematic errors due to MDS gapfilling and \(u^*\) threshold selection for NEE, GPP, and \(R_{eco}\) were calculated in REddyProc. The bootstrapping technique was used to generate 200 replicates of the dataset. For each of the replicates, a \(u^*\) threshold was estimated, and the results were pooled together. From the pool of \(u^*\) thresholds, 39 values from the 2.5\(^{th}\) to the 97.5\(^{th}\) percentile were extracted. Gap-filling and partitioning were then done repeatedly using each of the \(u^*\) threshold
estimates (Wutzler et al., 2018). The standard deviation of the 39 estimates was then calculated for each half-hourly value and aggregated to annual and seasonal cumulative values.

For gaps that were filled using the random forest approach (i.e., long gaps in winter 2016 and 2017 NEE and all periods of CH₄ fluxes), random and gap-filling errors were calculated by generating 20 iterations of random forest estimates. The standard deviation of the 20 estimates were then calculated for each half-hourly value and aggregated to get annual and seasonal sums. For periods of cumulative NEE that were gap-filled using both MDS and the random forest approach, the standard deviations calculated from these two approaches were added in quadrature.

To get the total uncertainty, random and systematic errors were added in quadrature and presented as the 95% confidence interval. At the annual scale, the contribution of random errors is very small relative to systematic errors and often negligible.

2.5 Data Analysis

2.5.1 Net Carbon (C) Balance

We analyzed five years of data starting from winter 2016 to summer 2021. One year cycle in this study is defined as the period between October 1st and September 30th the next year. Each period was divided into two seasons: non-growing and growing season. The non-growing season spanned from October 1st to March 31st, while growing-season spanned from April 1st to September 30th.
Net carbon balance values (in g C m\(^{-2}\)) were calculated for annual, growing season, and non-growing season each year from the sum of gap-filled half-hourly NEE (g CO\(_2\)-C m\(^{-2}\)) and CH\(_4\) flux (g CH\(_4\)-C m\(^{-2}\)). A positive net C budget represented net C loss, while a negative net C balance represented net C uptake by the bog. Note that lateral fluxes were not included in the net C balance estimates for the bog.

2.5.2 GHG Balance Calculation

GHG balance or radiative balance were calculated from gap-filled NEE and CO\(_2\)-equivalent emissions of CH\(_4\). To get CO\(_2\)-equivalent emission of CH\(_4\), we used two different metrics: global warming potential (GWP) and sustained-flux global warming potential (SGWP) (Neubauer, 2021; Neubauer & Megonigal, 2015; Forster et al., 2021).

Calculations of annual GHG budgets using a 20, 100, and 500-year GWP were done using the equations below:

\[
GHG \text{ budget}_{\text{GWP20}} = m_{CO_2} F_{CO_2} + (m_{CH_4} F_{CH_4} \times GWP_{20}) 
\]

\[
GHG \text{ budget}_{\text{GWP100}} = m_{CO_2} F_{CO_2} + (m_{CH_4} F_{CH_4} \times GWP_{100}) 
\]

\[
GHG \text{ budget}_{\text{GWP500}} = m_{CO_2} F_{CO_2} + (m_{CH_4} F_{CH_4} \times GWP_{500}) 
\]

where \(m_{CO_2}\) and \(m_{CH_4}\) refer to the molecular mass of CO\(_2\) (44.01 g mol\(^{-1}\)) and CH\(_4\) (16.04 g mol\(^{-1}\)) respectively; \(F_{CO_2}\) and \(F_{CH_4}\) refer to CO\(_2\) and CH\(_4\) fluxes in mol m\(^{-2}\) y\(^{-1}\); GWP\(_{20}\), GWP\(_{100}\), and GWP\(_{500}\) are the GHG metrics that describe the radiative effect of a pulse of CH\(_4\) emission.
relative to a pulse emission of an equal mass of CO$_2$ for 20, 100, and 500 year timeframes, respectively. Here, we used GWP$_{20}$ value of 79.7, GWP$_{100}$ of 27.0, and GWP$_{500}$ of 7.2 (Forster et al. 2021).

The annual GHG balances from using the 20, 100, and 500-year SGWP values were calculated as follows:

$$GHG \ budget_{SGWP_{20}} = F_{CO_2-seq} + (F_{CH_4} \times SGWP_{20})$$  \hspace{1cm} (2.6)

$$GHG \ budget_{SGWP_{100}} = F_{CO_2-seq} + (F_{CH_4} \times SGWP_{100})$$  \hspace{1cm} (2.7)

$$GHG \ budget_{SGWP_{500}} = F_{CO_2-seq} + (F_{CH_4} \times SGWP_{500})$$  \hspace{1cm} (2.8)

$$F_{CO_2-seq} = (F_{CO_2} + F_{CH_4}) \times m_{CO_2}$$  \hspace{1cm} (2.9)

where SGWP$_{20}$ ($= 96$), SGWP$_{100}$ ($= 45$), and SGWP$_{500}$ ($= 14$), are the GHG metrics that describe the radiative effect of a sustained emission of CH$_4$ relative to sustained sequestration of an equal mass of CO$_2$ over 20 and 100 year timeframes, respectively; and $F_{CO_2-seq}$ refers to annual net CO$_2$ sequestration (negative value for sequestration, positive value for emission) calculated as the sum of annual NEE and the amount of carbon lost as CH$_4$ (Neubauer & Megonigal, 2015).

### 2.5.3 Relative Influence of GPP and Reco on the variability of NEE

To determine the contribution of GPP and $R_{eco}$ to the interannual variability of NEE, their relative influences were calculated following (Schaefer et al., 2002):
\[ f_{GPP} = \frac{\sigma_{GPP}^2}{\sigma_{GPP}^2 + \sigma_{Reco}^2} \]  
\[ f_{Reco} = \frac{\sigma_{Reco}^2}{\sigma_{GPP}^2 + \sigma_{Reco}^2} \]

where \( f_{GPP} \) and \( f_{Reco} \) are relative influences, \( \sigma_{GPP}^2 \) and \( \sigma_{Reco}^2 \) are variances of GPP and Reco across years, respectively. Since \( f_{Reco} + f_{GPP} = 1 \), \( f_{Reco} = 0 \) indicates that Reco has no influence on interannual NEE variability and \( f_{Reco} = 1 \) indicates that respiration entirely controls interannual NEE variability. \( f_{GPP} \) and \( f_{Reco} \) were calculated across all years for annual, growing season, and non-growing season timeframes.

### 2.5.4 Light Response Curves

Light response curves were used to demonstrate how daily GPP varied as a function of half-hourly PAR between years in the growing season. GPP-PAR relationship was represented by a rectangular hyperbola function (Frolking et al., 1998; Thornley & Johnson, 1990) as follows:

\[ GPP = \frac{\alpha \times PAR \times P_{max}}{\alpha \times PAR + P_{max}} \]  

where \( \alpha \) is the slope of increase in GPP at low light levels, also known as the light-use efficiency (\( \mumol \) CO\(_2/\mumol \) photon) and \( P_{max} \) is the maximum GPP at high light levels (\( \mumol \ m^{-2} \ s^{-1} \)).

To compare the year-to-year differences of the GPP-PAR relationship, we fitted two light response curves: one model where \( \alpha \) and \( P_{max} \) were identical between years and another model
where \( \alpha \) and \( P_{\text{max}} \) varied between years. An F-test was then used to compare the two models. If the null hypothesis was rejected (\( p<0.05 \)) we concluded that at least one of the years had significantly different \( \alpha \) and \( P_{\text{max}} \).

### 2.5.5 Surface Conductance (Gs)

Surface conductance was calculated following Baldocchi and Meyers (1998) by inverting the Penman-Monteith equation to get:

\[
\frac{1}{G_s} = \frac{1}{G_a} \left\{ \frac{s}{\gamma} \left( R_n - G \right) + \frac{\rho C_p G_G VPD}{\gamma} \frac{LE}{\gamma} - \frac{s}{\gamma} \right\} - 1
\]

(2.13)

where \( G_a \) is the aerodynamic conductance, \( s \) is the slope of relation between saturation vapor pressure and air temperature, \( \gamma \) is the psychrometric constant, \( R_n \) is the net radiation, \( G \) is the ground heat flux, \( \rho \) is the air density, \( C_p \) is the specific heat of air, VPD is the vapour pressure deficit and LE is the latent heat flux. \( G_a \) was calculated as follows:

\[
\frac{1}{G_a} = \frac{1}{G_{a,m}} + \frac{1}{G_b}
\]

(2.14)

\[
\frac{1}{G_{a,m}} = \frac{u}{u^*^2}
\]

(2.15)

\[
\frac{1}{G_b} = \frac{kB^{-1}}{k u_*}
\]

(2.16)

where \( G_{a,m} \) is the aerodynamic conductance for momentum transfer, \( G_b \) is the laminar boundary layer conductance, \( u \) is the mean wind speed, \( u^* \) is the friction velocity, \( k \) is the von Karman constant (0.4), and \( kB^{-1} \) is a constant that depends on the surface roughness. Here, we used \( kB^{-1} = 2 \) for short grass following (Garratt & Hicks, 1973).
2.5.6 Temperature Sensitivity of $R_{eco}$ and FCH$_4$

To analyse how C fluxes respond to variations in soil temperature, we calculated the temperature sensitivity (Q10) of $R_{eco}$ and CH$_4$ flux. Q10 describes the relative increase in daily $R_{eco}$ or CH$_4$ flux per 10°C rise in daily soil temperature. Here, we estimated Q10 for the growing season, non-growing season, and the entire year of measurements separately for $R_{eco}$ and CH$_4$ flux using the following equation:

$$Q10_{R_{eco}} = e^{10b_{R_{eco}}}$$ (2.17)

$$Q10_{FCH_{4}} = e^{10b_{FCH_{4}}}$$ (2.18)

where $b_{R_{eco}}$ and $b_{FCH_{4}}$ are the fitting parameters obtained from the function relating $T_{s,5cm}$ to $R_{eco}$ and CH$_4$ flux (FCH$_4$), respectively. The relationship between $R_{eco}$ and $T_{s,5cm}$ were modeled using a linear fit of the logarithmically transformed $R_{eco}$ (Equation (2.19)), while the relationship between CH$_4$ flux and $T_{s,5cm}$ were modeled using an exponential function (Equation (2.20)) as follows:

$$ln(R_{eco}) = A + b_{R_{eco}}T_{s,5cm}$$ (2.19)

$$FCH_{4} = ae^{b_{FCH_{4}}T_{s,5cm}}$$ (2.20)

where $A$ and $b_{R_{eco}}$ are the intercept and slope of the linear model of $ln(R_{eco})$, $a$ is the initial CH$_4$ flux at $T_{s,5cm} = 0$, and $b_{FCH_{4}}$ is the growth of the exponential function of $T_{s,5cm}$.

We fitted the temperature response of $R_{eco}$ and CH$_4$ flux for each year separately and for all years combined and compared the two estimates using F-test. If the null hypothesis was rejected
(p<0.05) we concluded that at least one of the years had a significantly different Q10 relative to the Q10 for the full period.

2.5.7 Drivers of CO₂ and CH₄ Interannual Variability

2.5.7.1 Year-to-year Differences in Daily Drivers of C fluxes

To analyze the variation of daily drivers of C fluxes between years, we determined the significant predictors of daily non-gapfilled CO₂ and CH₄ fluxes for each year and compared them across years. Two sets of climatic variables (i.e., Tₜ₅cm, RH, PAR, VPD, precipitation, Pa, Tₐ, WTD, and GPP for CH₄; and excluding GPP for CO₂) were used as inputs for forward stepwise multilinear regression models for each year. The combination of climatic variables that produced the best model (lowest AIC) were considered as the significant drivers of daily C fluxes for the particular year.

2.5.7.2 Homogeneity of Slopes (HOS) Model

Homogeneity of slopes (HOS) model was used to determine the contribution of direct and indirect effects of environmental conditions on seasonal and interannual variability of CO₂ and CH₄ fluxes (Hui et al., 2003). Using HOS, variability of C fluxes could be partitioned into seasonal and interannual components. The interannual components could then be further partitioned into direct effects (driven by climatic variability) or indirect effects (driven by functional changes).

For the model input, we calculated the weekly averages of daily sums of non-gapfilled CO₂ and CH₄ fluxes (only taking daily sums with more than 30% of half-hourly values available), and the
weekly averages of climatic variables to attenuate daily fluctuations. For modeling CO₂, we used a set of climatic variables (i.e., T₅cm, RH, PAR, VPD, precipitation, Pa, Tₐ and WTD) as predictors. Similarly, we used the same set of predictor variables for modeling CH₄ with the addition of GPP.

Before conducting the HOS analysis, we first identified which predictor variables were relevant to include in the model. To do this, we combined measurements from all years and performed a forward stepwise multiple linear regression (MLR) analysis using the set of climatic variables as the independent variables and CO₂ or CH₄ flux as the dependent variable. We selected a combination of a maximum of three relevant variables that gave the lowest akaike information criterion (AIC) for CO₂ and CH₄ flux each. PAR, T₅cm and WTD were found to be relevant predictors for CO₂, while WTD, GPP, and Tₐ were found to be relevant predictors for CH₄.

Using the selected predictors, a HOS model that considered the interaction of climatic variable and year was constructed:

$$ Y_{ij} = a + \sum_{k=1}^{m} b_k X_{ijk} \sum_{k=1}^{m} b_k X_{ijk} + \sum_{k=1}^{m} b_{ik} X_{ijk} + e_{ij} $$

(2.21)

where \(i\) is the \(i^{th}\) year; \(j\) is the \(j^{th}\) day of a year; \(k\) is the \(k^{th}\) predictor variable; \(Y_{ij}\) is the observed dependent variable (CO₂ or CH₄ flux) in \(i^{th}\) year and \(j^{th}\) day; \(X_{ijk}\) is the observed predictor variable in \(i^{th}\) year and \(j^{th}\) day for the \(k^{th}\) predictor; \(b_k\) is the slope of regression for the \(k^{th}\) predictor; \(b_{ik}\) is the slope of the interaction term between the \(k^{th}\) predictor and the \(i^{th}\) year; \(e_{ij}\) is the random error associated with \(Y_{ij}\).
To investigate the presence of functional changes, we tested the null hypothesis (H$_0$: $b_{ik} = 0$) for all years against the alternative hypothesis (H$_1$: $b_{ik} \neq 0$) for any of the years. If H$_0$ could not be rejected, the model had a single slope to predict C fluxes from climatic variables for all years, indicating that functional changes were not significant. Equation (2.21) was then simplified to a single-slope MLR model:

$$Y_{ij} = a + \sum_{k=1}^{m} b_k X_{ijk} + e_{ij}$$  \hspace{1cm} (2.22)

If H$_0$ was rejected, the relationship between climatic variables and C fluxes varied between years. The varying responses were assumed to be caused by the presence of functional changes. Equation (2.21) was then simplified to a separate-slopes MLR model:

$$Y_{ij} = a + \sum_{k=1}^{m} b_{ik} X_{ijk} + e_{ij}$$  \hspace{1cm} (2.23)

If functional change was detected, variations of observed C fluxes were classified into direct effects of seasonal climatic variation, direct effects of interannual climatic variability, functional changes (indirect effects), and random errors. Statistically, the classification was done by partitioning the sum of squares (SS) of the total deviation (SS$_T$) into sum of squares of functional changes (SS$_f$), sum of squares of the interannual climatic variability (SS$_{ic}$), sum of squares of the seasonal climatic variability (SS$_{sc}$), and sum of squares of error (SS$_e$) as follows:

$$SS_T = SS_f + SS_{ic} + SS_{sc} + SS_e$$  \hspace{1cm} (2.24)
SS_i, SS_e, SS_{sc}, and SS_{ic} were calculated respectively by:

\[
SS_f = \sum_{i=1}^{y} \sum_{j=1}^{n} (\hat{Y}_{ij}' - \hat{Y}_{ij})^2
\]  
(2.25)

\[
SS_e = \sum_{i=1}^{y} \sum_{j=1}^{n} (Y_{ij} - \hat{Y}_{ij}')^2
\]  
(2.26)

\[
SS_{ic} = \sum_{i=1}^{y} \sum_{j=1}^{n} (\hat{Y}_{ij} - \bar{Y}_j)^2
\]  
(2.27)

\[
SS_{sc} = \sum_{i=1}^{y} \sum_{j=1}^{n} (\bar{Y}_j - \bar{Y})^2
\]  
(2.28)

where \(\hat{Y}_{ij}\) is the estimated C flux from Equation (2.22); \(\hat{Y}_{ij}'\) is the estimated C fluxes from Equation (2.23); \(\bar{Y}\) is the mean of all estimated C fluxes; \(\bar{Y}_j\) is the mean of estimated C fluxes across all years on the \(j^{th}\) day.

If functional change was not significant in the model, \(SS_T\) were partitioned into three components only:

\[
SS_T = SS_{ic} + SS_{sc} + SS_e
\]  
(2.29)

where \(SS_e, SS_{sc},\) and \(SS_{ic}\) were calculated using Equation (2.26), (2.27), (2.28), respectively.
2.5.7.3 Correlation Analysis

To investigate how annual environmental variables affect annual C fluxes, we conducted a bivariate correlation analysis, with an assumption of linear relationship between variables. The correlation between cumulative fluxes (i.e., NEE, GPP, R\textsubscript{eco}, and CH\textsubscript{4} fluxes) and environmental variables (i.e., T\textsubscript{a,5cm}, PAR, precipitation, Pa, T\textsubscript{a}, WTD, LUE, Q10) for each year were analyzed separately for the growing season, the non-growing season, and the whole year.
Chapter 3: Results

3.1 Environmental Variables

Water table depth (WTD) at Burns Bog showed clear seasonality, with lower WTD in the growing season (-3.2 ± 3.7 cm; mean ±SD across years; negative value indicates depth below the surface) and higher WTD in the non-growing season (6.2 ± 1.2 cm; positive value indicates height above the surface). On a five-year average, the water table reached its highest level in January (10.5 cm ± 1.1 cm) and reached its minima in September (-14.8 ± 3.2 cm) with varied timing of water table drawdown from June to July. This pattern followed precipitation, which is the primary input of water in the bog, and was also inversely related to evapotranspiration (ET), which was the dominant process of water loss in the summer (Figure 3.1). The 2016-2021 average annual precipitation was 1167.6 ± 89.5 mm and was on par with the 1981-2010 average of 1189 mm. On average, precipitation peaked around December (186.5 ± 30.3 mm month\(^{-1}\)) and reached its lowest in July (15.2 ± 17.7 mm month\(^{-1}\)). Meanwhile, average annual ET was 640.2 ± 80.3 mm with a peak around July (130.3 ± 33.5 mm month\(^{-1}\)) (Table 3.1).
Figure 3.1 Daily hydrological variables (black lines) along with their monthly anomalies (grey bars) for (a) water table depth (WTD), (b) precipitation, and (c) evapotranspiration (ET). Monthly anomalies were calculated as deviations from the monthly means across five years.

Annual photosynthetically active radiation (PAR) ranged from 9776 to 11296 mol m\(^{-2}\) y\(^{-1}\) with an average of 10401 ± 643 mol m\(^{-2}\) y\(^{-1}\) (± SD across years) (Table 3.1). PAR was consistently higher in the growing season (8274 ± 393 mol m\(^{-2}\)) than in the non-growing season (2127 ± 293 mol m\(^{-2}\)). Generally, PAR reached its maxima in July (1795.9 ± 67.5 mol m\(^{-2}\) mo\(^{-1}\)) and reached its minima in December (135.4 ± 25.3 mol m\(^{-2}\) mo\(^{-1}\)), coinciding with the timing of the lowest and highest precipitation, respectively. Over the five-year period, the highest growing season PAR was observed in the 2018-2019 period (8764 mol m\(^{-2}\)), while the lowest growing season
PAR was observed in the 2017-2018 period (7779 mol m$^{-2}$). Daily PAR and its monthly anomalies are shown in Figure 3.2.

Mean annual air temperature ($T_a$) from 2016 to 2021 varied between 10.3 and 10.8°C, with an average of 10.5°C, which is slightly above the 1981-2010 average of 10.4°C (Figure 3.2b; Table 3.1). The five-year average growing season and non-growing season $T_a$ was 15.3 ± 0.2°C and 5.7 ± 0.3°C, respectively (table). Monthly $T_a$ peaked around July (18.2 ± 0.7°C), stayed high until August (17.8 ± 0.3°C), and started to decrease again in September each year. On average, the coldest month was February (2.9 ± 1.6°C). $T_{s,5cm}$ followed a similar seasonal pattern, with an annual average of 11.4 ± 0.03°C, a growing season average of 15.8 ± 0.3°C, and a non-growing season average of 6.9 ± 0.3°C (Figure 3.2c).

Mean annual vapour pressure deficit (VPD) ranged from 0.25 to 0.30 kPa, with a mean of 0.28 ± 0.02 (± SD across years) over the five years (Table 3.1). The growing season VPD (0.42 ± 0.03 kPa) was consistently higher than the non-growing season VPD (0.13 ± 0.01 kPa). Peak monthly VPD generally occurred in July (0.54 ± 0.09 kPa), while its minima occurred in December (0.06 ± 0.03). Throughout the study period, the highest daily (24-h) VPD was observed in late July 2021 when it reached 1.98 kPa (Figure 3.2d).
Figure 3.2 Daily means (black line) and monthly anomalies (grey bars) for (a) photosynthetically active radiation (PAR) (b) air temperature ($T_a$), and (c) soil temperature at 5 cm depth ($T_{s,5cm}$), (d) 24-h vapour pressure deficit (VPD). Monthly anomalies were calculated as deviations from the monthly means across five years.

The coldest year was 2016-2017, with an annual $T_a$ of 10.3°C, which was slightly below the five-year average of 10.5°C. This was also the wettest year, with annual precipitation and mean annual WTD reaching 1296.6 mm and 4.78 cm, respectively. Non-growing season 2016 started
with a warmer fall (October-November), which was followed by a colder winter (December-February) compared to the five-year average (Figure 3.3). Due to higher-than-normal precipitation in spring 2017 (March-May), WTD stayed high in 2017 and only started declining to a level below the surface in mid-July.

Monthly $T_a$ and WTD in 2017-2018 were close to the five-year average, except in the summer months. Due to lower precipitation in the growing season (289.3 mm), WTD dropped below 0 in mid-June and continued to drop to an average of -19.4 cm in August. However, summer $T_a$ stayed close to the five-year average, and was slightly colder at the end of the growing season.

2018-2019 was overall a dry year, with 11 months of anomalously lower WTD (Figure 3.3). WTD throughout autumn and winter stayed low this year due to less non-growing season precipitation (710.2 mm) compared to other years. However, summer WTD was close to the five-year average due to high water input in June. $T_a$ during this period was relatively close to the five-year average, except for February 2019 when $T_a$ dropped to 0.33°C.

2019-2020 was the second wettest year, with annual precipitation and WTD of 1168.9 mm and 2.29 cm, respectively. This was mainly due to high input of water in the spring and summer months, which allowed WTD to decline later in mid-July and stay high throughout summer. Monthly $T_a$ during this period was close to the five-year average.

2020-2021 was the warmest and driest year with an annual $T_a$ of 10.9°C and annual average WTD of -0.1 cm. This is mostly due to growing season anomalies, where three summer months
(June to August) had a lower WTD and higher $T_a$ than the five-year averages (Figure 3.3). Maximum daily mean $T_a$ in summer 2021 reached 29°C, which was ~5°C higher than the previous years. Additionally, due to low precipitation in spring, this period had an earlier WTD drawdown in early June followed by a rapid decline of WTD until mid-July.

![Figure 3.3 Monthly water table depth (WTD) and air temperature ($T_a$) anomalies. Anomalies were calculated by comparing individual months to their monthly averages across the five-year study period.](image)

Figure 3.3 Monthly water table depth (WTD) and air temperature ($T_a$) anomalies. Anomalies were calculated by comparing individual months to their monthly averages across the five-year study period.
Table 3.1 Annual, non-growing season (NGS) and growing season (GS) means of environmental variables (i.e., precipitation (P), evapotranspiration (ET), and water table depth (WTD), soil temperature at 5cm depth ($T_{s,5cm}$), and air temperature ($T_a$), photosynthetically active radiation (PAR), and 24-h vapor pressure deficit (VPD) in Burns Bog

<table>
<thead>
<tr>
<th>Period</th>
<th>Precipitation (mm)</th>
<th>ET (mm)</th>
<th>WTD (cm)</th>
<th>$T_{s,5cm}$ ($^\circ$C)</th>
<th>$T_a$ ($^\circ$C)</th>
<th>PAR (mol m$^{-2}$)</th>
<th>VPD (kPa)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>2016-2017</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Annual</td>
<td>1296.6</td>
<td>656.3</td>
<td>4.78</td>
<td>11.07</td>
<td>10.30</td>
<td>9776.4</td>
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<tr>
<td>NGS</td>
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<td>62.5</td>
<td>7.32</td>
<td>8.28</td>
<td>5.34</td>
<td>1797.2</td>
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<tr>
<td>GS</td>
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<td>593.8</td>
<td>2.25</td>
<td>13.85</td>
<td>15.24</td>
<td>7979.2</td>
<td>0.46</td>
</tr>
<tr>
<td><strong>2017-2018</strong></td>
<td></td>
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</tr>
<tr>
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<td>756.2</td>
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<td>90.5</td>
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<td>2041.4</td>
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<td>0.46</td>
</tr>
<tr>
<td><strong>2018-2019</strong></td>
<td></td>
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<td></td>
<td></td>
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</tr>
<tr>
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<td>13.95</td>
<td>15.34</td>
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<td></td>
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<tr>
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<td>NGS</td>
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<td>5.60</td>
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<tr>
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<td>452.8</td>
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<td>GS</td>
<td>Mean</td>
<td>NGS</td>
<td>GS</td>
<td>SD across years</td>
</tr>
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<tr>
<td>GS</td>
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<td>562.4</td>
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<td>13.69</td>
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<td>8407.4</td>
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<tr>
<td><strong>Mean</strong></td>
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</tr>
<tr>
<td></td>
<td>1167.6</td>
<td>640.2</td>
<td>1.50</td>
<td>11.38</td>
<td>10.48</td>
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<td>NGS</td>
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<td>90.3</td>
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<td>6.91</td>
<td>5.66</td>
<td>2127.4</td>
<td>0.13</td>
</tr>
<tr>
<td>GS</td>
<td>307.6</td>
<td>549.9</td>
<td>-3.20</td>
<td>15.83</td>
<td>15.28</td>
<td>8274.5</td>
<td>0.42</td>
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<td><strong>SD across years</strong></td>
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<td></td>
</tr>
<tr>
<td></td>
<td>89.5</td>
<td>80.3</td>
<td>2.07</td>
<td>0.03</td>
<td>0.22</td>
<td>643.3</td>
<td>0.02</td>
</tr>
<tr>
<td>NGS</td>
<td>99.9</td>
<td>16.1</td>
<td>1.23</td>
<td>0.32</td>
<td>0.34</td>
<td>293.4</td>
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<tr>
<td>GS</td>
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<td>87.4</td>
<td>3.71</td>
<td>0.33</td>
<td>0.15</td>
<td>393.2</td>
<td>0.03</td>
</tr>
</tbody>
</table>
3.2 CO₂ Exchange

3.2.1 Annual and Seasonal CO₂ Balance

Seasonally, the site consistently alternated from being a net CO₂ sink in the growing season (-62.3 ± 17.3 g CO₂-C m⁻²; mean ± SD across years) to being a net CO₂ source in the non-growing season (50.0 ± 29.1 g CO₂-C m⁻²) (Table 3.2). The switch from net CO₂ source to sustained CO₂ sink generally occurred in May and continued until September (Figure 3.4a). On average, monthly net CO₂ uptake peaked in June with an average of 30.7 g CO₂-C m⁻² month⁻¹, when the ratio of GPP to Rₜ was the highest. Both GPP and Rₜ declined later in July and reached their lowest around December-January (Figure 3.4b and Figure 3.4c), coinciding with minima and maxima of Tₕ and Tₕ,5cm, respectively.

Across the study period, the magnitude of annual NEE and its components varied considerably between years. GPP showed a declining trend throughout the 5 year period, ranging from 458.7 ± 30.8 g CO₂-C m⁻² y⁻¹ (± 95% CI) in the first year to 378.7 ± 16.7 g CO₂-C m⁻² y⁻¹ in the last year. Similarly, Rₜ declined from 470.1 ± 38.6 in 2016-2017 to 357.0 ± 12.7 g CO₂-C m⁻² y⁻¹ in 2019-2020, although it increased again to 390.6 ± 25.2 g CO₂-C m⁻² y⁻¹ in the last year. Conversely, NEE did not show any interannual trend over the 5 year period. Based on annual NEE, the site was a weak net CO₂ sink in most years, with annual NEE ranging from -26.0 ± 5.5 g CO₂-C m⁻² y⁻¹ to -32.6 ± 21.5 g CO₂-C m⁻² y⁻¹, except for 2016-2017 and 2020-2021 when the bog was a net CO₂ source, emitting 11.5 ± 16.1 g CO₂-C m⁻² y⁻¹ and 11.9 ± 15.1 g CO₂-C m⁻² y⁻¹, respectively.
Annual GPP and $R_{eco}$ were determined mainly by their growing season sums. Growing season $R_{eco}$ constituted 66-76% of annual $R_{eco}$, while growing season GPP constituted 84-87% of annual GPP. The lowest proportion of growing season $R_{eco}$ to annual $R_{eco}$ was observed in 2016-2017 (66%), the year when the bog was a CO$_2$ source. In contrast, the highest proportion of growing season $R_{eco}$ to annual $R_{eco}$ was observed in 2018-2019 (76%), the year when the bog was the strongest CO$_2$ sink.

Figure 3.4 Daily gap-filled fluxes in g CO$_2$-C m$^{-2}$ d$^{-1}$ (black lines) along with their monthly anomalies in g CO$_2$-C m$^{-2}$ month$^{-1}$ (grey bars) for (a) net ecosystem exchange (NEE), (b) gross primary production (GPP), (c) ecosystem respiration ($R_{eco}$). Monthly anomalies were calculated as deviations from the monthly means across five years.
Table 3.2 Annual, non-growing season (NGS), and growing season (GS) net ecosystem exchange (NEE), (GPP), and ecosystem respiration ($R_{eco}$) of Burns Bog in g CO$_2$-C m$^{-2}$ and their uncertainties ($\pm$ 95% CI)

<table>
<thead>
<tr>
<th>Period</th>
<th>Season</th>
<th>NEE (g C m$^{-2}$)</th>
<th>GPP (g C m$^{-2}$)</th>
<th>$R_{eco}$ (g C m$^{-2}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2016-2017</td>
<td>Annual</td>
<td>11.5 ± 16.1</td>
<td>458.7 ± 30.8</td>
<td>470.1 ± 38.6</td>
</tr>
<tr>
<td></td>
<td>NGS</td>
<td>88.7 ± 15.3</td>
<td>71.2 ± 17.2</td>
<td>159.9 ± 12.4</td>
</tr>
<tr>
<td></td>
<td>GS</td>
<td>-77.2 ± 4.1</td>
<td>387.4 ± 24.7</td>
<td>310.2 ± 28.5</td>
</tr>
<tr>
<td>2017-2018</td>
<td>Annual</td>
<td>-26.0 ± 5.5</td>
<td>454.6 ± 7.7</td>
<td>428.7 ± 7.1</td>
</tr>
<tr>
<td></td>
<td>NGS</td>
<td>40.0 ± 3.3</td>
<td>71.4 ± 4.2</td>
<td>111.3 ± 3.2</td>
</tr>
<tr>
<td></td>
<td>GS</td>
<td>-66.0 ± 6.7</td>
<td>383.3 ± 6.5</td>
<td>317.3 ± 5.4</td>
</tr>
<tr>
<td>2018-2019</td>
<td>Annual</td>
<td>-32.6 ± 21.5</td>
<td>409.0 ± 15.5</td>
<td>376.4 ± 9.6</td>
</tr>
<tr>
<td></td>
<td>NGS</td>
<td>26.6 ± 18.8</td>
<td>62.9 ± 18.0</td>
<td>89.6 ± 1.9</td>
</tr>
<tr>
<td></td>
<td>GS</td>
<td>-59.3 ± 5.3</td>
<td>346.1 ± 6.3</td>
<td>286.8 ± 8.2</td>
</tr>
<tr>
<td>2019-2020</td>
<td>Annual</td>
<td>-26.4 ± 9.9</td>
<td>383.3 ± 5.7</td>
<td>357.0 ± 12.7</td>
</tr>
<tr>
<td></td>
<td>NGS</td>
<td>48.7 ± 9.1</td>
<td>50.3 ± 8.8</td>
<td>99.0 ± 3.6</td>
</tr>
<tr>
<td></td>
<td>GS</td>
<td>-75.0 ± 3.0</td>
<td>333.1 ± 12.8</td>
<td>258.0 ± 13.1</td>
</tr>
<tr>
<td>2020-2021</td>
<td>Annual</td>
<td>11.9 ± 15.1</td>
<td>378.7 ± 16.7</td>
<td>390.6 ± 25.2</td>
</tr>
<tr>
<td></td>
<td>NGS</td>
<td>46.1 ± 13.2</td>
<td>57.9 ± 11.4</td>
<td>103.9 ± 8.5</td>
</tr>
<tr>
<td></td>
<td>GS</td>
<td>-34.2 ± 4.4</td>
<td>320.9 ± 20.8</td>
<td>286.7 ± 23.9</td>
</tr>
</tbody>
</table>

| Mean       | Annual | -12.3              | 416.9              | 404.6                    |
|            | NGS    | 50.0               | 62.7               | 112.7                    |
|            | GS     | -62.3              | 354.1              | 291.8                    |

| SD across years | Annual | 20.4               | 38.1               | 45.1                      |
|                 | NGS    | 29.1               | 9.0                | 27.5                      |
|                 | GS     | 17.3               | 29.9               | 23.4                      |
3.2.2 Contribution of GPP and $R_{\text{eco}}$ to Interannual Variability of CO$_2$

In the non-growing season, interannual variability in NEE was strongly influenced by $R_{\text{eco}}$ ($f_{R_{\text{eco}}} = 0.90$, $f_{\text{GPP}} = 0.10$) due to $R_{\text{eco}}$ being more variable than GPP ($\sigma_{R_{\text{eco}}} = 27.53$ g CO$_2$-C m$^{-2}$, $\sigma_{\text{GPP}} = 9.0$ g CO$_2$-C m$^{-2}$). As shown in Figure 3.5, divergence of daily cumulative $R_{\text{eco}}$ between years in the winter was more apparent than GPP. High variability in $R_{\text{eco}}$ was due to higher-than-average $R_{\text{eco}}$ in autumn 2016, in which monthly $R_{\text{eco}}$ reached $>45$ g CO$_2$-C m$^{-2}$ in October and November that year. As a result, the 2016-2017 non-growing season NEE was considerably higher than the other years. Although GPP also varied in the early part of the non-growing season due to higher GPP in autumn 2016 and 2018, the difference was compensated by a lower GPP rate in early spring of those years. Consequently, although 2018-2019 cumulative daily NEE diverged from other years initially, it started to converge again later in the non-growing season (Figure 3.5a).

On the contrary, interannual variability in growing season NEE was more strongly influenced by GPP ($f_{\text{GPP}} = 0.62$, $f_{R_{\text{eco}}} = 0.38$) than $R_{\text{eco}}$ due to slightly higher variability in growing season GPP than $R_{\text{eco}}$ ($\sigma_{\text{GPP}} = 29.90$ g CO$_2$-C m$^{-2}$, $\sigma_{R_{\text{eco}}} = 23.26$ g CO$_2$-C m$^{-2}$). Cumulative GPP between years started to diverge in mid May when 2017-2018 GPP increased rapidly (69.26 g CO$_2$-C m$^{-2}$ month$^{-1}$, Fig 3.5), and was followed by the increase of 2016-2017 GPP in June (89.81 g CO$_2$-C m$^{-2}$ month$^{-1}$). Variability in $R_{\text{eco}}$ was less noticeable, except for a lower increase in daily cumulative $R_{\text{eco}}$ for 2019-2020 period in August.

Overall, this led to the influence of $R_{\text{eco}}$ and GPP on the variability of annual NEE being similar, although $R_{\text{eco}}$ was slightly more dominant ($f_{R_{\text{eco}}} = 0.58$, $f_{\text{GPP}} = 0.42$).
3.2.3 Drivers of Interannual Variability in CO₂ Fluxes

3.2.3.1 GPP

Over the years, there was a consistent decline in annual and growing season GPP. We found a significant positive correlation between annual GPP and mean annual VPD \( (r = 0.93, p<0.05) \) as
shown in Figure 3.7a, but no significant correlation with other climatic variables (i.e., $T_{s,5cm}$, RH, PAR, precipitation, Pa, $T_a$, WTD).

To further investigate the interannual drivers of GPP, light response curves were used to demonstrate how half-hourly GPP varied as a function of PAR between years in the growing season (Figure 3.6). The curve fit parameters of the light response curves ($\alpha$ and $P_{\text{max}}$) had a declining trend and were significantly different across the years ($p < 0.05$) (Table 3.3).

Light-saturated photosynthetic capacity ($P_{\text{max}}$) declined from 6.58 µmol m$^{-2}$ s$^{-1}$ in 2016-2017 to 5.28 µmol m$^{-2}$ s$^{-1}$ in 2020-2021, indicating that for a given PAR, maximum photosynthesis was lower in more recent years. As expected, $P_{\text{max}}$ also acted as a constraint for GPP, as shown by the significant positive correlation between $P_{\text{max}}$ and annual GPP ($r = 0.99$, $p < 0.05$) (Figure 3.7b).

Light use efficiency ($\alpha$) declined from 0.02 µmol CO$_2$ (µmol photon)$^{-1}$ in the first year to 0.012 µmol CO$_2$ (µmol photon)$^{-1}$ in the last year. Since $\alpha$ describes the initial slope of light response curve, lower $\alpha$ in more recent years indicated a lower ability of the bog in fixing CO$_2$ at low light. Based on the correlation analysis, interannual variability of $\alpha$ was influenced by $T_{s,5cm}$, in which higher $\alpha$ was associated with higher mean growing season $T_{s,5cm}$ ($r = 0.89$, $p < 0.05$) Figure 3.7c.

To assess the physiological response of plants to water and light availability, we analyzed the relationship between surface conductance (Gs) and VPD, ET, and PAR (Figure 3.8). Growing season Gs significantly increased with higher growing season VPD ($r = 0.96$, $p<0.05$) and higher
growing season ET \( (r = 0.87, p<0.01) \). Conversely, Gs significantly decreased with increasing growing season PAR \( (r = -0.91, p<0.05) \).

![Graph showing comparison of light response curves]

**Figure 3.6** Comparison of light response curves (i.e., Gross primary production (GPP) as a function of photosynthetically active radiation (PAR)) between years. The data points are half-hourly non-gap-filled growing season GPP.

**Table 3.3** Curve fitting parameters (i.e., light use efficiency \( (\alpha) \) and light-saturated photosynthetic capacity \( (P_{\text{max}}) \)) for the yearly light response curves.

<table>
<thead>
<tr>
<th>Period</th>
<th>( \alpha ) ( \text{(\mu mol CO}_2/\text{\mu mol photon}-1) )</th>
<th>( P_{\text{max}} ) ( \text{(\mu mol m}^{-2} \text{s}^{-1}) )</th>
<th>RMSE ( \text{(\mu mol m}^{-2} \text{s}^{-1}) )</th>
</tr>
</thead>
<tbody>
<tr>
<td>2016-2017</td>
<td>0.02186</td>
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</tr>
<tr>
<td>2017-2018</td>
<td>0.01527</td>
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<td>1.76</td>
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<td>2018-2019</td>
<td>0.01218</td>
<td>5.65</td>
<td>1.50</td>
</tr>
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<td>2019-2020</td>
<td>0.01204</td>
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<td>2020-2021</td>
<td>0.01203</td>
<td>5.28</td>
<td>1.53</td>
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</table>
Figure 3.7 Correlation analysis between (a) annual gross primary production (GPP) and annual vapor pressure deficit (VPD), (b) growing season (GS) light-saturated photosynthetic capacity ($P_{\text{max}}$) and growing season GPP, (c) growing season light use efficiency ($\alpha$) and growing season soil temperature at 5 cm depth ($T_{5\text{cm}}$).

Figure 3.8 Growing season correlations between (a) surface conductance (Gs) and vapor pressure deficit (VPD), (b) Gs and evapotranspiration (ET), and (c) Gs and incoming photosynthetically active radiation (PAR).

### 3.2.3.2 $R_{\text{eco}}$

We observed no significant bivariate correlation ($p>0.05$) between annual, growing season, and non-growing season $R_{\text{eco}}$ with annual or seasonal mean environmental variables. However, we
found that annual \( R_{\text{eco}} \) was significantly correlated with annual GPP \((r = 0.87, p<0.01)\), in which years with higher GPP tend to have higher \( R_{\text{eco}} \) (Figure 3.9).

![Figure 3.9 Annual ecosystem respiration \((R_{\text{eco}})\) in g C m\(^{-2}\) y\(^{-1}\) against annual gross primary production \((\text{GPP})\) in g C m\(^{-2}\) y\(^{-1}\)](image)

To understand the year-to-year variability in \( R_{\text{eco}} \), we looked at its temperature sensitivity \((Q_{10}^{\text{RECO}})\), which describes how much \( R_{\text{eco}} \) increases per 10°C rise in soil temperature. Annual Q10 was the lowest in 2016-2017 \((Q_{10}^{\text{RECO}} = 3.25)\) and the highest in 2018-2019 \((Q_{10}^{\text{RECO}} = 4.63)\) (Table 3.4). Daily \( R_{\text{eco}} \) as a function of \( T_{s,5\text{cm}} \) is shown in Figure 3.10.

The year-to-year variability of \( Q_{10}^{\text{RECO}} \) was mainly attributed to the hydrological conditions of the bog (Figure 3.11). Based on the correlation analysis, higher annual \( Q_{10}^{\text{RECO}} \) was associated with a lower annual WTD \((r = -0.95, p<0.05)\) and a lower annual precipitation \((r = 0.94, p<0.05)\), implying that \( R_{\text{eco}} \) was more sensitive to soil temperature during drier years. A similar pattern was observed in the non-growing season, in which \( R_{\text{eco}} \) had a stronger response to \( T_{s,5\text{cm}} \) (i.e., higher \( Q_{10}^{\text{RECO}} \)) in years with lower winter WTD \((r = -0.89)\). The \( Q_{10}^{\text{RECO}} \) – WTD relationship,
however, was not significant in the growing season when WTD was close to or below the surface (p>0.05).

![Figure 3.10 Ecosystem respiration (Reco) as a function of soil temperature at 5 cm depth (T_{s,5cm}) in different years. Data points are non-gapfilled daily Reco for the entire annual period; different years are represented by different colors. Curve fitting parameters shown in Table 3.4.](image)

Table 3.4 Comparison of curve fitting parameters (a and b) and temperature sensitivity of ecosystem respiration (Q10_{RECO}), and the model goodness-of-fit between years.

<table>
<thead>
<tr>
<th>Period</th>
<th>a</th>
<th>b</th>
<th>Q10_{RECO}</th>
<th>r^2</th>
<th>RMSE (g C m^{-2} d^{-1})</th>
</tr>
</thead>
<tbody>
<tr>
<td>2016-2017</td>
<td>0.24</td>
<td>0.12</td>
<td>3.25</td>
<td>0.79</td>
<td>0.27</td>
</tr>
<tr>
<td>2017-2018</td>
<td>0.17</td>
<td>0.14</td>
<td>4.12</td>
<td>0.82</td>
<td>0.27</td>
</tr>
<tr>
<td>2018-2019</td>
<td>0.12</td>
<td>0.15</td>
<td>4.63</td>
<td>0.80</td>
<td>0.30</td>
</tr>
<tr>
<td>2019-2020</td>
<td>0.16</td>
<td>0.13</td>
<td>3.68</td>
<td>0.70</td>
<td>0.33</td>
</tr>
</tbody>
</table>
### 3.2.3.3 NEE

Forward stepwise multiple linear regression (MLR) analysis was used to investigate the year-to-year differences in drivers of daily NEE (Table 3.5). The performance of the best model varied among years, ranging from an $R^2_{adj}$ value of 0.47 in 2017-2018 to 0.66 in 2016-2017. Out of the eight environmental variables used as inputs for the model selection (i.e., PAR, $T_s$,5cm, WTD, VPD, RH, precipitation, Pa, and $T_a$), only $T_s$,5cm consistently appeared as a significant predictor for daily NEE in all years. Even though PAR was the first or second predictor included in the model for most years, it was not significant for 2016-2017. Four out of five years also included WTD in the model, indicating its importance for predicting daily NEE. Meanwhile, the
inclusion of other variables such as RH, precipitation, and VPD could only explain an additional 1-2% of the variation in NEE. Details are provided in Appendix A.

In 2016-2017, T_{s,5cm} was the strongest driver of daily NEE. T_{s,5cm} was able to predict the seasonality of NEE, although it underestimated CO$_2$ source strength during autumn 2016 and late summer 2017. The inclusion of WTD to the model helped improve the estimation during those periods. Further inclusion of RH and precipitation only improved the model by ~2%. Overall, this year had the best model performance out of all other years ($R^2_{adj} = 0.66$).

Daily NEE in 2017-2018 was primarily driven by PAR, T$_{s,5cm}$, and WTD. The inclusion of T$_{s,5cm}$ and WTD to the model mainly improved the estimation of spring NEE, which was underestimated by PAR when it was included alone. However, the model performance for this year was the lowest of the years ($R^2_{adj} = 0.47$), mostly due to the overestimation of NEE in the peak of growing season (June-July).

In 2018-2019, T$_{s,5cm}$ mainly explained the seasonal pattern of daily NEE. Including PAR in the model helped improve the performance, especially during late summer 2019 when T$_{s,5cm}$ alone underestimated NEE. Further inclusion of precipitation only helped explain an additional ~0.4% of the variation in NEE.

For the 2019-2020 period, PAR was the strongest driver of daily NEE. However, including only PAR in the model resulted in underestimation of spring NEE and overestimation of peak growing season NEE (June – July). When T$_{s,5cm}$ was included in the model, spring and summer
estimated NEE was improved, but late summer NEE was underestimated. Further addition of precipitation and RH to the model resulted in better estimates in the peak and late growing season of 2020.

In 2020-2021, the seasonal pattern of daily NEE was mainly driven by PAR. When $T_{s,5cm}$, VPD, and WTD were included in the model, NEE estimates during spring and peak growing season were improved. However, the four variables still underestimated spring NEE and overestimated peak summer NEE ($R^2_{adj} = 0.61$).

Generally, PAR and $T_{s,5cm}$ were better predictors of daily NEE than other water-related variables (i.e., WTD, precipitation, VPD, and RH). PAR consistently underestimated spring daily NEE and overestimated peak summer daily NEE, whereas $T_{s,5cm}$ frequently underestimated late summer and autumn daily NEE.

Table 3.5 Forward stepwise multiple linear regression for non-gapfilled daily NEE

<table>
<thead>
<tr>
<th>Period</th>
<th>Variable</th>
<th>AIC</th>
<th>$R^2_{adj}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>2016-2017</td>
<td>$T_{s,5cm}$</td>
<td>-1.8</td>
<td>0.58</td>
</tr>
<tr>
<td></td>
<td>WTD</td>
<td>-20.6</td>
<td>0.64</td>
</tr>
<tr>
<td></td>
<td>RH</td>
<td>-23.9</td>
<td>0.65</td>
</tr>
<tr>
<td></td>
<td>Precipitation</td>
<td>-25.6</td>
<td>0.66</td>
</tr>
<tr>
<td>2017-2018</td>
<td>PAR</td>
<td>21.5</td>
<td>0.43</td>
</tr>
<tr>
<td></td>
<td>$T_{s,5cm}$</td>
<td>12.4</td>
<td>0.46</td>
</tr>
</tbody>
</table>
To determine the contribution of functional changes and year-to-year climatic variability to interannual variability in NEE, a homogeneity of slopes (HOS) model was used. Based on the model selection step, $T_{s,5cm}$, WTD, and PAR were identified as the three best predictors of NEE for the entire study period and were used to construct a single-slope regression model. We then included year as one of the predictor variables to detect if the slopes of regression vary among years. Based on the null-hypothesis test, we found that the interactions between year and climatic variables (i.e., the separate slopes model) were not significant ($p>0.05$), implying that the interannual variability in NEE was not caused by functional changes (Figure 3.12).

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>WTD</td>
<td>10.6</td>
<td>0.46</td>
<td></td>
</tr>
<tr>
<td>$T_{s,5cm}$</td>
<td>13.1</td>
<td>0.46</td>
<td>-99.6</td>
</tr>
<tr>
<td>PAR</td>
<td>-28.0</td>
<td>0.57</td>
<td>-101.8</td>
</tr>
<tr>
<td>Precipitation</td>
<td>-28.5</td>
<td>0.57</td>
<td>-102.4</td>
</tr>
<tr>
<td>PAR</td>
<td>21.5</td>
<td>0.52</td>
<td></td>
</tr>
<tr>
<td>$T_{s,5cm}$</td>
<td>-25.4</td>
<td>0.63</td>
<td></td>
</tr>
<tr>
<td>WTD</td>
<td>-34.6</td>
<td>0.65</td>
<td></td>
</tr>
<tr>
<td>Precipitation</td>
<td>-35.9</td>
<td>0.65</td>
<td></td>
</tr>
<tr>
<td>RH</td>
<td>-36.6</td>
<td>0.66</td>
<td></td>
</tr>
</tbody>
</table>
Figure 3.12 Comparison of single-slope and separate-slopes model for estimating weekly mean daily net ecosystem exchange (NEE) constructed from weekly mean daily soil temperature at 5 cm depth ($T_{s,5cm}$), water table depth (WTD), and photosynthetically active radiation (PAR).

The contribution of each component to the variation in weekly NEE were explained by the partitioning of sum of squares of the total deviation into $SS_t$, $SS_c$, and $SS_e$. Seasonal climatic variables together with random error contributed to more than half of the variation in NEE ($SS_{sc} = 45\%$, $SS_e = 35\%$), whereas the interannual variation in climatic variables (notably WTD, $T_a$ and PAR) accounted for 20% of year-to-year variability in weekly NEE.

At the annual scale, we found no significant bivariate correlation between cumulative NEE and mean annual climatic variables (i.e., PAR, $T_{s,5cm}$, WTD, VPD, RH, precipitation, PA, and $T_a$). Since climatic variables had no detectable direct effects on variability of a NEE, we looked at other related measures, such as $Q_{10_{Reco}}$, the ratio of GPP to $R_{eco}$ ($GPP/R_{eco}$), and their relationships in the growing and non-growing season.
In the growing season, NEE was negatively correlated with GPP/R_{eco} (r = -0.95, p < 0.05), indicating an increase in summer GPP relative to R_{eco} that resulted in a stronger net CO₂ sink status (Figure 3.13a). Higher GPP/R_{eco} was associated with lower number of days when WTD was deeper than 10 cm below the surface (i.e., relatively drier conditions) (p < 0.05) (Figure 3.13b). An increase in GPP/R_{eco} was also observed with decreasing summer T_{a} (r = -0.94, p < 0.05) (Figure 3.13c). Thus, years with a warmer and longer dry period in summer had a lower GPP to R_{eco} ratio, and consequently lower growing season net CO₂ uptake.

![Figure 3.13 Growing season correlations between (a) net ecosystem exchange (NEE) and the ratio of gross primary production to ecosystem respiration (GPP/R_{eco}), (b) GPP/R_{eco} and the number of days with water table depth (WTD) lower than 10 cm below the surface, and (c) GPP/R_{eco} and mean air temperature (T_{a}).](image)

### 3.3 CH₄ Exchange

#### 3.3.1 Annual and Seasonal CH₄ Balance

Daily CH₄ fluxes along with their monthly anomalies are presented in Figure 3.14. CH₄ fluxes showed a clear seasonal pattern throughout the years. CH₄ flux was consistently higher in the growing season (11.7 ± 2.1 g CH₄-C m⁻²) and lower in the non-growing season (2.0 ± 0.5 g CH₄-
C m\(^{-2}\)). On average, the maxima of CH\(_4\) fluxes occurred in July (3.5 ± 0.5 g CH\(_4\)-C m\(^{-2}\) month\(^{-1}\)) and the minima occurred in December (0.1 ± 0.1 g CH\(_4\)-C m\(^{-2}\) month\(^{-1}\)). Daily cumulative CH\(_4\) fluxes along with the uncertainties (95% CI) are shown in Figure 3.15.

Annually, the bog was consistently a net CH\(_4\) source over the study period. During the first four years, annual CH\(_4\) fluxes declined from 18.0 ± 1.6 g CH\(_4\)-C m\(^{-2}\) y\(^{-1}\) to 11.6 ± 0.7 g CH\(_4\)-C m\(^{-2}\) y\(^{-1}\) before going up to 13.2 ± 0.8 g CH\(_4\)-C m\(^{-2}\) y\(^{-1}\) in the last year (Table 3.6).)

![Figure 3.14 Daily CH\(_4\) fluxes in g CH\(_4\)-C m\(^{-2}\) d\(^{-1}\) (black lines) along with their monthly anomalies in g CH\(_4\)-C m\(^{-2}\) month\(^{-1}\) (grey bars). Monthly anomalies were calculated as deviations from the monthly means across five years.](image-url)
Figure 3.15 Daily cumulative CH₄ fluxes. Dashed lines indicate the end of the non-growing season and the start of growing season. Uncertainty is presented as 95% CI.

Table 3.6 Annual, non-growing season (NGS), and growing season (GS) sums of CH₄ fluxes in g CH₄-C m⁻². Flux uncertainty is presented as the 95% CI.

<table>
<thead>
<tr>
<th>Period</th>
<th>CH₄ fluxes (g CH₄-C m⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Annual</td>
</tr>
<tr>
<td>2016-2017</td>
<td>18.0 ± 1.6</td>
</tr>
<tr>
<td>2017-2018</td>
<td>13.2 ± 1.0</td>
</tr>
<tr>
<td>2018-2019</td>
<td>12.2 ± 0.6</td>
</tr>
<tr>
<td>2019-2020</td>
<td>11.6 ± 0.7</td>
</tr>
<tr>
<td>2020-2021</td>
<td>13.2 ± 0.7</td>
</tr>
<tr>
<td>Mean</td>
<td>13.7</td>
</tr>
<tr>
<td>SD across years</td>
<td>2.5</td>
</tr>
</tbody>
</table>

3.3.2 Drivers of Interannual Variability of CH₄ Fluxes

Year-to-year differences in daily drivers of CH₄ fluxes were examined using forward stepwise multilinear regression (MLR) analysis. The performance of the best model varied among years, ranging from $R^2_{adj}$ value of 0.78 in 2017-2018 to 0.89 in 2018-2019 (Table 3.7). Out of the nine
environmental variables used as inputs for the model selection (i.e., GPP, PAR, T_{s,5cm}, WTD, VPD, RH, precipitation, Pa, and T_a), WTD, GPP, and temperature (i.e., T_a and T_{s,5cm}) consistently appeared as the strongest significant predictors for daily CH_4 fluxes in all years. Inclusion of other variables such as PAR, VPD, and Pa could only improve the R^2_{adj} values by ~1%. Details are provided in Appendix B.

For the 2016-2017 period, daily CH_4 flux was best explained by T_a, which accounted for 67% of variability in NEE. Although T_a could predict the general seasonality of CH_4 flux, it underestimated CH_4 loss in February and August, and overestimated CH_4 loss in the spring. Including WTD improved the model during those periods, except for September, where it overestimated CH_4 flux. GPP further improved the goodness of fit of the model, especially in winter 2016 and peak CH_4 loss around August and September 2017.

2017-2018 CH_4 flux was best explained by T_a, followed by WTD, T_{s,5cm}, GPP, and Pa. Similar to the previous year, T_a overestimated CH_4 loss in spring and underestimated CH_4 loss in February and August. With WTD included in the model, model performance was increased, but September CH_4 flux was overestimated. Together, T_{s,5cm}, GPP and Pa explained an additional 9% of variations in CH_4 fluxes, mainly refining spring and peak CH_4 loss in summer. Overall, model performance this year was the lowest among other years (R^2_{adj} = 0.78) due to greater model residuals in July–September.

WTD was the strongest driver of daily CH_4 fluxes in 2018-2019. However, estimated peak of CH_4 loss from WTD lagged behind the peak of measured CH_4 loss by almost a month. Including
GPP in the model minimized the lag but resulted in underestimation of peak CH$_4$ loss in July. After the addition of T$_{s,5cm}$, summer CH$_4$ estimates were closer to the measured values and the model performance increased to $R^2_{adj}$ value of 0.89, which was also the best among all years.

CH$_4$ flux in 2019-2020 was mainly driven by T$_a$, which explained 63% of variations in the daily sums. T$_a$ on its own overestimated CH$_4$ flux in spring and underestimated CH$_4$ flux during its peak in July-August. The inaccuracy in spring estimates was improved by WTD and GPP; however, late summer (September) CH$_4$ was overestimated. Further inclusion of T$_{s,5cm}$ and Pa improved the model performance by 2% but still did not produce a good fit for the July-September period.

The first significant driver of CH$_4$ included in the model for 2020-2021 was WTD. Similar to 2018-2019, the summer peak CH$_4$ predicted from WTD was a month behind the observed value. Adding GPP to the model improved this, but still resulted in a poor fit in September. When T$_{s,5cm}$, VPD, and Pa were included in the model, the performance only improved by 1%.

Overall, no single predictor exhibited sufficient explanatory power on its own for effectively estimating the daily CH$_4$ flux. When used as a single predictor for the model, T$_a$ consistently overestimated CH$_4$ loss in spring, while WTD consistently yielded peak CH$_4$ that lagged the observed values by approximately a month. Even after including several predictors, the best model for each year were often not able to accurately predict CH$_4$ flux during its peak period (July-August).
Table 3.7 Forward stepwise multiple linear regression model performance for non-gapfilled daily CH₄ flux by year

<table>
<thead>
<tr>
<th>Period</th>
<th>Variable</th>
<th>AIC</th>
<th>adjR²</th>
</tr>
</thead>
<tbody>
<tr>
<td>2016-2017</td>
<td>Ta</td>
<td>-839</td>
<td>0.67</td>
</tr>
<tr>
<td></td>
<td>WTD</td>
<td>-888</td>
<td>0.78</td>
</tr>
<tr>
<td></td>
<td>GPP</td>
<td>-934</td>
<td>0.85</td>
</tr>
<tr>
<td></td>
<td>PAR</td>
<td>-935</td>
<td>0.85</td>
</tr>
<tr>
<td>2017-2018</td>
<td>Ta</td>
<td>-1088</td>
<td>0.61</td>
</tr>
<tr>
<td></td>
<td>WTD</td>
<td>-1125</td>
<td>0.69</td>
</tr>
<tr>
<td></td>
<td>Ts,5cm</td>
<td>-1149</td>
<td>0.73</td>
</tr>
<tr>
<td></td>
<td>GPP</td>
<td>-1181</td>
<td>0.78</td>
</tr>
<tr>
<td></td>
<td>Pa</td>
<td>-1182</td>
<td>0.78</td>
</tr>
<tr>
<td>2018-2019</td>
<td>WTD</td>
<td>-1461</td>
<td>0.77</td>
</tr>
<tr>
<td></td>
<td>GPP</td>
<td>-1553</td>
<td>0.86</td>
</tr>
<tr>
<td></td>
<td>Ts,5cm</td>
<td>-1600</td>
<td>0.89</td>
</tr>
<tr>
<td>2019-2020</td>
<td>Ta</td>
<td>-1232</td>
<td>0.63</td>
</tr>
<tr>
<td></td>
<td>WTD</td>
<td>-1294</td>
<td>0.74</td>
</tr>
<tr>
<td></td>
<td>GPP</td>
<td>-1331</td>
<td>0.79</td>
</tr>
<tr>
<td></td>
<td>Ts,5cm</td>
<td>-1349</td>
<td>0.81</td>
</tr>
<tr>
<td></td>
<td>Pa</td>
<td>-1352</td>
<td>0.81</td>
</tr>
<tr>
<td>2020-2021</td>
<td>WTD</td>
<td>-1611</td>
<td>0.75</td>
</tr>
<tr>
<td></td>
<td>GPP</td>
<td>-1768</td>
<td>0.87</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>--------</td>
<td>-------</td>
<td>-------</td>
<td></td>
</tr>
<tr>
<td>T, s, 5cm</td>
<td>-1775</td>
<td>0.88</td>
<td></td>
</tr>
<tr>
<td>VPD</td>
<td>-1778</td>
<td>0.88</td>
<td></td>
</tr>
<tr>
<td>Pa</td>
<td>-1780</td>
<td>0.88</td>
<td></td>
</tr>
</tbody>
</table>

To determine the contribution of functional changes and year-to-year climatic variability to CH₄ fluxes interannual variability, the HOS approach was used. We constructed a single-slope regression model for the entire study period using the three best predictors (i.e., WTD, GPP, and Tₐ). We then included year as one of the predictor variables to detect if the slopes of regression vary among years. Based on the null-hypothesis test, having separate slopes significantly improved CH₄ flux estimates (p < 0.05), especially for the 2016-2017 period (Figure 3.16). The different CH₄ response to climatic variables between years was then assumed to be caused by functional changes.

![Comparison of single-slope and separate-slopes models for estimating weekly mean daily CH₄ flux constructed from weekly mean daily water table depth (WTD), gross primary production (GPP), and air temperature (Tₐ).](image)

**Figure 3.16** Comparison of single-slope and separate-slopes models for estimating weekly mean daily CH₄ flux constructed from weekly mean daily water table depth (WTD), gross primary production (GPP), and air temperature (Tₐ).
We looked at the annual, growing season, and non-growing season temperature sensitivity (Q10\textsubscript{FCH4}) to investigate the year-to-year variability in the relationship between daily CH\textsubscript{4} flux and T\textsubscript{s,5cm}. Q10\textsubscript{FCH4} describes the increase in CH\textsubscript{4} flux per 10°C rise in soil temperature. We found that Q10\textsubscript{FCH4} in the study site was higher in the growing season (Q10\textsubscript{FCH4}= 22) than in the non-growing season (Q10\textsubscript{FCH4}= 5.7), with an annual Q10\textsubscript{FCH4} value of 20.5 (Table 3.8). Both seasonal and annual Q10\textsubscript{FCH4} did not differ between years. The exponential relationship between T\textsubscript{s,5cm} and CH\textsubscript{4} fluxes is shown in Figure 3.17.

Figure 3.17 Daily CH\textsubscript{4} fluxes as a function of soil temperature at 5 cm (T\textsubscript{s,5cm}) in different years. Data points are non-gapfilled daily CH\textsubscript{4} fluxes for the entire annual period; different years are represented by different colors.
Table 3.8 Comparison of curve fitting parameter (a and b) and temperature sensitivity (Q10) of CH$_4$ flux, and the model goodness-of-fit between years

<table>
<thead>
<tr>
<th>Period</th>
<th>a</th>
<th>b</th>
<th>Q10$_{CH4}$</th>
<th>RMSE (g C m$^{-2}$ d$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Annual</td>
<td>0.0005</td>
<td>0.30</td>
<td>20.48</td>
<td>0.029</td>
</tr>
<tr>
<td>Non-growing season</td>
<td>0.0032</td>
<td>0.17</td>
<td>5.69</td>
<td>0.011</td>
</tr>
<tr>
<td>Growing season</td>
<td>0.0005</td>
<td>0.31</td>
<td>22.03</td>
<td>0.032</td>
</tr>
</tbody>
</table>

To determine the contribution of functional changes to the interannual variability of CH$_4$ flux, we partitioned the sum of squares of the total deviation into SS$_t$, SS$_{ic}$, SS$_{sc}$, and SS$_c$. Variations in weekly CH$_4$ flux were mainly accounted for by seasonal climatic variables and random error (SS$_{sc} = 53.8\%$, SS$_c = 23.3\%$). Interannual variability in WTD, GPP, and T$_a$ contributed to 11.6% of variations in weekly CH$_4$ flux, while functional changes contributed to 11.3% of the variations in weekly CH$_4$ flux.

3.4 Net C Balance

The annual net C balance (as sum of NEE and FCH$_4$) of the bog ranged from -20.4 ± 21.5 g C m$^{-2}$ y$^{-1}$ in 2018-2019 to 29.5 ± 16.2 g C m$^{-2}$ y$^{-1}$ in 2016-2017 (Table 3.9). Over the 5 years, the bog consistently lost carbon in the non-growing season (5-year average 52.0 ± 23.7 g C m$^{-2}$), while being a C sink (5-year average 50.7 ± 16.7 g C m$^{-2}$) in the growing season. Averaged over the five years, CH$_4$ emissions (13.7 ± 2.5 g CH$_4$-C m$^{-2}$ y$^{-1}$) completely offset NEE (-12.3 ± 20.4 g CO$_2$-C m$^{-2}$ y$^{-1}$), resulting in the site losing an average of 1.3 ± 23.9 g C m$^{-2}$ y$^{-1}$. 
Table 3.9 Annual and seasonal carbon balance of Burns Bog calculated from net ecosystem exchange (NEE) and CH₄ fluxes in g C m⁻². Uncertainty is presented as the 95% CI.

<table>
<thead>
<tr>
<th>Period</th>
<th>Season</th>
<th>NEE (g CO₂-C m⁻²)</th>
<th>CH₄ flux (g CH₄-C m⁻²)</th>
<th>Net C balance (g C m⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2016-2017</td>
<td>Annual</td>
<td>11.5 ± 16.1</td>
<td>18.0 ± 1.6</td>
<td>29.5 ± 16.2</td>
</tr>
<tr>
<td></td>
<td>NGS</td>
<td>88.7 ± 15.3</td>
<td>2.8 ± 0.7</td>
<td>91.4 ± 15.3</td>
</tr>
<tr>
<td></td>
<td>GS</td>
<td>-77.2 ± 4.1</td>
<td>15.3 ± 1.2</td>
<td>-61.9 ± 4.2</td>
</tr>
<tr>
<td>2017-2018</td>
<td>Annual</td>
<td>-26.0 ± 5.5</td>
<td>13.2 ± 1.0</td>
<td>-12.8 ± 5.6</td>
</tr>
<tr>
<td></td>
<td>NGS</td>
<td>40.0 ± 3.3</td>
<td>2.1 ± 0.4</td>
<td>42.1 ± 3.3</td>
</tr>
<tr>
<td></td>
<td>GS</td>
<td>-66.0 ± 6.7</td>
<td>11.2 ± 0.8</td>
<td>-54.8 ± 6.8</td>
</tr>
<tr>
<td>2018-2019</td>
<td>Annual</td>
<td>-32.6 ± 21.5</td>
<td>12.2 ± 0.6</td>
<td>-20.4 ± 21.5</td>
</tr>
<tr>
<td></td>
<td>NGS</td>
<td>26.6 ± 18.8</td>
<td>1.5 ± 0.4</td>
<td>28.1 ± 18.8</td>
</tr>
<tr>
<td></td>
<td>GS</td>
<td>-59.3 ± 5.3</td>
<td>10.7 ± 0.5</td>
<td>-48.5 ± 5.3</td>
</tr>
<tr>
<td>2019-2020</td>
<td>Annual</td>
<td>-26.4 ± 9.9</td>
<td>11.6 ± 0.7</td>
<td>-14.7 ± 10.0</td>
</tr>
<tr>
<td></td>
<td>NGS</td>
<td>48.7 ± 9.1</td>
<td>1.6 ± 0.3</td>
<td>50.3 ± 9.2</td>
</tr>
<tr>
<td></td>
<td>GS</td>
<td>-75.0 ± 3.0</td>
<td>10.0 ± 0.6</td>
<td>-65.0 ± 3.1</td>
</tr>
<tr>
<td>2020-2021</td>
<td>Annual</td>
<td>11.9 ± 15.1</td>
<td>13.2 ± 0.8</td>
<td>25.1 ± 15.2</td>
</tr>
<tr>
<td></td>
<td>NGS</td>
<td>46.1 ± 13.2</td>
<td>2.1 ± 0.3</td>
<td>48.1 ± 13.2</td>
</tr>
<tr>
<td></td>
<td>GS</td>
<td>-34.2 ± 4.4</td>
<td>11.1 ± 0.7</td>
<td>-23.0 ± 4.4</td>
</tr>
<tr>
<td>Mean across years</td>
<td>Annual</td>
<td>-12.3</td>
<td>13.7</td>
<td>1.3</td>
</tr>
<tr>
<td></td>
<td>NGS</td>
<td>50.0</td>
<td>2.0</td>
<td>52.0</td>
</tr>
<tr>
<td></td>
<td>GS</td>
<td>-62.3</td>
<td>11.7</td>
<td>-50.7</td>
</tr>
<tr>
<td>SD across years</td>
<td>Annual</td>
<td>20.4</td>
<td>2.5</td>
<td>23.9</td>
</tr>
<tr>
<td></td>
<td>NGS</td>
<td>29.1</td>
<td>0.5</td>
<td>23.7</td>
</tr>
<tr>
<td></td>
<td>GS</td>
<td>17.3</td>
<td>2.1</td>
<td>16.7</td>
</tr>
</tbody>
</table>
3.5 GHG Balance (GHGB)

The annual GHGB of Burns Bog was calculated from annual CO\textsubscript{2} flux and annual CO\textsubscript{2}-eq emission of CH\textsubscript{4} weighted using a 20, 100, and 500-year GWP and SGWP. Regardless of the GHG metrics used in the calculation for the 20 and 100-year timeframe, the GHG balance of the bog was positive over the 5-year period (Table 3.10). However, in 2018-2019, the bog was a small GHG sink in the 500-year timeframe when calculated using GWP.
Table 3.10 Annual GHG balance of Burns Bog calculated using 20, 50, and 100-year timeframe sustained global warming potential (SGWP) and global warming potential (GWP). Uncertainty is presented as the 95% CI.

<table>
<thead>
<tr>
<th>Period</th>
<th>GHGSGWP20 (g CO₂-eq m⁻² y⁻¹)</th>
<th>GHGSGWP100 (g CO₂-eq m⁻² y⁻¹)</th>
<th>GHGSGWP500 (g CO₂-eq m⁻² y⁻¹)</th>
<th>GHGGWP20 (g CO₂-eq m⁻² y⁻¹)</th>
<th>GHGGWP100 (g CO₂-eq m⁻² y⁻¹)</th>
<th>GHGGWP500 (g CO₂-eq m⁻² y⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2016-2017</td>
<td>2422.2 ± 209.8</td>
<td>1192.9 ± 111.4</td>
<td>445.7 ± 66.1</td>
<td>1963.2 ± 177.2</td>
<td>692.9 ± 81.7</td>
<td>215.7 ± 60.9</td>
</tr>
<tr>
<td>2017-2018</td>
<td>1648.2 ± 128.9</td>
<td>747.7 ± 63</td>
<td>200.4 ± 27.5</td>
<td>1312 ± 107.6</td>
<td>381.5 ± 41</td>
<td>31.9 ± 22.2</td>
</tr>
<tr>
<td>2018-2019</td>
<td>1488.9 ± 112.7</td>
<td>658.2 ± 87.3</td>
<td>153.2 ± 79.6</td>
<td>1178.7 ± 103.3</td>
<td>320.3 ± 81.9</td>
<td>-2.2 ± 78.9</td>
</tr>
<tr>
<td>2019-2020</td>
<td>1439.7 ± 98.8</td>
<td>646.2 ± 56.4</td>
<td>163.9 ± 38.8</td>
<td>1143.4 ± 84.5</td>
<td>323.4 ± 44.6</td>
<td>15.4 ± 37.0</td>
</tr>
<tr>
<td>2020-2021</td>
<td>1783.7 ± 112.9</td>
<td>885 ± 72.2</td>
<td>338.7 ± 57.4</td>
<td>1448.1 ± 98.7</td>
<td>519.4 ± 62</td>
<td>170.5 ± 56.0</td>
</tr>
</tbody>
</table>
Chapter 4: Discussion

The aim of this study was to analyze the interannual variability in C fluxes of a restored temperate peatland. Here, we measured five years (2016 – 2021) of ecosystem scale CO\textsubscript{2} and CH\textsubscript{4} fluxes in Burns Bog nine years after rewetting. Analyses were conducted to evaluate the annual C budgets and GHG balances of the site and how they varied between years. To identify the drivers of interannual variability in CO\textsubscript{2} and CH\textsubscript{4} fluxes of the bog, we evaluated the relationship between fluxes, environmental variables, and functional changes across five years at different timescales.

4.1 Interannual Variability in CO\textsubscript{2} Fluxes

Based on the yearly multiple linear regression analyses, daily net CO\textsubscript{2} flux (NEE) was primarily controlled by PAR, T\textsubscript{s,5cm}, and WTD and/or precipitation (Table 3.5). Overall, the models were able to predict the seasonality well, in which lower daily NEE (i.e., more CO\textsubscript{2} uptake) coincided with higher PAR, higher T\textsubscript{s,5cm}, and deeper WTD, typically observed in the growing season.

There are a strong physical and physiological relationships between PAR, soil temperature, and metabolic processes. PAR is a well-known dominant control of photosynthesis (Bubier et al., 1998; Frolking et al., 1998). At the same time, PAR affects soil temperature, which in turn regulates plant growth and respiration (Bubier et al., 1998). Despite being able to explain the seasonal pattern of NEE well, PAR alone consistently overestimated spring CO\textsubscript{2} uptake in Burns Bog. The inclusion of T\textsubscript{s,5cm} in the model helped improve the estimates, suggesting that T\textsubscript{s,5cm} serves as a limiting factor during this period. This is most likely due to the low photosynthetic activity in the early spring when soil temperature is not warm enough to support plant growth.
(Walker et al., 2017). However, in the late autumn, $T_{s, 5cm}$ typically underestimated NEE (i.e., overestimated CO$_2$ uptake). As fresh C input accumulated throughout the growing season, heterotrophic respiration might persist well after plant senescence (Goulden et al., 1998; Kross et al., 2014; Lund et al., 2010), resulting in a higher observed NEE in the autumn.

Mean daily WTD in Burns Bog typically ranged from ~20 cm below the surface in the growing season to 15 cm above the surface in the non-growing season. This seasonal variation in WTD determines the depth of aerobic and anaerobic zones of the peat layer, which in turn affects heterotrophic respiration (Bubier et al., 1998). Waterlogged conditions may inhibit respiration and plant growth of species that are not well adapted to high water levels, while WTD that is too low can lead to water stress in plants (Helfter et al., 2015). In this study, larger daily net CO$_2$ uptake was observed when WTD was relatively close to the surface, when the aerobic zone of the soil profile was shallow enough to limit heterotrophic respiration without causing water stress to the vegetation (Tuittila et al., 2004; Walker et al., 2017).

During periods of low WTD, precipitation events provided water to the moss layer, thus increasing its capitulum moisture and supporting photosynthesis. However, precipitation could only explain an additional 1-2% of the model variance in this study, presumably due to the similar rate of increase in photosynthesis and respiration (resulting in a minimal change in NEE) during the short period after precipitation events (Strack & Price, 2009).

Based on the HOS result, interannual variability in weekly NEE was mainly driven by interannual variability in $T_{s, 5cm}$, PAR, and WTD, which agrees with our finding on the daily
drivers of NEE. However, we detected no impact of functional changes in explaining the interannual variability of weekly NEE. Here, we interpret functional changes as non-climatic parameters that regulate photosynthesis and respiration (e.g., shifts in vegetation composition, phenology, plant physiology, nutrient status, etc.) following the definition by Hui et al. (2003). In contrast to our observation, McVeigh et al. (2014) reported a significant, although relatively small, contribution of functional changes to variations in NEE at Glencar blanket bog in Ireland. In their review, Niu et al. (2017) also highlighted the considerable effect of changes in plant traits on interannual variability in NEE across different ecosystem types.

Interestingly, although our HOS results didn’t detect a role of functional changes in explaining interannual variability in NEE, we found evidence of a functional change (i.e., vegetation composition shift) happening at this site based on our analysis at the annual scale (as discussed in the next section). In our case, the HOS approach is presumably not sensitive enough to detect functional changes because: (i) GPP and \( R_{eco} \) responded similarly to the change, leading to undetectable differences in NEE, or (ii) the response was not large enough at the weekly timescale.

Annual GPP of Burns Bog across five years (416.9 ± 38.1 g C m\(^{-2}\) y\(^{-1}\); mean ± SD across years) was comparable to annual GPP in other restored northern bogs (412 to 743 g C m\(^{-2}\) y\(^{-1}\)) (Nugent et al., 2018; Swenson et al., 2018). In this study, higher annual GPP was associated with higher mean annual VPD (Figure 3.7a). VPD could affect GPP through regulating stomatal aperture, in which the opening of stomata leads to higher surface conductance, thus enhancing CO\(_2\) diffusion into the leaves and photosynthetic rate (Chaves et al., 2004). Depending on climate and plant
water usage strategy, an increase in VPD could either increase or decrease surface conductance and evapotranspiration (Massmann et al., 2019). Some studies have found that high VPD (> 1 kPa) constrained GPP due to VPD-induced stomatal closure (Aurela et al., 2007; Cai et al., 2010; Goodrich, Campbell, Clearwater, et al., 2015; Otieno et al., 2012). In Burns Bog, VPD rarely reached 1 kPa, except in the very dry summer 2021, in which the high VPD only lasted a few days and did not significantly increase the mean growing season VPD. In this lower range of VPD, plants might prioritize photosynthesis over water conservation, as seen by the positive correlation between VPD and surface conductance (Gs) and evapotranspiration (ET) at the site (Figure 3.8). Similarly, Alekseychik et al. (2017) reported that high VPD favored GPP in a bog in Finland as long as the dry period did not last too long.

The magnitude and interannual variability of $R_{eco}$ at this study site (404.6 ± 45.1 g C m$^{-2}$ y$^{-1}$; mean ± SD across years) was within the range of that reported in other restored temperate peatlands over multiple observation years: from 175.0 ± 100.0 g C m$^{-2}$ y$^{-1}$ at Bellacorick Bog in Ireland (Wilson et al., 2016) to 650.7 ± 28.7 g C m$^{-2}$ y$^{-1}$ at Bois-des-Bel Bog in Canada (Nugent et al., 2018). At Bellacorick Bog, interannual variability in $R_{eco}$ was mostly affected by water availability and temperature, in which years with a below-average precipitation, a drop in WTD, and a high mean soil temperature had higher annual $R_{eco}$ (Wilson et al., 2016).

Although we could not identify any direct primary climatic driver of annual $R_{eco}$, to further investigate the relationship between $R_{eco}$, temperature, and WTD at Burns Bog, we looked at the year-to-year variability in temperature sensitivity ($Q_{10_{RECO}}$). $Q_{10_{RECO}}$ at Burns Bog varied considerably between years, ranging from 3.25 to 4.64 (Table 3.4). All values fell within the
range of $Q_{10\text{RECO}}$ measured using soil temperature at 5 cm depth in other studies, e.g., 2.16 at a boreal bog in Russia (Mamkin et al., 2021), 2.8 to 4.95 at Rzecin peatland in Poland (Acosta et al., 2017; Juszczak et al., 2013), and 3.91 in the growing season at Mer Bleue bog, Canada (Lafleur et al., 2005). We found that annual $Q_{10\text{RECO}}$ increased with drier conditions (less annual precipitation and lower WTD) in the bog (Figure 3.11 The relationship between temperature sensitivity of ecosystem respiration ($Q_{10\text{RECO}}$) and hydrological variables. (a) Annual $Q_{10\text{Reco}}$ against annual precipitation in mm, (b) annual $Q_{10\text{Reco}}$ against mean annual WTD in m, (c) non-growing season (NGS) $Q_{10\text{Reco}}$ against non-growing season WTD in m. Figure 3.11). Similarly, Juszczak et al. (2013) reported greater $Q_{10\text{RECO}}$ in the year with deeper minimum WTD. With lower WTD, oxygen diffusion into the peat layer is enhanced, thus the depth of the aerobic zone increases, while the anaerobic zone decreases. Higher $Q_{10\text{RECO}}$ values under aerobic conditions are presumably due to enhanced heterotrophic respiration, as some microbial enzyme activities for decomposition (e.g., phenol oxidase) require oxygen (Chen et al. 2018; Szafranek-Nakonieczna and Stêpniewska 2014).

As noted above, although no direct climatic driver explained interannual variability in $R_{\text{eco}}$, we did observe higher annual $R_{\text{eco}}$ in years with higher annual GPP (Figure 3.9). It should be noted that this relationship may be spurious, due to possible self-correlation between GPP and $R_{\text{eco}}$ resulted from NEE partitioning (Ueyama et al., 2014; Vickers et al., 2009). However, there is a widely accepted physical and physiological basis for the relationship between $R_{\text{eco}}$ and GPP, in which some portion of CO$_2$ taken up during photosynthesis is released back to the atmosphere via autotrophic and heterotrophic respiration (Lund et al., 2010; Nugent et al., 2018; Tuittila et al., 2000).
When averaged over the five-year period, Burns Bog was CO\textsubscript{2} neutral (-12.3 ± 20.4 g CO\textsubscript{2}-C m\textsuperscript{-2}; mean ± SD across years). Annual net CO\textsubscript{2} uptake at Burns Bog was generally lower than that measured in undisturbed northern bogs with multiple years of EC measurements (Figure 4.1). Drollinger et al. (2019) reported a two-year mean NEE of -54 ± 42 g CO\textsubscript{2}-C m\textsuperscript{-2} in a low-shrub pine bog in Austria (Puergschachen Moor, 47°34.873′N, 14°20.810′E). Similarly, Roulet et al. (2007) estimated a mean NEE of -40.2 ± 40.5 g CO\textsubscript{2}-C m\textsuperscript{-2}) across six years in an intact temperate bog in Ontario, Canada (Mer Bleue Bog, 45.40°N, 75.50°W). Helfter et al. (2015) measured a 12-year mean NEE of -64.1 ± 33.6 g CO\textsubscript{2}-C m\textsuperscript{-2} in a near-intact bog in Scotland (Auchencorth Moss Bog, 55°47′32″N, 3°14′35″ W). Larger net CO\textsubscript{2} uptake and interannual variability was reported by Ueyama et al. (2020) for an intact temperate bog in Japan (Bibai Mire, 43°19′22.82″N, 141°48′38.51″E) with a four-year mean NEE of -147 ± 65 g CO\textsubscript{2}-C m\textsuperscript{-2}. In contrast, degraded peatlands are generally stronger net CO\textsubscript{2} sources compared to Burns Bog. Aslan-Sungur et al. (2016) reported a three-year mean NEE of 384 ± 241 g CO\textsubscript{2}-C m\textsuperscript{-2} in a drained, harvested, and grazed temperate peat meadow in Turkey (Yenicaga peatland, 40°47′24″N, 32°1′44″E), while Holl et al. (2020) reported a similar mean NEE of 233 ± 53 g CO\textsubscript{2}-C m\textsuperscript{-2} across two years in a drained and harvested bog in Germany (Himmelmoor bog, 53°44′23.3″ N, 9°50′55.8″ E).

Annual NEE of Burns Bog was within the range of NEE measured in restored peatlands. For a single year of EC measurements, Schaller et al. (2021) reported a positive net CO\textsubscript{2} flux of 38 g CO\textsubscript{2}-C m\textsuperscript{-2} 18 years after rewetting in a previously drained and harvested bog in Germany (Uchter Moor, 52° 30’ 30” N, 8° 49’ 33” E). Conversely, Wilson et al. (2016) found that an
Atlantic blanket bog in Ireland (Bellacorick bog, 54°7'29.9"N, 9°33'22.2"W) was a net CO₂ sink (mean NEE across five years = -84 g CO₂-C m⁻²) with large interannual variability (SD = 103 g CO₂-C m⁻²) seven years after rewetting. Nugent et al. (2018) estimated even greater net CO₂ uptake with a three-year mean NEE of -90 ± 18 g CO₂-C m⁻² (mean ± SD across years) 14 years after restoration using a moss layer transfer technique in Bois-des-Bel Bog, Canada (47°58'1.95"N, 69°25′ 43.10"W). Large between-site and between-year variability of NEE in restored peatlands may be a result of different restoration management practices (Drollinger et al., 2019) and a transition in vegetation community and water table dynamics (Wilson et al., 2016).

![Figure 4.1 Comparison of annual net ecosystem exchange (NEE) between degraded, restored, and intact (undisturbed) temperate and boreal peatlands with long-term (>1 year) measurements (Aslan-Sungur et al., 2016; Drollinger et al., 2019; Fortuniak et al., 2021; Helfter et al., 2015; Holl et al., 2020; MacDonald, 2017;].

Figure 4.1 Comparison of annual net ecosystem exchange (NEE) between degraded, restored, and intact (undisturbed) temperate and boreal peatlands with long-term (>1 year) measurements (Aslan-Sungur et al., 2016; Drollinger et al., 2019; Fortuniak et al., 2021; Helfter et al., 2015; Holl et al., 2020; MacDonald, 2017;
McVeigh et al., 2014; Nugent et al., 2018; Olson et al., 2013; Peichl et al., 2014; Rinne et al., 2018; Roulet et al., 2007; Strachan et al., 2016; Swenson et al., 2018; Ueyama et al., 2020; Wilson et al., 2016). Data points and error bars depict mean and standard deviation across years.

Some studies across different ecosystems have found that the variability in NEE is driven more by $R_{\text{eco}}$ (Schaefer et al., 2002; Ueyama et al., 2014; Wilson et al., 2016), while others have found GPP to be more influential (Baldocchi et al. 2018; Lund et al. 2010). In our study, we found an almost equivalent influence of GPP and $R_{\text{eco}}$ on interannual variability in NEE. However, we observed different dominant controls in different seasons.

In the non-growing season, $R_{\text{eco}}$ determined interannual variability of NEE at the study site. Similarly, Mamkin et al. (2021) reported that NEE was regulated by an increase in $R_{\text{eco}}$ during positive anomalies in winter temperature at Staroselsky Mokh bog in Russia. In Burns Bog, high variability in non-growing season $R_{\text{eco}}$ was mainly due to anomalously high $R_{\text{eco}}$ in autumn 2016 (Figure 3.5). This period of high $R_{\text{eco}}$ coincided with higher-than-average monthly soil and air temperature in October and November 2016, suggesting that warmer autumns can significantly enhance non-growing season NEE. With higher autumn temperatures, studies have found that the increase of $R_{\text{eco}}$ exceeded that of GPP, presumably due to limited radiation for photosynthesis (Piao et al., 2008; Ueyama et al., 2014). Although $R_{\text{eco}}$ drove the interannual variability of NEE in the non-growing season, we could not identify any significant relationship between temperature, WTD, or precipitation with NEE, indicating that its interannual variability could not be explained by only a single climatic variable. Furthermore, the low number of non-gap-filled CO$_2$ flux observations in the non-growing season (14% to 37%; Table 2.1), especially during
long measurement gaps in January – February 2017 and 2018 limits the reliability of our estimates.

In the growing season, interannual variability in NEE at Burns Bog was mostly driven by the variability in growing season GPP. Although VPD explained GPP at the annual scale, mean growing season VPD could not explain a declining trend in growing season GPP over the years. Lower growing season GPP along with lower light use efficiency ($\alpha$) and lower values for maximum GPP at light saturation ($P_{\text{max}}$) in recent years might be an indication of a shift in vegetation composition from more sedge-dominated to more moss-dominated. Mosses are widely known to have a lower photosynthetic capacity than sedges and other vascular plants on a dry mass or area basis (Green & Lange, 1995; Korrensaloo et al., 2016; Laine et al., 2016; Martin & Adamson, 2001; Yuan et al., 2014).

We also observed a positive relationship between $\alpha$ and mean growing season soil temperature (Figure 3.7c). Previous studies have found that an increase in fractional moss cover resulted in colder summer soil temperature due to its insulating effect (Chen et al., 2019; Park et al., 2018). The insulating properties of moss can be attributed to: (1) reduced heat transfer into the soil due to lower thermal conductivity of the air-filled pores in the moss layer during dry periods (Dolley et al., 2022; Gornall et al., 2007); (2) the moss layer acting as a physical barrier against direct solar radiation (Shulgin 1957, as cited in Gornall et al. 2007). In a previous study done in a different part of our study site, Howie et al. 2008 found that the percent cover of $Sphagnum$ increased significantly within a year after rewetting. Studies in other restored peatlands also found an increase in moss cover 1 to 19 years after rewetting (Boudreau & Rochefort, 2008;
Gagnon et al., 2018; Mazzola et al., 2021), further supporting the possibility of a shift in vegetation community towards moss-dominated after years of restoration.

Summer drought has been reported to cause an increase in growing season NEE by suppressing GPP (Kross et al., 2014; Lund et al., 2012; Shurpali et al., 1995) or enhancing $R_{eco}$ (Aurela et al., 2007; Cai et al., 2010; Drollinger et al., 2019; Lund et al., 2012; Pugh et al., 2018). Lund et al. (2012) suggested that the timing and period of the drought mattered, where short and severe droughts triggered an increase in $R_{eco}$ due to an increase in decomposition (Chimner et al., 2017), while long droughts mainly decreased GPP through water stress in vegetation that is adapted to a high WTD. On the other hand, at a peatland with vegetation composition that is more adapted to lower WTD, Flanagan and Syed (2011) found that warmer and drier summers increased GPP and $R_{eco}$ at an equal rate, resulting in no effect of drought on NEE.

In this study, we did not find any clear evidence of suppression or enhancement of GPP and $R_{eco}$ during drier and warmer summer. This is presumably due to the site undergoing a shift in vegetation composition. Differences in the proportion of vascular and moss population can result in contrasting GPP and $R_{eco}$ responses to WTD (Sulman et al., 2010), which implies that transitioning ecosystems may have unclear responses to drier and warmer summer. However, we observed an overall decrease in the ratio of growing season GPP to $R_{eco}$ ($GPP/R_{eco}$) in the summers with higher mean air temperature and more days with deeper WTD (Figure 3.13), suggesting that warmer and drier summer ultimately enhanced growing season NEE. The effect of warm and dry summer at the bog was most evident in 2020-2021 period, when the mean growing season WTD reached -7.25 cm and the mean air temperature reached 15.45°C, resulting
in the smallest growing season CO₂ uptake among all years (NEE = -34.2 ± 4.4 g C m⁻²; ± 95% CI) and lowest growing season GPP.

Although some studies have found that annual NEE components (i.e., GPP and Reco) were mostly determined by their growing season sums due to their larger contributions (Alekseychik et al., 2021; Mamkin et al., 2021), we found that both non-growing and growing season fluxes played an important part in regulating the net CO₂ status of Burns Bog. In the 2018-2019 period, the bog’s status as a net CO₂ source was attributed to the high respiration in the early non-growing season due to the anomalously warm autumn. Then, during the three years when the climatic conditions were close to the five-year average (i.e., 2017 to 2021), the bog switched to being a weak CO₂ sink. Nonetheless, due to the very dry and warm summer of 2021, the bog switched to being a net CO₂ source again in the 2020-2021 period. Based on this observation, we can conclude that the interannual variations in the CO₂ source or sink status of the bog were largely explained by anomalies in climatic conditions, mainly temperature and WTD which had different impacts at different times of the year.

4.2 Interannual Variability in CH₄ Fluxes

Burns Bog was consistently an annual CH₄ source over the five-year period, emitting an average of 13.7 ± 2.5 g CH₄-C m⁻² y⁻¹ (± SD across years) over the five-year period. This value is comparable to annual CH₄ fluxes of natural temperate and boreal peatlands with available long-term EC measurements (Figure 4.2). Intact peatlands are known as important CH₄ sources with considerable variability between sites (Abdalla et al., 2016). Ueyama et al. (2020) reported a mean annual emission of 16.9 g CH₄-C m⁻² y⁻¹ from an intact temperate bog in Japan (Bibai
Mire, 43°19′22.82″N, 141°48′38.51″E). Similarly, Olson et al. (2013) estimated a mean emission of 16.3 ± 7.5 g CH₄-C m⁻² y⁻¹ from a poor fen in Minnesota. Other studies have reported mean annual CH₄ balance in the lower range, for example: 4.8 ± 0.6 g CH₄-C m⁻² y⁻¹ in a low-shrub pine bog in Austria (Drollinger et al., 2019), 3.7 ± 0.5 g CH₄-C m⁻² y⁻¹ in Mer Bleue Bog, Canada (Roulet et al., 2007), and 2.5 ± 0.3 g CH₄-C m⁻² y⁻¹ at an intact boreal bog in Canada (Wang et al., 2018). Compared to natural peatlands, drained peatlands often have lower CH₄ emissions (Abdalla et al., 2016). Wang et al. (2017) reported a near-zero CH₄ emission (0.2 ± 0.2 g CH₄-C m⁻² y⁻¹) in an abandoned peatland pasture with active drainage in Canada, while Holl et al. (2020) measured a higher mean of 9.5 ± 3.4 g CH₄-C m⁻² y⁻¹ in a drained and harvested temperate bog in Germany.

Comparing the interannual variability in CH₄ balances of rewetted peatlands is difficult, as there are not many studies with long-term continuous EC measurements. Compared to our findings, Nugent et al. (2018) reported a significantly lower mean and variability of annual CH₄ flux (4.4 ± 0.15 g CH₄-C m⁻² y⁻¹; mean ± SD across years) from three years of EC measurements in a restored bog in Quebec, Canada (Bois-des-Bel bog, 47°58′1″95″N, 69°25′43″10″W) 14 years after restoration. Similarly, Schaller et al. (2021) estimated a lower annual CH₄ balance of 6.5 g CH₄-C m⁻² y⁻¹ from a restored bog in Germany 18 years after rewetting (Uchter Moor, 52° 30’ 30″ N, 8° 49’ 33″ E), although EC measurements were only carried out for a year. The mean annual CH₄ balance in Burns Bog was more similar to that of a restored blanket bog in Ireland seven years after rewetting (11.2 ± 9 g CH₄-C m⁻² y⁻¹), as reported by Wilson et al. (2016) based on a five-year record of chamber measurements. However, chamber-derived CH₄ fluxes are known to yield higher estimates than EC-derived CH₄ fluxes due to chamber method not being
able to capture high spatial and temporal variations of CH$_4$ fluxes (Fortuniak et al., 2017; Korrensalо et al., 2018). Variability in CH$_4$ fluxes between rewetted peatlands might be caused by different initial disturbances, restoration strategies, and peatland types (Abdalla et al., 2016).

**Figure 4.2** Comparison of CH$_4$ balance between degraded, restored, and intact temperate and boreal peatlands with long-term (>1 year) eddy covariance measurements (Drollinger et al., 2019; Fortuniak et al., 2021; Goodrich, Campbell, Roulet, et al., 2015; Holl et al., 2020; Nilsson et al., 2008; Nugent et al., 2018; Olson et al., 2013; Rinne et al., 2018; Roulet et al., 2007; Ueyama et al., 2020; Wang et al., 2017, 2018). Error bars indicate standard deviations across years.

Based on the yearly multiple linear regression models, temperature (T$_a$ and T$_{s,5cm}$), WTD, and GPP are the primary drivers of daily CH$_4$ flux in our study site for all years (Table 3.7). Generally, daily CH$_4$ fluxes were higher in the growing season when temperatures and GPP were high and WTD was low.
Temperature is known as an important control of methanogenesis, in which higher soil temperatures are optimum for growth of methanogens (Whalen, 2005). Previous studies have found that CH$_4$ fluxes increase exponentially with rising temperature at the daily to monthly timescale (Hommeltenberg et al., 2014; Pugh et al., 2018; Rinne et al., 2018; Ueyama et al., 2020). We found that CH$_4$ flux sensitivity to soil temperature at this study site (annual $Q_{10\text{CH}_4} = 20.5$) was at the higher end of the $Q_{10\text{CH}_4}$ range of peatland ecosystems, which range from 1 to 35 (Lupascu et al., 2012; Whalen, 2005). It should be noted that these reported $Q_{10\text{CH}_4}$ values were estimated from various soil temperature depths and peatland types, thus producing a wide range of values (Rinne et al., 2018; Whalen, 2005). Non-growing season $Q_{10\text{CH}_4}$ ($5.7$) was lower than the growing season $Q_{10\text{CH}_4}$ ($22$), in line with the findings by Ueyama et al. (2020).

Another important driver of daily CH$_4$ fluxes was WTD. Here, we observed increasing CH$_4$ fluxes as WTD decreased in spring. Increased CH$_4$ fluxes during water table drawdown was likely due to the release of CH$_4$ through ebullition when the lowering of WTD exposed trapped bubbles to the atmosphere (Moore and Dalva 1993; Tokida, Miyazaki, and Mizoguchi 2013). Additionally, lower WTD was associated with warmer temperature, indicating that the increase of CH$_4$ fluxes in spring is presumably a result of the interaction between declining WTD and warmer temperature. In our model, WTD tends to overestimate CH$_4$ fluxes in the late growing season (mid August – September), during which mean monthly WTD was at its lowest level (~15 cm below the surface) and could reach a mean daily WTD of 20 cm below the surface. This suggests that CH$_4$ fluxes increased with decreasing WTD only within a certain threshold. Rinne et al. (2018) reported a threshold of -25 cm at a fen with Sphagnum-Carex sp. vegetation, Alekseychik et al. (2017) observed a limit of -20 cm at a bog with Sphagnum-Rhynchospora alba.
vegetation, while Turetsky et al. (2014) estimated an optimum WTD of -23.8 cm from 15 intact bog sites in the northern hemisphere. Low water table could reduce CH\textsubscript{4} fluxes by: (1) decreasing CH\textsubscript{4} production zone and increasing CH\textsubscript{4} oxidation zone (Lai, 2009; Whalen, 2005), (2) inhibiting the roots of vascular plants from reaching the anaerobic zone, thus decreasing plant-mediated CH\textsubscript{4} transport and limiting substrate supply for methanogenesis (Waddington et al., 1996). Typically, bog vascular vegetation have more than half of their root biomass within 10 cm of the bog surface, but some species are able to adapt and have their roots penetrate to up to ~30 cm depth below the surface during drier condition (Backeus, 1990).

In this study, using WTD and air temperature as single predictors consistently overestimated CH\textsubscript{4} fluxes in springtime periods. Inclusion of GPP in the model helped improve the estimation, indicating that early growing season CH\textsubscript{4} production was limited by substrate availability. In the early growing season, C uptake from photosynthesis might not be sufficient to yield fresh litter and root exudates for methanogenesis (Wang et al. 2017). The importance of substrate availability as a driver of CH\textsubscript{4} has been reported in previous studies (Gong et al., 2021; Mazzola et al., 2021; Tuittila et al., 2000; Waddington et al., 1996).

Although the model performance was generally high for all years (R\textsuperscript{2ad} = 0.78 to 0.89), WTD, temperature, and GPP were not able to capture CH\textsubscript{4} flux well during its peak period (July – August). Rather than controlled by CH\textsubscript{4} production, we speculate that CH\textsubscript{4} flux in the summer may be driven more by plant-mediated transport of CH\textsubscript{4} to the atmosphere in the study site. Previous studies had found that transport of CH\textsubscript{4} through plant aerenchyma made up 30-70% of total CH\textsubscript{4} flux in the growing season (Korrensalo et al., 2021; Noyce et al., 2014). Turner et al.
(2020) also found that the presence of aerenchymatous vegetation increased summer CH₄ fluxes, and high CH₄ emissions might persist until late summer as long as there was continuous C input for methane production.

Based on the HOS result, we found that interannual variabilities in WTD, GPP, and T_a were not sufficient in explaining the interannual variability in weekly CH₄ fluxes over the five-year period. The partitioning of variance indicates that ~49% of interannual variability in CH₄ flux was explained by functional changes (Chapter 3.3.2). Similarly, Rinne et al. (2018) observed a significant contribution of functional changes (~43%) in a boreal fen. Here, we interpret functional changes as non-climatic parameters that control CH₄ production, oxidation, and transport, e.g. microbial activities and vegetation phenology. Our finding is supported by Moore et al. (2011), in which they reported that vegetation cover was a more important driver of CH₄ fluxes than WTD and temperature over a longer time period. Since interannual variability in temperature and water table can affect biomass and the timing of plant growth and senescence (Noyce et al., 2014), plant species inherently carry information on the effects of climatic variables in addition to its own functions (Korrensalo et al., 2021). This indication of the presence of functional changes at the bog aligns with our speculation about shifting vegetation from vascular plant-dominated to moss-dominated ecosystem (as discussed in the previous CO₂ section). Additionally, Juottonen et al. (2021) reported that methanogens are very sensitive to changes in acidity and moss cover, further underlining the importance of functional changes as one of the drivers of CH₄ fluxes.
Although some studies in wetland ecosystems have found higher annual CH$_4$ fluxes in warmer and/or wetter years (Olson et al. 2013; Drollinger, Maier, and Glatzel 2019; Knox et al. 2016), we found no significant correlation ($p > 0.05$) between annual or growing season CH$_4$ fluxes and mean annual environmental variables (WTD, $T_a$, $T_{s,5cm}$). Similarly, Moore et al. (2011), Ueyama et al. (2020), and Rinne et al. (2018) did not find any correlation between annual CH$_4$ and summer WTD and precipitation. In contrast to findings from Rinne et al. (2018) where $Q_{10_{FCH_4}}$ varied interannually from 3.8 to 12 across 11 years, we found no significant difference in $Q_{10_{FCH_4}}$ across years in this study. However, even with variations in $Q_{10_{FCH_4}}$, Rinne et al. (2018) reported that growing season soil temperature could not explain interannual variability in CH$_4$ fluxes in their study site. Besides hydrological and climatic drivers, some studies have observed a positive correlation between annual CH$_4$ fluxes and vegetation (i.e., GPP or green area index) (Rinne et al., 2018; Wilson et al., 2016), however, this was not observed in our study.

The difficulty in assessing drivers of interannual variability at this site may arise from several factors. First, interannual variation in environmental conditions across the five-year study period may not be large enough to produce considerable differences in CH$_4$ fluxes. The difference in mean air temperature between the coldest and warmest year in Burns Bog was only 0.3°C, similar to that of a blanket bog in Ireland where no interannual variability in CH$_4$ fluxes was observed (Laine et al., 2007). Additionally, Belyea (2009) argued that peatlands exhibit nonlinear behavior; they maintain a persistent state when “stabilizing forces (i.e., negative feedback) dominate, and undergo rapid transformation when destabilizing forces (i.e., positive feedback mechanisms) dominate”. Thus, measurements at a longer timescale may be needed to capture wider climate conditions and disturbances that exceed the resilience threshold of the bog.
(Belyea, 2009; Ueyama et al., 2020). Second, a single variable may not be enough to explain interannual variability in CH$_4$ in this site. For example, we speculate that 2016-2017 had the highest annual CH$_4$ flux due to a combination of several factors, including: (i) higher soil temperatures and GPP (i.e., greater C input) throughout the growing season enhanced CH$_4$ production, (ii) a later timing of water table drawdown and higher spring-summer WTD (i.e. longer period of optimum WTD for CH$_4$ release, combined with warm spring-summer temperature) may enhance plant-mediated CH$_4$ transport and limit the depth of the methane oxidation zone, in line with the findings from Feng et al. (2020) where later timing of elevated WTD increased annual CH$_4$ fluxes by 9-15%. In 2019-2020, the year with the lowest annual CH$_4$ emission, we observed a similarly high WTD in the summer but with lower soil temperature. This shows that WTD or soil temperature alone did not necessarily promote or inhibit CH$_4$ emissions, and that interaction between these variables is more important.

### 4.3 Net C Balance

When accounting for both CO$_2$ (NEE) and CH$_4$ fluxes, the bog alternated between an annual net C sink and net C source, ranging from -20.4 ± 21.5 to 29.5 ± 16.2 to g C m$^{-2}$ y$^{-1}$. When averaged over the 5-year period, the site was C neutral, emitting 1.3 ± 23.9 g C m$^{-2}$ y$^{-1}$ (mean ± SD across five years). Compared to other peatlands, the mean net C balance of Burns Bog was within the range of other restored sites (Schaller et al., 2021; Wilson et al., 2016). Degraded peatlands are typically greater net C sources, while intact peatlands tend to be greater net C sinks (Figure 4.3).
The ratio of annual CH$_4$ flux to NEE ranged from -0.5 to 1.6, indicating that the inclusion of CH$_4$ emissions in the net balance either decreased the C sink strength or increased the C source strength of the bog. As a result, CH$_4$ fluxes at this site is not negligible in terms of the C balance, and its exclusion would result in an overestimation of the net C sink strength of the bog.

It is important to note that the net C balances we present here only included CO$_2$ and CH$_4$ fluxes and does not represent the full net ecosystem carbon balance (NECB) of the study site. In addition to surface–atmosphere exchange of CO$_2$ and CH$_4$, a full assessment of NECB typically includes carbon monoxide (CO) and volatile organic C (VOC) fluxes, and leaching or lateral transfer of dissolved organic C (DOC), dissolved inorganic C (DIC) and particulate C (PC) (Chapin et al., 2006). For peatland ecosystems in particular, since DOC loss through runoff is reportedly considerable, NECB is commonly estimated from CH$_4$, CO$_2$, and lateral transfer of DOC fluxes (Limpens et al., 2008; Roulet et al., 2007). In a previous study done by D'Acunha (et al. 2019) at Burns Bog for the 2016-2017 annual cycle, DOC loss in this site (15.6 ± 3.2 g C m$^{-2}$ y$^{-1}$) made up a significant proportion of the NECB (i.e., fCO$_2$ + fCH$_4$ + fDOC = -29.7 ± 17.0 g C m$^{-2}$ y$^{-1}$). This indicates that only accounting for CH$_4$ and CO$_2$ fluxes at Burns Bog may result in underestimation of the annual NECB.

Across multiple years, Nugent et al. (2018) reported a mean annual DOC loss of 6.9 ± 2.2 g C m$^{-2}$ y$^{-1}$ (± SD across years) at the Bois-des-Bel restored peatland in Canada, contributing only 6% to the site’s annual NECB; while Roulet et al. (2007) reported a higher mean annual DOC loss of 16.4 ± 3.4 g C m$^{-2}$ y$^{-1}$ (± SD across years) at the undisturbed Mer Bleue peatland in Canada, which equates to 37% of the site’s mean NEE. Despite varying contributions of annual DOC to
NECB at the two sites, both studies found that NEE was still the largest and the most variable component of the interannual variability in net C balance. Given that, even if the net C balance reported in our study might be an underestimate of the NECB, the exclusion of DOC may be relatively minor when assessing interannual variability in the overall C balance of the bog.

Figure 4.3 Comparison of net C balance between degraded, restored, and intact temperate and boreal peatlands (Drollinger et al., 2019; Fortuniak et al., 2021; Holl et al., 2020; Nilsson et al., 2008; Nugent et al., 2018; Olson et al., 2013; Peichl et al., 2014; Rinne et al., 2018; Roulet et al., 2007; Schaller et al., 2021; Swenson et al., 2018; Ueyama et al., 2020; Wilson et al., 2016). Error bar indicates standard deviations across measurement years.

4.4 GHG Balance

To understand the role of Burns Bog in regulating global climate, we quantified its annual greenhouse gas (GHG) balance from CH₄ and CO₂ fluxes. Since CH₄ and CO₂ differ in their
perturbation life and effectiveness in trapping heat in the atmosphere, calculations of the net GHG balance commonly involve normalizing the average radiative forcing of CH₄ flux to that of CO₂ flux using GHG metrics over a defined timeframe (Balcombe et al., 2018). The two common metrics that have been widely used in the literature are the global warming potential (GWP) and the sustained global warming potential (SGWP). These two metrics were derived based on different assumptions about how the GHG fluxes were emitted: the GWP assumes a pulse emission, while the SGWP assumes a sustained emission over the defined timeframe (Neubauer, 2021).

Here, we calculated the net GHG balance of Burns Bog using GWP and SGWP metrics over 20, 100, and 500-year timeframes. Due to its sustained emission assumption, the GHG balance estimates using the SGWP had higher magnitudes than the estimates using the GWP, and this deviation increased with longer timeframes (Table 3.10).

For the 20 and 100-year timeframes, the bog consistently had a positive radiative balance regardless of the metrics used. Interestingly, a significantly lower estimate (GHG_{GWP100} = -22 g CO₂-eq m⁻² y⁻¹) in the previous year (i.e., 2015-2016) at the study site was reported by Lee et al. (2017). This discrepancy is likely due to the difference in the GWP value used and the flux gap-filling approach, along with a higher CO₂ uptake during their study period. Overall, our GHG balances were within the range of estimates from other peatland sites: Schaller, Hofer, and Klemm (2021) found that a restored peatland in Germany still acted as a GHG source (GHG_{GWP100} = 309 g CO₂-eq m⁻² y⁻¹) 18 years after rewetting; Ueyama et al. (2020) reported that a nearly intact bog in Japan served as a GHG source (GHG_{GWP100} = 215 to +395 g CO₂-eq m⁻² y⁻¹).
for most years except for a wet summer year when its annual CO₂ sink was the strongest (GHG\textsubscript{GWP100} = -3 g CO₂-eq m\textsuperscript{-2} y\textsuperscript{-1}); and Drollinger, Maier, and Glatzel (2019) documented that an intact pine bog in Austria alternated between being a GHG sink (GHG\textsubscript{GWP100} = -110 g CO₂-eq m\textsuperscript{-2} y\textsuperscript{-1}) and a source in a drought year (GHG\textsubscript{GWP100} = +75 g CO₂-eq m\textsuperscript{-2} y\textsuperscript{-1}). Using this shorter timescale, the impact of methane emission is considered more potent than CO₂ emission (Pugh et al., 2018). For example, although the bog was a net C sink in 2017-2020, the relatively strong radiative forcing of CH\textsubscript{4} made even small emissions of CH\textsubscript{4} significant in the GHG balance during those three years.

On the other hand, when quantified using the GWP for the 500-year timeframe, the bog was a GHG sink in the 2018-2019 period (GHG\textsubscript{GWP500} = -2.2 g ± 78.9 CO₂-eq m\textsuperscript{-2} y\textsuperscript{-1}). During this period, the bog was the strongest CO₂ sink compared to other years. As CH\textsubscript{4} perturbation lifetime is shorter (12.4 years; Myhre et al. 2013) than that of CO₂ (37 years; Neubauer and Megonigal 2015), the impact of CH\textsubscript{4} may be less significant in the GHG context of the bog at longer timeframes.

Despite mainly acting as GHG source after 9 to 14 years after rewetting, restoration efforts at Burns Bog have most likely provided more benefits than leaving the bog drained. Studies have reported that without rewetting, drained peatlands will emit more GHG due to continuous peat oxidation (Günther et al., 2020; Leifeld et al., 2019). Additionally, Nyberg (2021) compared two locations in Burns Bog with different rewetting strategies (i.e., active vs. passive/minimal rewetting), and found that the site with active rewetting (this site) had a lower annual GHG balance. This suggests that rewetted peatlands, especially those in a further stage of rewetting,
have a net cooling impact on the climate over long time periods more potential in returning to
GHG sinks.

It should be noted, however, that we did not include N$_2$O flux in our calculation of GHG balance.
Peatland ecosystems generally have very small N$_2$O fluxes (Frolking et al., 2011; Hendriks et al.,
2007; Wilson et al., 2016), and specifically for our site, Christen et al. (2016) found N$_2$O fluxes
to be negligible.
Chapter 5: Conclusion

Five years of eddy covariance (EC) measurements were conducted at Burns Bog, a restored temperate ombrotrophic peatland in British Columbia, Canada, 9 to 14 years after rewetting. During the study period, the bog switched between being a weak annual net CO$_2$ source and sink, ranging from $-32.6 \pm 21.5$ g CO$_2$-C m$^{-2}$ y$^{-1}$ to $11.9 \pm 15.1$ g CO$_2$-C m$^{-2}$ y$^{-1}$ ($\pm 95\%$ CI). This interannual variability in CO$_2$ fluxes at the bog was mainly explained by anomalies in climatic conditions (mainly WTD and temperature), in which the site was a CO$_2$ source during the year with a warmer and drier summer (i.e., 2020-2021 period). Concurrently, the bog was a consistent CH$_4$ source, emitting $11.6 \pm 0.7$ g CH$_4$-C m$^{-2}$ to $18.0 \pm 1.6$ g CH$_4$-C m$^{-2}$ ($\pm 95\%$ CI) over the five years. We could not identify any direct climatic drivers of the variability in annual CH$_4$ fluxes, however, we found that WTD, GPP, temperature, and functional changes together drove the interannual variability in weekly CH$_4$ fluxes. Overall, based on the HOS results and the declining light use efficiency (LUE) over time, there may have been a shift in the vegetation community of the bog from sedge-dominated towards moss-dominated, also in part explaining interannual variability in net CO$_2$ exchange at the site.

Averaged across the five years, CH$_4$ emissions ($13.7 \pm 2.5$ g CH$_4$-C m$^{-2}$ y$^{-1}$; $\pm$ SD across years) offset NEE (-12.3 $\pm$ 20.4 g C m$^{-2}$ y$^{-1}$), resulting in the site being net C neutral ($1.3 \pm 23.9$ g C m$^{-2}$ y$^{-1}$). A large contribution of CH$_4$ fluxes to the net C balance shows that excluding CH$_4$ flux results in a significant overestimation of net C uptake at the bog. Compared to other peatlands, Burns Bog seems to be at a transition stage between drained peatlands that are typically large CO$_2$ sources and intact peatlands that are typically CO$_2$ sinks.
Regardless of the GHG metrics (i.e., GWP and SGWP) used in the estimation of GHG balance for the 20 and 100-year timeframes, Burns Bog consistently had a positive radiative balance due to the strong radiative forcing of CH₄ emissions. However, when calculated using GWP for the 500-year timeframe, the bog had a negative radiative balance in the year when it was a large CO₂ sink (i.e., 2018-2019). Since CH₄ has a shorter lifetime in the atmosphere, CO₂ has a greater impact in the GHG balance of the bog at longer timeframes. Despite the bog acting mainly as a GHG source 9 to 14 years after rewetting, the rewetting effort will likely have a cooling effect on the climate over long timescales in the future.

However, there are some limitations in this study that need to be addressed. First, data gaps in the winter introduced considerable uncertainty in annual and non-growing season sums, thus limiting our confidence in interpreting non-growing season fluxes and their potential drivers. Second, there is no available vegetation survey around the flux footprint area to confirm our speculation about the change of vegetation composition towards a more moss-dominated community. Freely available satellite images (e.g., Landsat and MODIS) are also too coarse in their spatial and temporal resolutions, making interpretation difficult. Third, despite the reportedly more important role of soil moisture compared to WTD and precipitation in driving C fluxes (Strack & Price, 2009), we did not have reliable soil moisture measurements during the study period (i.e., no replicates for hummocks and hollows, and inconsistent placement of the sensors throughout the years).
Despite the limitations, as one of the few studies with multiple-year measurements of ecosystem scale CO$_2$ and CH$_4$ fluxes in a rewetted peatland, this study provides useful insights. To the best of our knowledge, there are only two studies with full annual CO$_2$ and CH$_4$ balances with >1 year of EC measurements in temperate restored peatlands currently (e.g., Nugent et al. 2018; Schaller et al. 2021). Here, we present full annual balances of C fluxes and demonstrate that short-term monitoring is not sufficient in characterizing the C dynamics of restored peatlands. Climatic variability along with functional changes may lead to peatlands switching between C sink and C sources within the span of a few years. Furthermore, with predicted increases in the frequency of droughts due to climate change, the re-establishment of the role of restored peatlands as C sinks may be disrupted. For future work, longer term measurements (> 5 years) are necessary to capture the response of peatlands to disturbances, climate trends, and climate extremes, and to detect more reliable relationships between fluxes and their potential drivers at the interannual scale.
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Appendices

Appendix A  Forward stepwise multiple linear regression of daily NEE

Figure A.1 Observed (black dots) and predicted (colored lines) daily net ecosystem exchange (NEE) in 2016-2017. Different colors show different combinations of variables used in the forward stepwise multiple linear regressions.

Figure A.2 Observed (black dots) and predicted (colored lines) daily net ecosystem exchange (NEE) in 2017-2018. Different colors show different combinations of variables used in the forward stepwise multiple linear regressions.
Figure A.3 Observed (black dots) and predicted (colored lines) daily net ecosystem exchange (NEE) in 2018-2019. Different colors show different combinations of variables used in the forward stepwise multiple linear regressions.

Figure A.4 Observed (black dots) and predicted (colored lines) daily net ecosystem exchange (NEE) in 2019-2020. Different colors show different combinations of variables used in the forward stepwise multiple linear regressions.
Figure A.5 Observed (black dots) and predicted (colored lines) daily net ecosystem exchange (NEE) in 2020-2021. Different colors show different combinations of variables used in the forward stepwise multiple linear regressions.
Appendix B  Forward stepwise multiple linear regression of daily CH$_4$ Fluxes

Figure B.1 Observed (black dots) and predicted (colored lines) daily CH$_4$ fluxes in 2016-2017. Different colors show different combinations of variables used in the forward stepwise multiple linear regressions.

Figure B.2 Observed (black dots) and predicted (colored lines) daily CH$_4$ fluxes in 2017-2018. Different colors show different combinations of variables used in the forward stepwise multiple linear regressions.
Figure B.3 Observed (black dots) and predicted (colored lines) daily CH₄ fluxes in 2018-2019. Different colors show different combinations of variables used in the forward stepwise multiple linear regressions.

Figure B.4 Observed (black dots) and predicted (colored lines) daily CH₄ fluxes in 2019-2020. Different colors show different combinations of variables used in the forward stepwise multiple linear regressions.
Figure B.5 Observed (black dots) and predicted (colored lines) daily CH$_4$ fluxes in 2020-2021. Different colors show different combinations of variables used in the forward stepwise multiple linear regressions.