Controls on autotrophic and heterotrophic respiration in an ombrotrophic bog

Tracy Rankin

Geography Department, McGill University, Montreal

May 2022

A thesis submitted to McGill University in partial fulfillment of the requirements of the degree of Doctor of Philosophy in Geography

Abstract

Northern peatlands are globally significant carbon (C) stores. However, a peatland may flip between a source and a sink of C due to annual variations in climate. Most of the variation occurs because of changes in gross primary productivity and autotrophic respiration (AR, respiration by plant parts), and we understand these components reasonably well. However, peatland models and dark respiration measurements only crudely partition ecosystem respiration into its autotrophic and heterotrophic (HR, respiration by microbial bacteria in the soil, fungi, etc.) components, using constant ratios to parameterize growth respiration. This may lead to an overestimation of C sequestration through unexpected allocations of C to labile pools with different turnover rates. Additionally, HR is not as straight forward as we once thought, and is more intimately linked to vegetation dynamics, where plant-soil-root relationships seem to play an important role. This is especially true in sedge-dominated ecosystems, but this more dynamic nature of HR is not as well documented in shrub-dominated ecosystems, like bogs, where the water table is further away from the surface. The objectives of this study were to partition AR and HR at Mer Bleue, an ombrotrophic bog, and to determine the factors that determine the spatial and temporal variability in AR and HR for the dominant shrubs and the sparser sedges at the site. Plot level measurements were used to partition AR and HR (using automatic and manual chamber methods) and were coupled with the use of stable ($\delta^{13}C$) and radiocarbon ($\Delta^{14}C$) isotopes of C through end-member analysis as well as root and nutrient analyses. Results show that AR contributions ranged between 60 and 75% depending on environmental conditions, such as temperature and moisture, and the methodology used to conduct the measurements. The findings also show that a plant's response to changes in climate is related to the plants' root structure, which indicates different mechanisms of obtaining water and nutrient resources and utilizing associations with other plants around them. It is suggested that the mosses have a stronger association with the shrubs than with the sedges, which may lead to a plant-associated contribution to HR, highlighting the important role that plant-soil-root interactions play in peatland respiration dynamics. We believe this study will improve our understanding of peatland C cycling, be useful to incorporate peatland-specific climate feedbacks in land surface schemes and improve the conceptualization of HR.

Résumé

Les tourbières sont des réserves de carbone (C) importants et mondialement significatives. Cependant, une tourbière peut osciller entre une source et une réserve de C en raison des variations annuelles du climat. La majorité de la variation se produit en raison de changements dans la productivité primaire et la dynamique de la respiration autotrophique (AR, respiration par les plantes), et nous comprenons assez bien ces composants. Cependant, les modèles des tourbières et les mesures directes de la respiration ne partitionnent que grossièrement la respiration de l'écosystème en ses composantes autotrophique et hétérotrophique (HR, respiration par les bactéries microbiennes, les mycorhizes, etc.), en utilisant des valeurs constantes pour paramétrer la respiration grossesse. Cela peut conduire à une surestimation de la séquestration du C par des allocations inattendues de C à des pools labiles avec des taux de rotation différents. De plus, la HR n'est pas aussi simple que nous le pensions autrefois et est plus intimement liée à la dynamique de la végétation, où les relations plante-sol-racine semblent jouer un rôle important. Cela est particulièrement vrai dans les écosystèmes dominés par les carex, mais cette nature plus dynamique de HR n’est pas aussi bien documentée dans les écosystèmes dominés par les arbustes, comme les bogs, où la nappe phréatique est plus éloignée de la surface. Les objectifs de cette étude étaient de partitionner AR et HR à Mer Bleue, une tourbière ombrotrophique, et de déterminer les facteurs qui déterminent la variabilité spatio-temporelle de AR et HR pour les arbustes dominants et les carex plus clairsemés du site. Des mesures au niveau des plantes ont été utilisées pour partitionner AR et HR (en utilisant des méthodes de chambre automatiques et manuelles) et ont été accouplées à l'utilisation d'isotopes stables ($\delta^{13}C$) et radiocarbon ($\Delta^{14}C$) de C par le biais d'une analyse des membres finaux ainsi que des analyses des racines et des nutriments. Les résultats montrent que les contributions de AR variaient entre 60 et 75 % en fonction des conditions environnementales, comme la temperature et humidité, ainsi que de la méthodologie utilisée pour effectuer les mesurements. Les résultats montrent également que la réponse d'une plante aux changements climatiques est liée à la structure racinaire des plantes, ce qui indique différents mécanismes d'obtention des ressources en eau et nutrients et d'utilisation des associations avec d'autres plantes qui les entourent. En particulier, il est suggéré que les mousses ont une association plus forte avec les arbustes qu'avec les carex, ce qui peut etre consideré comme une contribution associée-plantes aux HR, soulignant le rôle important que jouent les interactions plantes-sol-racines dans la dynamique de la respiration des tourbières. Nous pensons que ce projet améliorera notre compréhension du cycle du carbone des tourbières, sera utile pour intégrer les rétroactions climatiques spécifiques aux tourbières dans les schémas de surface terrestre et améliorera la conceptualisation de HR.

Table of Contents

List of Figures

List of Tables

List of Abbreviations

C – Carbon

CO_2 - Carbon Dioxide

CH_4 - Methane

ER – Ecosystem Respiration

NEE – Net Ecosystem Exchange

GPP – Gross Primary Production

HR – Heterotrophic Respiration

AR – Autotrophic Respiration

T – Temperature

WT – Water Table

WTD – Water Table Depth

VWC – Volumetric Water Content

SOM – Soil Organic Matter

Acknowledgements

I would like to thank first and foremost my supervisor, Dr. Nigel Roulet, for all his wonderful guidance, advice and financial and emotional support throughout the last five years, and my committee member, Dr. Tim Moore, who provided helpful advice and constructive criticism. Thank you both very much for the great opportunity!

I would like to also thank my other committee members, Dr. Peter Douglas, Dr. Christian Von Sperber and Dr. Elyn Humphreys for their valuable suggestions and sharing with me their extensive knowledge of peatlands, isotopes, and nutrient analyses. I will be forever grateful to Mike Dalva, the wonderful lab technician who was always available to answer questions and help with equipment malfunctions, and the many student research assistants who helped me with my field work: Maya Hassa, Kevin Hutchins, Zoe Humeau, and Miranda Hunter. And I would also like to extend a very big thank you to my very close colleagues, Tanja Prsa, Manuel Helbig, Siya Shao, and Martina Schlaifer, who helped me survive as a graduate student by providing ample support as well as contributed to my overall understanding of peatlands and their carbon cycle feedbacks.

Finally, I would not be where I am today without my family and friends; thank you for providing me with the love and support I needed to succeed! I would like to especially thank my dad who helped construct many of my field structures, and of course, my partner Nicholas Soulard, who kept me calm through all the stressful times and watched our son, Luke, while I worked. I love my boys very much!

Contribution to Original Knowledge

This thesis contributes to our understanding of peatland carbon dynamics by exploring respiration and its components in an ombrotrophic bog. In particular, the thesis speaks to the lack in understanding of the conceptualization of heterotrophic respiration (HR) and its strong link with vegetation dynamics. The thesis shows, through different methods of CO_2 flux measurements and measures of belowground processes, that plant-root-soil interactions play a much greater role in heterotrophic respiration for woody shrubs than previously thought; a phenomenon mainly found in sedge-dominated ecosystems like fens or in permafrost ecosystems. This thesis will ultimately improve the conceptualization of HR.

Contribution of Authors

This thesis is presented in the manuscript-based thesis format.

This thesis is the original work of Tracy Rankin with a few exceptions. The collection of the manual flux measurements and environmental variables were carried out by the author, Tracy Rankin, except for the biomass measurements, which was provided by Miranda Hunter and reported in an honour's thesis (not published in the thesis archives of McGill University). Dr. Elyn Humphreys provided the data and the Matlab code for performing post-processing, cleaning, and gap-filling procedures on the automatic chamber measurements. But all the data from the automatic chambers was analysed by Tracy Rankin. All the other data was also analysed by Tracy Rankin, as well as the creation of all the figures and tables. Dr. Nigel Roulet provided expert advice and financial support for the project as well as edited the manuscripts. All the committee members contributed to the editing process of the thesis as well.

Chapter 1: Introduction

1.1 Background and motivation

Northern peatlands play a significant role in the global carbon (C) cycle, covering 12% of Canada's terrestrial surface (Tarnocai et al., 2011), yet containing ~ 50% of the organic carbon stored in Canadian soils (Tarnocai, 2006). Peat accumulates due to decomposition rates being less than net primary production, making natural peatlands long term sinks of atmospheric C. However, on shorter time scales, a natural peatland may be a source or a sink of carbon depending on the environmental and biogeochemical conditions of a given year (Dorrepaal et al. 2009; Roulet et al. 2007). Ecosystem respiration (ER) includes an autotrophic respiration (AR) component that consists of respiration by plant parts, and a heterotrophic respiration (HR) component that consists of respiration of microbial bacteria communities and fungi.

Although most of the variability in CO_2 exchange comes from changes in gross primary production (GPP) and AR (Blodau, 2002; Heimann and Reichstein, 2008), the dynamics of HR is not straight forward. HR is a variable that is correlated with environmental and substrate variables (Minkkinen et al., 2007; St-Hilaire et al., 2008), but has also recently been shown to be linked more to vegetation dynamics than previously thought. For example, Fan et al. (2013) suggest that long-term exposure to warmer conditions may lead to an increase in HR outpacing an increase in C input and C sequestration will weaken, which they attribute to root-soil interactions and a change in the transport of labile C. Similarly, Basiliko et al. (2012) highlight the difficulties in separating root respiration from HR, and organic C that is supplied as a substrate by the vascular plants (plant-associated HR), causing a priming effect, is not easily discernible from root respiration itself.

Belowground processes are more connected to aboveground production than just the slow decomposition of dead organic matter, especially when root dynamics are considered (Ryan and Law, 2005; Van Hees et al., 2005), which has been seen in sedge - dominated (Järveoja et al., 2018; Kurbatova et al. 2013; Wang et al. 2014) and in permafrost ecosystems (Crow and Wieder, 2005; Hicks Pries et al. 2015). For example, partitioning of respiration has been observed in fen sites, such as Degero Stormyr, a poor fen in northern Sweden, explored by Järveoja et al. (2018). While some peatland carbon models have come a long way from crudely simulating HR (He et al., 2018; Shao et al., 2022), the role of vegetation dynamics, and how the more complex nature of HR will change ecosystem structure, is still not well documented, particularly in peatlands dominated by woody shrubs – e.g., mid-continental bogs. My thesis addresses the influence of vegetation on HR in a mid-continental, raised bog (Mer Bleue) and will help to improve our conceptualization of HR.

Additionally, many studies that have explored the partitioning of AR and HR using either an automatic or manual chamber system, seem to only do so by using values found in the literature, constant ratios or fixed decomposition rates (Bond-Lamberty et al., 2004), which may lead to an overestimation of C sequestration due to unexpected allocations of C to labile pools with different turnover rates (Hungate et al., 1997; Phillips et al., 2017). Direct methods of partitioning AR and HR are not well documented. Studies seem to also differ in their descriptions of AR and HR. Bond-Lamberty et al. (2004) suggest there is no standard practice on whether to include rhizosphere respiration with AR or HR. This may be due to the difficulty in separating their impact on the C balance from other root functions (Chapin et al., 2006).

The distinction between AR and HR becomes less clear when there are strong links between soil organisms and plant roots, such as with mycorrhizal fungi (Figure 1.1). Shrubs, for example, have mycorrhizae that help improve their nutrient uptake (Shao, 2022), and it has not been well documented how to separate HR by the mycorrhizae and AR by the roots of the plants themselves (Baldwin and Batzer, 2012). My thesis used a combination of measurement methods (manual and automatic chambers and biogeochemical approaches) to partition HR and AR, and a variety of environmental variables to understand the temporal and spatial variability in respiration and its components. AR was then calculated as a residual of the ER - HR. Below ground processes were explored and coupled to above ground production.

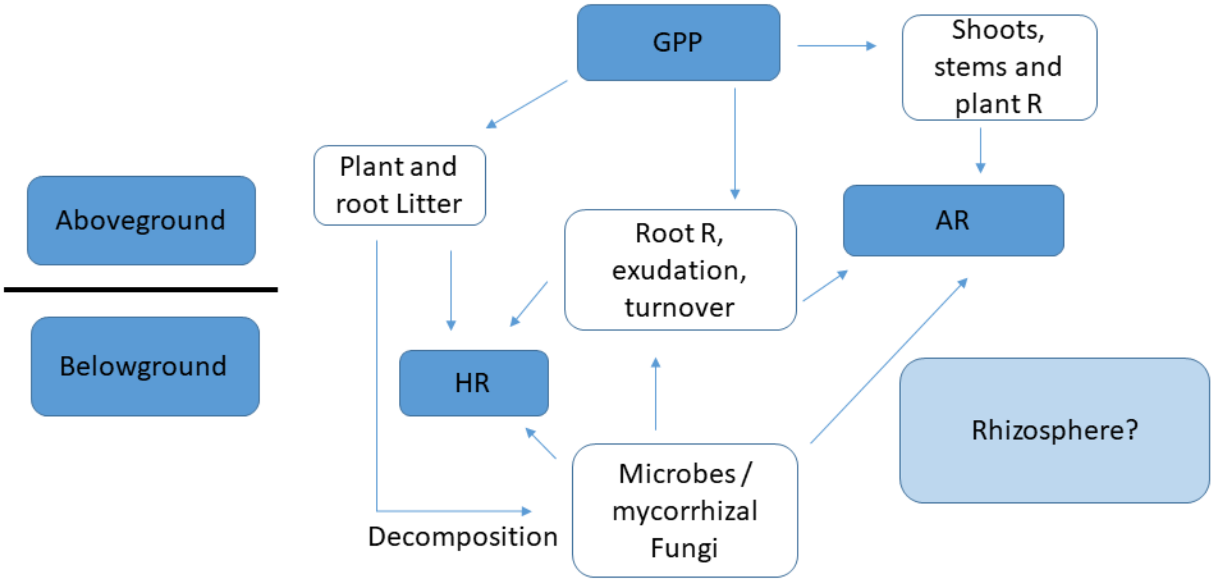


Figure 1.1 Respiration pathways, inspired by Jacoby et al. (2017), Ryan and Law (2005), and Van Hees et al. (2005).

1.2 Research objectives and hypotheses

There is a need for a better understanding of the processes and mechanisms that influence the changes in respiration and its components. My conceptualization of HR leads to questions on how to handle certain processes, such as plant-associated HR and mycorrhizal fungi, that highlight the intimate link between soil organisms and plant functioning. It is also important to provide empirically derived estimates of the partitioning to help further testing and the development of models. Thus, the goal of my study was to empirically determine the autotrophic and heterotrophic contributions to ER at a temperate, ombrotrophic bog in south-eastern Ontario (Mer Bleue) to get a better understanding of the processes and mechanisms that affect respiration. I also aimed to determine how the contributions of AR and HR at Mer Bleue compare with the values/ratios reported for other ecosystems. The contributions of my thesis chapters are as follows.

Chapter 3:

Using manual chambers, I aimed to establish the environmental controls on ER, AR, and HR at Mer Bleue for both the dominant shrubs as well as the sparse sedges. Looking at both plant types allowed the role of plant-associated HR to be explored and the dependence of plant type on the AR and HR contributions to ER to be examined. Finally, I explored the relationship between the mosses and the vascular plants and their associated feedback. My hypotheses were that 1) respiration from the shrubs will be more affected by changing weather conditions than the sedges, and 2) that the mosses will inhibit the decomposition of the microbes below.

Chapter 4:

Using a variety of methodologies that incorporated belowground processes, such as nutrient and root exudate analyses as well as isotopic analyses, I aimed to determine whether the woody shrubs at the Mer Bleue bog mediate belowground processes and whether the shrub-dominated bog contains a plant-associated HR component that exceeds peat respiration, as has been observed in sedge-dominated peatlands. My hypotheses were that 1) the presence of roots from woody vascular plants prime the decomposition of organic matter, and 2) that the woody shrubs are more intimately associated with the mosses and the peat surrounding them are the sedges.

Chapter 5:

Using an automatic chamber set up, I aimed to determine the average contributions of AR and HR and the temporal/spatial variability of AR and HR at the Mer Bleue bog. Then I compared the contributions with those of the Degero Stormyr Fen in Umea (Sweden) and other ecosystems. I also explored the benefits and disadvantages of using darkened chambers to directly measure respiration fluxes directly during the day versus estimating respiration from relationships between temperature and night-time respiration. My hypotheses were that 1) ER measured directly using darkened chambers will be lower than ER derived from night-time relationships with temperature, and that 2) The AR/HR ratio will be higher in shrub-dominated peatlands than in sedge-dominated peatlands.

1.3 Experimental design

I used a variety of methodological approaches to partition AR and HR at MB as well as to characterise the spatial and temporal variability in AR and HR. These included (1) conducting CO_2 measurements at the plot level, using both automatic and manual chamber methods, whereby manipulations of the plots were applied in early 2018 (e.g., clipping experiments), (2) nutrient and root exudate analyses, whereby peat and pore water samples were obtained to determine whether they support the CO_2 fluxes, and (3) the use of stable ($\delta^{13}C$) and radiocarbon isotopes ($\Delta^{14}C$) of C. Isotopic methods are a less invasive way to determine the portion of respiration that comes from either recently fixed plant C or that which is derived from older C sources in the soil.

In 2017, before manipulations were applied to the manual plots (Chapter 3), I established a baseline for the CO_2 fluxes in the plots covering the dominant shrubs and the sparse sedges at the site and conducted a cluster analysis on the matrix of respiration values forcing them into one of two groups in the R statistical software (RStudio, version 4.0.2). I performed a “pam” clustering approach on distance matrices, calculated using the “daisy” distance function, on the standardized matrix along the rows (i.e., clustering the plots into 2 groups). I decided to use this method because it is a more robust version of the commonly known “k-means” approach, but it also allows missing values. I did, however, perform a “k-means” clustering approach, filling in the missing values with the mean CO_2 flux for that day and given plant type. I found that the plants behaved as expected, where all the shrub plots behaved similarly to one another and all the sedge plots behaved similarly to one another, but the plots behaved differently between the two sections (Figure A1).

I also established a baseline for the CO_2 fluxes in the automatic chamber plots (Chapter 5) across the growing season of 2017. I used five of the automatic chambers, separated into two clusters. The two clusters responded differently, but similarly among the automatic chamber plots within the same cluster (Figure A2). The chambers from Cluster 1 had growing season ER flux averages of 425 and 392 mg CO_2 m^{-2} hr^{-1}, and the chambers from Cluster 2 had growing season ER flux averages of 327 and 311 mg CO_2 m^{-2} hr^{-1}. One of the CO_2 flux time series is missing in Figure A2 from Cluster 1 due to instrument error. Based on the ecosystem respiration fluxes from previous years, that chamber fit better with Cluster 1 than Cluster 2 (Personal Communication, Dr. Elyn Humphreys).

Chapter 2: Literature Review

2.1 Peatlands and their role in the carbon cycle

Northern peatlands play a significant role in the global carbon (C) cycle, covering 12% of Canada's terrestrial surface (Tarnocai et al., 2011) yet containing ~ 50% of the organic carbon stored in Canadian soils (Tarnocai, 2006). Peatlands take up carbon dioxide (CO_2) through photosynthesis by the surface vegetation and release CO_2 through plant respiration, litter, and peat decomposition. On average, gross production is greater than ecosystem respiration where low temperatures and anoxic conditions both lead to the favouring of biomass production over decomposition (Blodau, 2002; Humphreys et al., 2014). Peat accumulates due to decomposition rates being less than net primary production, making natural peatlands long term sinks of C (Normand et al., 2021; Xu et al., 2018). Following the last glaciation, peatlands have accumulated C at an average rate of 23-26 g m^{-2} yr^{-1} (Charman et al., 2013; Loisel et al., 2014). However, on shorter time scales, an undisturbed peatland can be a source or a sink of carbon depending on the environmental conditions of a given year (Dorrepaal et al., 2009; Roulet et al., 2007).

Carbon enters an ecosystem as gross primary productivity (GPP) through photosynthesis by the surface vegetation. Together, the aboveground and belowground portions of the plants return about half of that C to the atmosphere as autotrophic respiration (AR). Net primary productivity (NPP) is the difference between GPP and AR. Most NPP is transferred to soil organic matter (SOM) through litter, dead roots and exudates, and most C that enters the soil is lost through heterotrophic respiration (HR) by microbial bacteria in the soil, macrobes (e.g. earthworms), decomposition of organic matter, leaching of dissolved organic and inorganic C and methane gas (Blodau, 2002; Chapin et al., 2002). Net ecosystem production (NEP) is the net

C gain or loss by an ecosystem. It is the difference between GPP (gain of carbon) and ecosystem respiration (ER). In a steady state system, where no disturbance is present, GPP would be balanced equally by all avenues of C loss. But most ecosystems never reach a complete steady state, resulting in either a net gain or loss of C from the system due to the imbalance between production and decomposition, and exacerbated by disturbances such as climate change. This would affect the C that has been stored for hundreds to thousands of years in soils like peatlands, and hence would have an impact on the global C (Lafleur, 2008).

2.2 Partitioning autotrophic and heterotrophic respiration

Respiration dynamics have been explored in peatlands, mainly through eddy covariance techniques (e.g., Cai et al., 2010; Humphreys et al., 2014; Peichl et al., 2014) and using darkened chambers (e.g., Järveoja et al., 2018; Lai, 2012), which measure C exchange at a scale that towers cannot. Models have also been developed that attempt to project how the components of the C exchange (e.g., ER) will vary with a changing climate (e.g., Abdalla et al., 2014; Frolking et al., 2002). Most peatland carbon models simulate autotrophic and heterotrophic components differently; AR is embedded within the photosynthesis part of a model while HR comprises the soil part. Some current models have simulated the influence of hydrological and vegetation dynamics (Abdalla et al., 2014; Heinemeyer et al., 2010) as well as roles of nutrients (Wu et al., 2013) on soil respiration, and some peatland carbon models have come a long way from assuming HR as a function of litter and soil quality, temperature and moisture by simulating HR, such as through exudation (He et al., 2018; Shao et al., 2022). However, the more dynamic nature of HR through plant-soil-root interactions is still not as well understood, particularly in peatlands dominated by woody shrubs – e.g., mid-continental bogs.

Although most of the variability in CO_2 exchange comes from changes in gross primary production (GPP) and AR (Blodau, 2002; Heimann and Reichstein, 2008), the dynamics of HR is more complicated than previously thought. HR is correlated with environmental and substrate variables (Minkkinen et al., 2007; St-Hilaire et al., 2008), but has also recently been shown to be more complicated, made up of various components that are likely to change differently as environmental conditions are altered. For example, Fan et al. (2013) suggest that long-term exposure to warmer conditions may lead to an increase in HR outpacing an increase in carbon input, and carbon sequestration will weaken, which they attribute to root-soil interactions and a change in the transport of labile C. Similarly, Basiliko et al. (2012) highlight the difficulties in separating root respiration from HR, and CO_2 that is supplied as a substrate by the vascular plants (plant-associated HR), causing a priming effect, is not easily discernible from root respiration itself. Belowground processes are more connected to aboveground production than just the slow decomposition of dead organic matter, especially when root dynamics are considered (Ryan and Law, 2005; Van Hees et al., 2005), which has been seen in sedge-dominated (Järveoja et al., 2018; Kurbatova et al., 2013; Wang et al., 2014) and in permafrost ecosystems (Crow and Wieder, 2005; Hicks Pries et al., 2015). However, it is unknown whether this same level of vegetation influence on HR exists in shrub-dominated peatlands as well.

A peatland's response in respiration to climate change has been attributed to the plant's carbon use efficiency (Bunsen and Loisel, 2020). A shift in microbial community composition because of a change in temperature for example, could potentially counteract an accelerated loss of carbon (Lin et al., 2014). However, different outcomes in a peatland’s C cycle following a change in climate may also occur, depending on which respiration source dominates the response. For example, a positive feedback in climate change may occur if HR dominates the response because the system would lose C to the atmosphere that had been stored for hundreds to thousands of years. In contrast, if AR dominates the response, the system may fix more C, causing a negative feedback to climate change (Hicks Pries et al., 2013).

Considering that plant type influences AR and perhaps HR, the contributions of AR and HR to total respiration may be ecosystem specific (Griffis et al., 2000; Ojanen et al., 2012). Moore et al. (2002) for example, estimated that HR contributed about 46% to total ER at the Mer Bleue bog. However, the study used values reported in the literature for base metabolic rates and temperature effects, not direct observations. Stewart (2006) also found a higher contribution of HR (~ 63%) at the Mer Bleue and this was measured using direct methods. Similarly, Robroek et al. (2016) found that plant type affected the quality of dissolved SOM and soil activity, which resulted in an increase in vascular plant cover leading to the destabilization of SOM and consequently greater C losses (greater HR). Hicks Pries et al. (2013), on the other hand, found that HR contributed only 6-18% to total ER at a tundra site in Alaska underlain by permafrost using direct methods. However, they also state that although the C losses were compensated by an increase in net productivity as the permafrost thaw deepened, with increased warming, the HR may increase substantially if soil respiration from older, deeper peat eventually outpaces productivity. They then contradict this statement in a later study, where long-term warming experiments did not lead to an increase in HR, but rather an increase in both AR/HR ratios and the contribution of AR to total ER (Hicks Pries et al., 2015). It would be reasonable to assume then, that sites not underlain with permafrost, and perhaps not as sensitive to changes in temperature, would show lower HR contributions.

More predominant research on peatlands found in the literature compares the carbon exchange and processes between fens and bogs. Where fens make up a greater proportion of peatlands in European and Scandinavian countries (Janska et al., 2017; Jimenez-Alfaro, 2018), bogs make up about 70% of peatlands in Canada (Tarnocai et al., 2011). Thus, this distinction is very important when considering respiration dynamics of peatlands, where future changes in climate could have an impact on Canada’s overall greenhouse gas emissions. Bogs receive water inputs from precipitation and tend to reside in higher elevated areas, whereas fens receive water inputs from both precipitation and from the groundwater below and reside in lower elevated areas such as valleys (Baldwin and Batzer, 2012). Although a 50/50 split in AR and HR contributions to ER could make sense in fens, as was found at the Degero Stormyr (Järveoja et al., 2018), where water tables are quite high for most of a growing season, this may not be a valid assumption in bogs, where the water tables are mainly below the surface, which leads to more aerobic conditions (Mitsch and Gosselink, 2007; Moore, 2008). Therefore, it may be reasonable to assume that bogs would show a greater contribution of HR to total ER than fens. Many of the studies that look at the partitioning of AR and HR are done in forests, where root structures expand further in both the horizontal and vertical directions than in peatland ecosystems (Hahn et al., 2006; Kurbatova et al., 2013). It may also be reasonable to assume that bogs, with low-lying shrubs, would show a higher contribution of HR to total ER than forested ecosystems, if we assume that roots can be associated with the AR component.

Jacoby et al. (2017) suggest that aboveground respiration and productivity of plants are very much influenced by microbial - soil - plant interactions. Some plants take advantage of associations they have with other plants around them and may act as plant-associated HR, where the plants fix the respired CO_2 from the vegetation that surrounds them rather (much like a heterotroph that assimilates C) than using the CO_2 directly from the atmosphere in the process of photosynthesis, which has been shown to be the case for *Sphagnum* mosses (Kuiper et al., 2014;

Turetsky and Wieder, 1999). This is important since *Sphagnum* mosses are sensitive to changes in CO_2 concentrations (Serk and Schleucher, 2021). So, vascular plant coverage (i.e., shrub biomass) may influence ER and possibly the magnitude of HR if the presence of shrubs to provide C to be fixed by the mosses is altered (Shao, 2022). This also indicates a problem in our conceptualization of HR; We cannot simply partition AR and HR contributions when there is clearly an intermediate form (plant-associated HR) of what is traditionally thought of as HR, in that the C is assimilated from other sources, but where the rate of litter supply is related to plant production through root-soil interactions and belowground processes rather than through plant biomass. Phillips et al. (2017) argue that creating a large database with more robust, and improved soil respiration data will benefit further developments of models that aim to incorporate terrestrial C cycling.

Manual measurements only crudely partition AR and HR and studies that have explored the partitioning of AR and HR using either an automatic or manual chamber system, seem to only do so by using values found in the literature, constant ratios or fixed decomposition rates (Bond-Lamberty et al., 2004), which may lead to an overestimation of C sequestration due to unexpected allocations of C to labile pools with different turnover rates (Hungate et al., 1997). How the role of vegetation dynamics, and the more complex nature of HR, will change ecosystem structure is still not well documented. In fact, studies even seem to differ in their descriptions of AR and HR. Bond-Lamberty et al. (2004) suggest that there is no standard practice on whether to include rhizosphere respiration with AR or HR. This may be due to the difficulty in separating their impact on the C balance from other root functions (Chapin et al., 2006). The distinction between AR and HR becomes less clear when there are strong links between soil organisms and plant roots, such as with mycorrhizal fungi. Shrubs, for example, have quite a bit of mycorrhizae that help improve their nutrient uptake (Shao, 2022), and it’s not universally determined whether the respiration of the mycorrhizae should be considered HR or AR (Baldwin and Batzer, 2012). It is important to provide empirically derived estimates of the partitioning to help test and develop models and to understand the temporal and spatial dynamics in partitioning respiration, and below ground processes must be coupled to above ground production.

Additionally, ER measurements may be influenced by the methods used. For example, at a treed fen in Alberta, they found that direct measurements made with dark chambers during the day resulted in smaller ER fluxes than when the ER during the day was estimated by night-time relationships with temperature (Cai et al., 2010), as is the typical way of calculating respiration during the day with eddy covariance towers (Humphreys et al., 2014; Peichl et al., 2014). Photorespiration may be the cause of this discrepancy, as photorespiration tends to be reduced in dark respiration measurements (Pirk et al., 2016). But environmental variables may be a factor as well as photorespiration has also been shown to be stimulated in high temperature and water stress conditions (Dusenge et al., 2019; Lloyd, 2006). So, the difference between the two measurement methods may not be the same across the entire growing season or even across years either.

2.3 Factors explaining the variability in AR and HR contributions

The contributions of AR and HR to total respiration are also driven by different environmental factors. AR seems to be linked more to climatic factors (e.g. air and soil temperature and soil moisture) and vegetation dynamics, whereas HR seems to be linked more to belowground processes, such as quantity and quality of substrate, microbial biomass, nutrient availability and decomposition rates (Hicks Pries et al., 2015; Kurbatova et al., 2013). Wang et al. (2014) suggest both HR and AR are affected by changes in air temperature, but that HR does not acclimate as fast as AR, so we often see a shift towards higher HR/AR ratios in warming experiments. In contrast, Dorrepaal et al. (2009) found that both HR and AR did not acclimate to warming over the 8 years of their study, but instead they found that there was a shift in the contribution of deeper peat. An interesting study conducted by O'Connell et al. (2003) found that soil CO_2 fluxes from deeper soil were still being released from the frozen layers of soil in winter, which may imply that older soil carbon contributes more to HR in winter. Additionally, fresh plant litter and newly formed OM (e.g., exudates) contain a larger fraction of labile C (less decomposed) than older peat (Wang et al., 2016). Wang and Roulet (2017) found that since litter inputs are generally located at oxic zones near the surface, where the majority of HR takes place, litter quality and quantity are important to HR contributions and microbial activity. Similarly, Straková et al. (2012) found that litter quality may help determine the quality of substrate as a source of energy and nutrients for decomposers. Straková et al. (2012) also found indirect effects on litter and substrate quality as well, where a shift in vegetation dynamics following a drawdown in water table led to a decrease in pH and an increase in nutrient concentrations, consequently resulting in an alteration of litter quality and decomposability. Keiser et al. (2019) also found that substrate type was the driving factor of increased respiration in most cases with increasing temperatures, due to a greater photosynthesis allowing for increased decomposition and leaching of root exudates to belowground decomposers.

There seems to also be support for the presence of both spatial and temporal variability in the contributions of AR and HR, and the variability may be driven by the difference in their response and sensitivity to changes in temperature (Iversen et al., 2022; Keiser et al., 2019). Q_{10} values, which represent temperature sensitivity, measure the rate of change in biological and chemical reactions to an increase in temperature of 10°C (Wang et al., 2014), and hence give some indication of the sensitivity of microbial activity (decomposition rates). For example, Grogan and Jonasson (2005) found that the decomposition rates of newly photosynthesized C by plants was more sensitive to changes in temperature than the decomposition rates of C derived from older stores of SOM deeper in the peat. Nutrient availability may explain this difference in temperature sensitivity. Juszczak et al. (2013) found that the temperature response of HR depends on the chemical composition of substrates and nutrient availability. In contrast, Bubier et al. (2007) found that a change in nutrient availability led to a change in plant production and productivity, which affected the peatland's ability to sequester CO_2. They attribute this to a loss of *Sphagnum* production, which contributed to slowly decomposing litter, whereas the shrub production increased somewhat, but its litter decomposes faster. Similarly, Hungate et al. (1997) found that if demands for belowground resources (e.g. nutrients, water) are not met or if the growth of the plants is constrained, this will lead to a higher loss of C from plants through root turnover, respiration and exudation; highlighting the presence of complex interactions and the potential coupling of effects on both AR and HR simultaneously, as well as the importance of understanding the link between belowground processes and aboveground production.

A plant's response to a change in environmental conditions can also be explained by the various mechanisms by which plants obtain water resources (Migliavacca et al., 2021). Malhotra et al. (2020) found that environmental changes (e.g., warming) can alter fine root production, affecting water and nutrient uptake and hence ER and C storage. Sedges have root structures that extend vertically downwards, sometimes up to 50 cm depth, and can consequently tap into the water table at deeper depths even during the drier parts of the season as well as support a greater aboveground biomass than shrubs, especially when WT depths fluctuate a lot (Buttler et al., 2015; Pouliot et al., 2012). In contrast, shrubs allocate more of their energy to belowground roots, which tend to spread out laterally rather than vertically with root lengths limited to within the first 20-30 cm of the surface (Iversen et al., 2018; Murphy et al., 2009b), hence supporting a greater belowground biomass than sedges. Shrubs also allocate energy to small, needle-like stems (small in diameter but great in height) to make use of whatever water is available to the plants in the soil, while minimizing the loss of water through transpiration (Bonan, 2008). The stems are also buried annually by the mosses, contributing significantly to the greater belowground biomass (Murphy et al., 2009a). This seems to be true mostly for shrubs like *Chamaedaphne*, while other shrubs like *Rhododendron* tend to have thick leaves to prevent desiccation during drought periods (Warren et al., 2021), highlighting differences in hydraulic strategies of species that can affect ecosystem function. Oke & Hager (2020) suggest that plants, in bogs especially, are influenced by the hummock-hollow topography and that the plant's distribution depends on physiological tolerances and ecological strategies. Although shrubs are quite adapted for relatively wet and dry conditions, with studies finding a shift to greater shrub cover with water table draw-down (Murphy et al., 2009a), sedges are a more competitive plant functional type than shrubs, being one of the first colonizers in abandoned extracted peatlands (Lavoie et al., 2003).

2.4 Methods of partitioning ER into AR and HR

The various methods proposed in the literature include: (1) Root exclusion, which measures respiration in the soil with and without the roots present, (2) Component integration, which measures CO_2 production of all parts of the soil separately (litter, roots and sieved soil), (3) Girdling, which requires invasive stripping of bark on trees until xylem depth is reached to prevent photosynthates reaching tree roots (although, this method is only feasible in forested ecosystems), (4) Trenching, which also requires invasive removal of roots to prevent plant parts contributing to belowground HR, and (5) Clipping, which is less invasive, but similar to girdling in that it requires clipping the plant parts to the ecosystem surface to prevent photosynthates reaching the roots (Hardie et al., 2009; Wang et al., 2014). The idea is that after about 5-6 days, the roots of the clipped plants will decompose and become part of the heterotrophic component of respiration. However, this is an unrealistic assumption for most ecosystems. In cooler northern peatlands, fine roots *may* decompose fast enough, but any coarse roots that remain may take several months, not days, to decompose (Moinet et al., 2018). This is especially prevalent in bogs, where ombrotrophic plant functional types favour greater WT depths, and hence have decomposition rates that are much slower than in fens (Frolking et al., 2010).

A method that has gained much attention in recent decades is the use of both stable ($\delta^{13}C$) and radiocarbon ($\Delta^{14}C$) isotopes (natural and pulse labelling) of C in partitioning AR and HR (Hanson et al., 2000). Indeed, isotope measurements of CO_2 are a much less invasive method to determine the portion of respired CO_2 that comes from either recently fixed plant C and that which is derived from older C sources in the soil, providing valuable insight into the processes that control the storage and release of C in terrestrial ecosystems (Hahn et al. 2006; Werner et al. 2012). They can also be applied in non-forested ecosystems, unlike methods such as girdling and trenching (Hahn et al., 2006; Hardie et al., 2009). Therefore, both $\delta^{13}C$ and ^{14}C of soil respired CO_2 are good indicators for understanding respiration dynamics.

On the one hand, $\delta^{13}C$ separates respiration sources based on biological fractionation and relationships with water budgets (Yang et al. 2015). $\delta^{13}C$ may differ among sources because many enzymatic processes, such as C fixation, discriminate against the heavy isotope (Schuur and Trumbore, 2006). The less C-limited plants are, the more they discriminate against $\delta^{13}C$ (Ehleringer et al., 2000; Flanagan et al., 1999). Furthermore, a shift towards a greater contribution of deeper peat to total respiration would be reflected as an increase in the overall $\delta^{13}C$ signature of CO_2 emitted to the atmosphere due to the discrimination of $\delta^{13}C$ during decomposition being dominated by microbes of substrates differing in isotopic composition rather than by metabolic fractionation (Dorrepaal et al., 2009)

Additionally, $\delta^{13}C$ signatures vary across plant functional types due to different photosynthetic strategies and relationships with water. For example, along with a greater contribution of HR, Wang (2016) found higher $\delta^{13}C$ signatures (1.63 – 1.81 ‰) in the wet lawns compared to the dry lawns, suggesting that areas containing shrubs are more enriched in $\delta^{13}C$. However, Hardie et al. (2009) found that plant-mediated transport of CO_2 (through aerenchyma) produced in the catotelm accounted for ~ 10-23 %, a considerable component, of total ER. $\delta^{13}C$ becomes more enriched with depth in the soil as deeper soils allow for more microbial-derived enriched $\delta^{13}C$ relative to the depleted plant derived $\delta^{13}C$ near the surface (Hicks Pries et al., 2013). Hardie et al. (2009)'s findings would suggest then, that areas containing sedges would be more enriched in $\delta^{13}C$. Typical values for shrubs and sedges, based on values reported in the literature (Hardie et al., 2009; Wang, 2016.; Yang et al., 2015) are approximately -27 to -29 ‰ and -25 to -27 ‰, respectively.

On the other hand, ^{14}C isotope measurements act like a timestamp; after fractionation effects have been accounted for, they can help separate respiration sources by providing information about the "ecosystem age" (Gaudinski et al., 2000). There was an increase in ^{14}C content in atmospheric CO_2 that peaked around 1963 ('bomb peak') because of nuclear bomb testing in the atmosphere that occurred during the 1950s. A treaty was created because of these tests, so that since then, ^{14}C in atmospheric CO_2 has been steadily decreasing. The release of fossil fuels since this time has added to the decrease in ^{14}C in atmospheric CO_2 as well. HR has been shown to be enriched in ^{14}C compared with current atmospheric CO_2, whereas the ^{14}C content of AR corresponds to current atmospheric CO_2 (Hahn et al., 2006; Hicks Pries et al., 2015).

Chapter 3: Controls on autotrophic and heterotrophic respiration in an ombrotrophic bog

Bridging Statement to Chapter 3

This chapter introduces the main objective of my thesis, which was to partition autotrophic and heterotrophic respiration at Mer Bleue, an ombrotrophic bog. I measured the fluxes of CO_2 using manual chamber methods and obtained measures of the environmental variables (water table depth, air temperature and soil temperature) at the same time as the flux measurements to determine the controls on respiration and its components. Our findings show that a plant's response to changes in climate is related to different mechanisms of obtaining water resources and utilizing associations with other plants around them; highlighting the lack in our understanding of the conceptualization of HR, which is more related to vegetation dynamics than previously suggested.

© Rankin, T., Roulet, N. and Moore, T. (2022). *Biogeosciences*, 19, 3285-3303. https://doi.org/10.5194/bg-19-3285-2022.

Note: The heading numbers for chapter 3 were altered to follow the table of contents for the thesis.

3.1 Abstract

Northern peatlands are globally significant carbon stores, but the sink strength may vary from year-to-year due to variations in environmental and biogeochemical conditions. This variation is mainly brought about by changes in primary production and in autotrophic respiration (AR; respiration by plant parts), components that we understand reasonably well. Heterotrophic respiration (HR; respiration by the soil microbial community, mycorrhizal fungi, etc.), on the other hand, is crudely measured and simulated, which may lead to biased estimates if a change favours one form of respiration over another. HR has only recently been shown to be more intimately linked to vegetation dynamics than once thought, particularly in wetter, oligotrophic, sedge-dominated ecosystems. The objective of this study is to determine the factors that relate to the spatial and temporal variability in respiration and its autotrophic and heterotrophic components in an ombrotrophic bog (Mer Bleue) where woody shrubs are dominant, and to see if the more dynamic nature of HR in sedges also exists in this bog. Plot level measurements using manual chambers were used to partition respiration from both the dominant shrubs and the sparse sedges at the site, and the controls on respiration were explored by measuring a variety of environmental variables, such as air and soil temperatures (T) and water table (WT) depth. Results show that AR and HR correlate primarily with air and soil T, with WT depth playing an important role in some cases, and that a higher variability in respiration exists for the shrub plots than the sedge plots, especially when WT levels are more variable. Our findings also show that a plant’s response to changes in climate is related to the plants’ root structure, which indicates different mechanisms of obtaining water resources, and utilizing associations with other plants around them. These results will improve our understanding of peatland carbon cycling, as well as improve the conceptualization of HR.

3.2. Introduction

Northern peatlands play a significant role in the global carbon (C) cycle, covering 12% of Canada’s terrestrial surface (Tarnocai et al., 2011), and containing ~ 50% of the organic C stored in Canadian soils (Tarnocai, 2006). Slow decomposition of plant material in undisturbed peatlands leads to the accumulation of peat, making natural peatlands long term sinks of C. Following the last glaciation, peatlands have accumulated C at an average rate of 23-26 g m-2 yr-1 (Charman et al., 2013; Loisel et al., 2014). However, on shorter time scales, a natural peatland may be a source or a sink of C depending on the environmental conditions of a given year and on biogeochemical conditions (Dorrepaal et al., 2009; Roulet et al., 2007). Although most of the variability in CO_2 exchange comes from changes in gross primary production (GPP) and AR (Blodau, 2002; Heimann and Reichstein, 2008), the dynamics of heterotrophic respiration are not straightforward. HR is correlated with environmental and substrate variables, such as moisture and litter quality (e.g., Minkkinen et al., 2007; St-Hilaire et al., 2008), but has recently been shown to be more complicated, made up of various components that are likely to change differently as environmental conditions are altered. For example, Fan et al. (2013) suggest that long-term exposure to warmer conditions may lead to an increase in HR outpacing an increase in C input and C sequestration will weaken, which they attribute to root-soil interactions and a change in the transport of labile C. Similarly, Basiliko et al. (2012) highlight the difficulties in separating root respiration from HR, and organic C that is supplied as a substrate by the vascular plants, causing a priming effect (Robroek et al. 2016), is not easily discernible from root respiration. Belowground processes are more connected to aboveground production than just the slow decomposition of dead organic matter, especially when root dynamics are considered (Ryan and Law, 2005; Van Hees et al., 2005). This has been seen in sedge dominated or forested peatlands (Järveoja et al., 2018; Kurbatova et al., 2013; Wang et al., 2014) and in permafrost ecosystems (Crow and Wieder, 2005; Hicks Pries et al., 2015). However, it is unknown whether this same level of vegetation influence on HR exists in shrub dominated peatlands as well. This paper addresses the influence of vegetation on HR in a mid-continental, raised bog.

Ecosystem respiration dynamics have been explored in peatlands, mainly through eddy covariance techniques (e.g., Cai et al., 2010; Humphreys et al., 2014; Peichl et al., 2014) and using darkened chambers (e.g., Järveoja et al., 2018; Lai, 2012) which explore C exchange at a scale that towers cannot address. Models have been developed that attempt to predict how the components of the C balance (e.g., ER) will vary with a changing climate (e.g., Abdalla et al., 2014; Frolking et al., 2002). A peatland's response in respiration to climate change has been attributed to the plant's carbon use efficiency (Lin et al., 2014), and how the carbon accumulation will be altered (Bunsen and Loisel, 2020). However, different outcomes in a peatland’s C cycle following a change in climate may also occur, depending on which respiration source dominates the response. For example, if HR dominates the response, the system will lose C to the atmosphere that had been stored for hundreds to thousands of years, creating a positive feedback to climate change. In contrast, if AR dominates the response, the system will either turn over newly-photosynthesized C faster, causing a positive feedback to climate change, or may fix more C, causing a negative feedback to climate change (Hicks Pries et al., 2013). Consequently, the contributions of AR and HR to total respiration may be ecosystem specific (Griffis et al., 2000; Ojanen et al., 2012). Phillips et al. (2017) argue that creating a large database with more robust, improved soil respiration data will benefit further developments of models that aim to incorporate terrestrial C cycling.

Additionally, it is likely that a plant's response to a change in environmental conditions can also be explained by the various mechanisms in which the plants obtain water resources. Malhotra et al. (2020) suggest that environmental changes, such as warming and a lowering of the water table, can alter fine root production, affecting water and nutrient uptake and hence ER and C storage. Oke and Hager (2020) suggest that a plant's distribution, in bogs especially, depends on physiological tolerances and ecological strategies. Some plants may even take advantage of associations they have with other plants and may fix the respired CO_2 from the surrounding vegetation rather than using CO_2 directly from the atmosphere in the process of photosynthesis, which has been shown to be the case for Sphagnum mosses (Kuiper et al., 2014; Shao, 2022; Turetsky and Wieder, 1999). This also indicates a problem in the conceptualization of HR: one cannot simply partition AR and HR contributions when there is clearly an intermediate form of what is traditionally thought of as HR, in that the C is assimilated from other sources, but where the rate of litter supply is related to plant production through root-soil interactions and belowground processes rather than through plant biomass (Shao et al., 2022). While some peatland carbon models have simulated the influence of hydrological, vegetation, and microbial dynamics on soil respiration (Abdalla et al., 2014; He et al., 2018; Heinemeyer et al., 2010; Shao et al., 2022), most peatland models still crudely simulate HR, and manual measurements only crudely partition AR and HR using constant ratios or fixed decomposition rates, which may lead to an overestimation of C sequestration if a change favours one form of respiration over another (Hungate et al., 1997). How the role of vegetation dynamics, and the more complex nature of HR, will change ecosystem structure is still not well documented.

The objectives of this study are to determine the factors that control the spatial and temporal variability in ecosystem respiration and its autotrophic and heterotrophic components at

Mer Bleue, a mid-continental, temperate, ombrotrophic raised bog. More specifically, this paper aims to 1) determine the contributions of AR and HR at Mer Bleue, 2) establish the environmental controls on AR and HR, and 3) explore the dependence of AR and HR contributions to ER on plant functional type.

3.3 Methods

3.3.1 Study site

Mer Bleue is a 28 km2 ombrotrophic bog located near Ottawa, Ontario (45.41 °N, 75.52 °W). It is in a cool continental climate region, with a mean annual temperature of 6.4 °C ranging from -10.3 °C in January to 21.0 °C in July. Mean annual precipitation is 943 mm, 350 mm of which falls from May to August, with a mean annual snowfall of 223 cm (Environment Canada; 1981–2010 climate normals). Peat depth reaches about 5 to 6 m near the centre of the bog and is shallower (<0.3 m) near the beaver pond margin. Bog development began 7100–6800 years ago, and it has a hummock-lawn microtopography (Roulet et al., 2007). The surface of the bog is covered by *Sphagnum* mosses (*Sphagnum angustifolium, Sphagnum capillifolium, Sphagnum fallax, Sphagnum magellanicum*), and the vascular plant cover is dominated by low growing ericaceous evergreen shrubs that make up about 80% of the areal coverage (mainly *Chamaedaphne calyculata*, with some *Rhododendron groenlandicum*, and *Kalmia angustifolia*), and an occasional mix of sedges (*Eriophorum vaginatum* and *Carex oligosperma*) (Humphreys et al., 2014; Lai et al., 2014).

The sedges have root structures that extend vertically downwards, sometimes up to 50 cm depth, and can consequently tap into the water table at deeper depths even during the drier parts of the season as well as support a greater aboveground biomass than shrubs, especially when the water table (WT) fluctuates greatly (Buttler et al., 2015; Pouliot et al., 2012). In contrast, the shrubs allocate more of their biomass to belowground roots, which tend to spread out laterally rather than vertically with root lengths limited to within the first 20-30 cm of the surface (Iversen et al., 2018; Murphy et al., 2009a), hence supporting a greater relative belowground to aboveground biomass than sedges. Shrubs also allocate energy to small, needle-like stems (small in diameter but great in height) to make use of whatever water is available to the plants in the soil, while minimizing the loss of water through transpiration (Bonan, 2008). These stems are also buried annually by the mosses, contributing significantly to the greater belowground biomass (Murphy et al., 2009b). Stem burial occurs mostly for shrubs like C. *calyculata*, the dominant shrub species at the site, while other shrubs like R. *groenlandicum* tend to have thick leaves to prevent desiccation during drought periods (Warren et al., 2021), highlighting differences in hydraulic strategies of species that can affect ecosystem function.

Although shrubs are quite adapted for relatively wet and dry conditions, with studies finding a shift to greater shrub cover with water table draw-down (Murphy et al., 2009a), sedges are a more competitive plant functional type than shrubs, being one of the first colonizers in abandoned extracted peatlands as they can handle more extreme fluctuations in moisture conditions (Lavoie et al., 2003). Although the sedges cover only 3 to 17% of the surface area of Mer Bleue (Kalacska et al., 2013), the respiration dynamics of this plant functional type is quite important. The mosses are mixed with the other vegetation, so finding plots of just mosses was almost impossible. Therefore, the plots as described below, contained either *Eriophorum* and mosses (the ‘sedge section’) or *Chamaedaphne* and mosses (the ‘shrub section’).

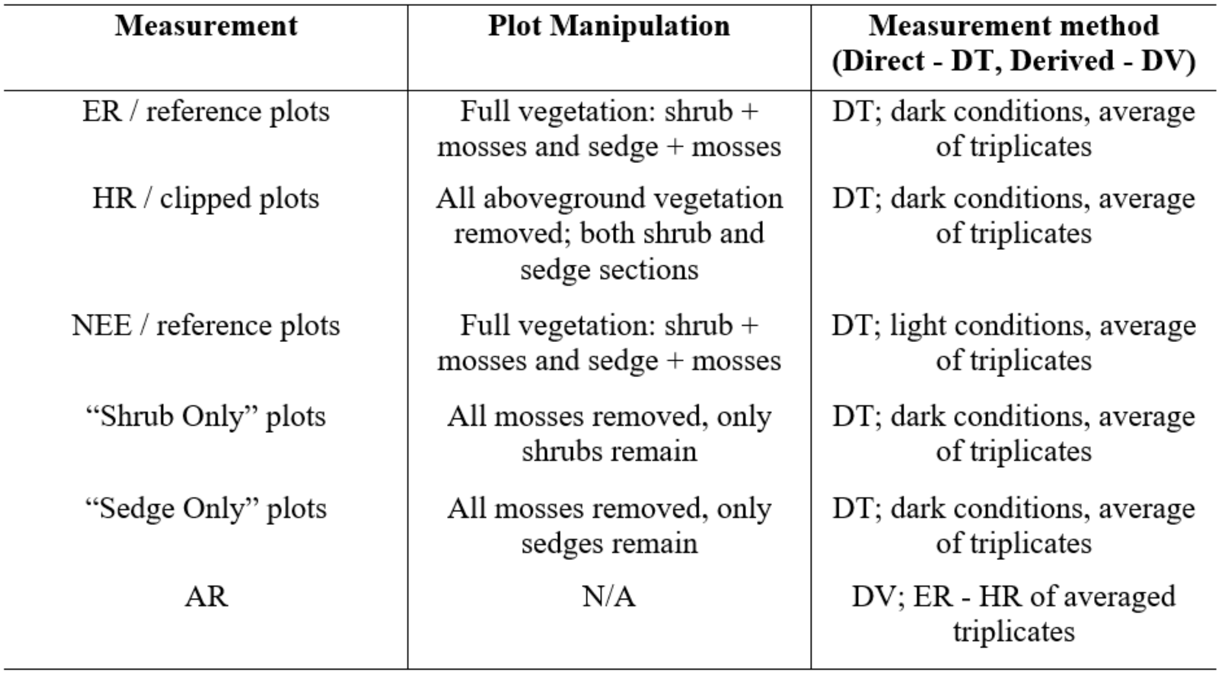
3.3.2 Chamber setup (CO_2 fluxes)

We conducted CO_2 measurements at the plot level using manual chambers (Pelletier et al., 2007). Nine circular collars of about 26 cm diameter were randomly placed over areas that were shrub-dominated (shrub section), and nine collars were placed over areas that were sedge-dominated (sedge section). All the collars were sampled weekly to bi-weekly, weather depending, from May through September in the 2018 and 2019 growing seasons.

Fluxes were obtained using a transparent static chamber (diameter of 26 cm and height of 50 cm) placed and sealed over permanent PVC collars inserted into the peat to a depth of 15 cm at each sampling location. The chamber contained a fan to allow for adequate mixing, and a cooling system was used to maintain ambient temperature conditions (Waddington et al., 2010). For each collar, a full light measurement was done using the transparent chamber, representing the net ecosystem exchange (NEE) for that plot, and a dark round was conducted using a covered chamber. This represented the ecosystem respiration (ER) for that plot.

In the spring of both 2018 and 2019, some of the plots were manipulated to be able to tease apart the influence of vegetation (Table 3.1); we applied two treatments and one control to each plot in each section. CO_2 measurements were started roughly two weeks after the manipulations. In each section, 3 plots were designated as reference plots with intact vegetation, representing NEE and ER for the measurements conducted under light and dark measurements, respectively; 3 plots had all the aboveground vegetation removed (“clipped plots”) where measurements were conducted under dark conditions only; and 3 plots were deemed “shrub only" and "sedge only", where only the mosses were removed (i.e., vascular plants remained), and where measurements were also conducted under dark conditions only. In the plots representing no vegetation ("clipped plots"), the roots surrounding the plots were trenched to kill the roots outside of the plots and root exclosures were set up to prevent roots from entering the plots from below. We assumed that the clipped plots represented HR, with the understanding that there will have been a residual component from the decomposing roots. However, re-clipping and re-trenching was done periodically throughout 2018 and 2019. A layer of green mesh was also placed on top of the bare peat in the clipped plots to minimize any confounding effects of temperature and moisture. We then assumed AR = ER – HR. We followed the ecosystem sign convention, where a positive NEE value represents a gain of C to the ecosystem and a positive value for ER represents a loss of C from the ecosystem.

Table 3.1 Manual chamber set up with descriptions of manipulations and reported measurements.



Measurement	**Plot Manipulation**	**Measurement method (Direct - DT, Derived - DV)**
ER / reference plots	Full vegetation: shrub + mosses and sedge + mosses	DT; dark conditions, average of triplicates
HR / clipped plots	All aboveground vegetation removed; both shrub and sedge sections	DT; dark conditions, average of triplicates
NEE / reference plots	Full vegetation: shrub + mosses and sedge + mosses	DT; light conditions, average of triplicates
"Shrub Only" plots	All mosses removed, only shrubs remain	DT; dark conditions, average of triplicates
"Sedge Only" plots	All mosses removed, only sedges remain	DT; dark conditions, average of triplicates
AR	N/A	DV; ER - HR of averaged triplicates

In 2018, the CO_2 concentrations were measured every 5 seconds over a period of 5 minutes, using an ultra-portable greenhouse gas analyser (Los Gatos Research (LGR), San Jose, California). The LGR was calibrated beforehand, and a round started when stabilized ambient concentrations of CO_2 were reached. In 2019, the site was too wet to safely carry in the LGR, so a smaller portable CO_2 gas analyser (EGM-4, PP systems, Amesbury, Massachusetts) was used instead. CO_2 concentrations were measured every 10 seconds for the first minute, then every 30 seconds after that, for a total of 5 minutes. The EGM-4 was zeroed before each round. In September of 2018, CO_2 measurements of a few collars were measured one after the other using both instruments to get a standardized set of fluxes. There was no significant difference between the fluxes measured with the two gas analysers (T = 1.59, P-value = 0.13). In both years, linear regression equations of concentrations over time were used to calculate a flux for CO_2 for each 5-minute period. Only regressions with R^2 values over 0.8 were kept, which resulted in less than 10% of the values being removed. There were no instances where CO_2 concentrations remained the same over the measurement period, which would have indicated a very low R^2 value.

3.3.3 Environmental variables

At the time of sampling, water table (WT) depth was determined manually using a permanently installed perforated PVC tube beside each set of 3 collars. Soil temperatures were obtained using a temperature probe inserted to depths of 0, 5 and 10 cm, roughly in the same location each time just outside of each collar. Daily air temperatures were obtained from the

Ottawa International Airport weather station, located about 18 km southwest of the site (Environment Canada, 2021).

To determine if there was any hysteresis between soil water content and WT depth, continuous measurements of both variables were conducted at the meteorological station next to the eddy covariance tower about 50 m away from the manual chamber set-up. Measures of volumetric water content (VWC) at 40 cm depth were measured using time-domain reflectometry (TDR) probes (model CS615, Campbell Scientific, Alberta, Canada) inserted in the peatland hummocks, and water table levels were determined using capacitance water level probes (Odyssey, Dataflow Systems PTY Limited, Christchurch, New Zealand). Signals from the sensors were monitored on a CR7X and a CR10X data logger every 5 seconds, averaged every 30 min (Lafleur et al., 2005) and the daily averages were used in the analysis.

Thermocouples were installed in the peat to measure soil temperatures at 10 cm and 40 cm depths. These were measured every second, with 30-minute averages as an output. However, daily daytime averages were used in the analysis (using excel pivot tables and filtering for values between 8AM and 6PM). Continuous 30-minute records of WT depths were also obtained in each area of the manual chamber locations, with capacitance water level probes, that were placed inside the same perforated PVC tubes previously inserted in the peat beside each set of 3 collars, as described above. Daily averages were used in the analysis.

3.3.4 Statistical analyses

Statistical analyses were performed using the R statistical software (RStudio, version 4.0.2). As 2018 was an anomalously warm year at Mer Bleue and elsewhere across the globe

(Lees et al. 2021; Arain et al. 2022), we analysed the respiration fluxes from the plant types separately for 2018 and 2019. First, simple linear and multiple regressions were conducted among the respiration fluxes (ER, HR, and AR) and the various environmental variables using the “stats” package in R. Second, regression trees were conducted with the “rpart” package in R, which uses stepwise regression models and recursive partitioning, to determine which environmental variable best predicted the respiration response (Brieman et al. 1984), similar to the regression trees conducted by Melling et al. (2005) who determined controls on soil CO2 fluxes in tropical peatlands. Analysis of Variance (ANOVA) is used to test the significance of the regression trees (Brieman et al. 1984). Third, repeated measures Analysis of Variance (ANOVA) tests were conducted using the “car” package in R to determine if the fluxes from the different treatments were significantly different, and two sample t-tests were conducted using the “stats” package to determine whether the fluxes were significantly different between the two plant types and whether the fluxes measured with the two gas analysers were significantly different. We consider individual p-values less than or equal to 0.10 as significant. Finally, coefficients of variation (standard deviation / mean of population) were conducted to determine the degree of variability in AR contributions to ER as described in Abdi (2010).

3.4 Results

3.4.1 Environmental variables

The growing season of 2018 was characterised by variable (more sporadic) weather conditions based on the manual measurements of WT depth and soil temperatures (Soil T) at 10 cm depth, and the mean daily air temperatures (Air T) taken from the weather station nearby

(Figure 3.1a; Environment Canada, 2021). Air temperatures ranged from 21 ℃ to 35 ℃, soil temperatures (at 10 cm depth) ranged between 12 ℃ and 27 ℃, and WT depth ranged between 23 cm and 47 cm depth (June – August mean WT = 34 cm depth). It was also a hot year compared to the normal averages, where the mean annual temperature for July, for example, is 21.0 °C (Environment Canada, 1981–2010 climate normals), and a drier start to the growing season than normal for June, and July, but generally a wetter August and September than normal (Teklemariam et al., 2010), with a significant rise in WT depth following a series of large rain events.

The growing season of 2019 had less variable weather conditions than 2018, despite a greater range in WT depth; it was wetter in May and June compared to the normal averages, then consistently became warmer and drier as the growing season progressed (Figure 3.1b), with WT depth similar to normal averages in July and August (Teklemariam et al., 2010). Mean daily air temperatures (23 ℃ to 31 ℃) and soil temperatures at 10cm depth (10 ℃ and 18 ℃) had a much smaller range than in 2018, and WT depth ranged between 20 cm and 55 cm depth (May – August mean WT = 36.5 cm depth).

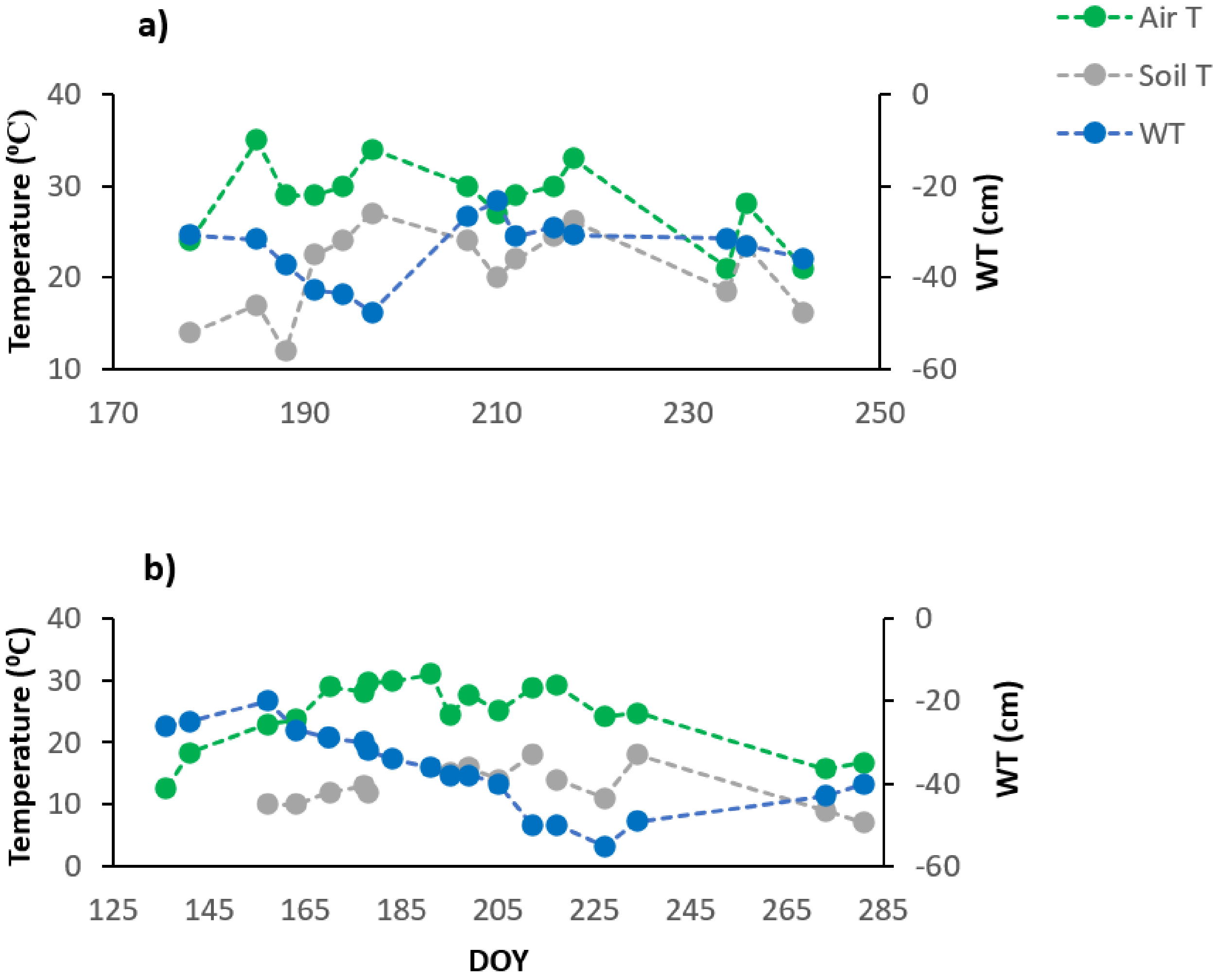


Figure 3.1 Environmental variables for the growing seasons of a) 2018 and b) 2019. Soil T is soil temperature at 10 cm depth, taken manually along with WT depth, while the mean daily air temperatures (Air T) were taken from the weather station nearby.

A hysteresis existed between volumetric water content (VWC) and WT depth in 2018 (Figure 3.2a), the growing season that showed an abrupt rise in water table position (Figure B1a). The hysteresis was not as pronounced in 2019 (Figure 3.2b); we had less data available for VWC and WT depth measurements in 2019, which may have led to the hysteresis being less obvious. Nonetheless, 2019 is where water table positions more consistently decreased over the growing season and only slightly rose in September with the start of the fall rains (Figure B1), which likely also played a role in the hysteresis loop being less obvious in 2019 than 2018. We do not have VWC measurements for the different treatments unfortunately, only the data from the probes near the eddy covariance tower. Although it is important to acknowledge the hysteresis present, we could show that the relationship between WT depth and VWC are correlated (Figure 3.2), thus WT depth is a reasonable surrogate for changes in VWC.

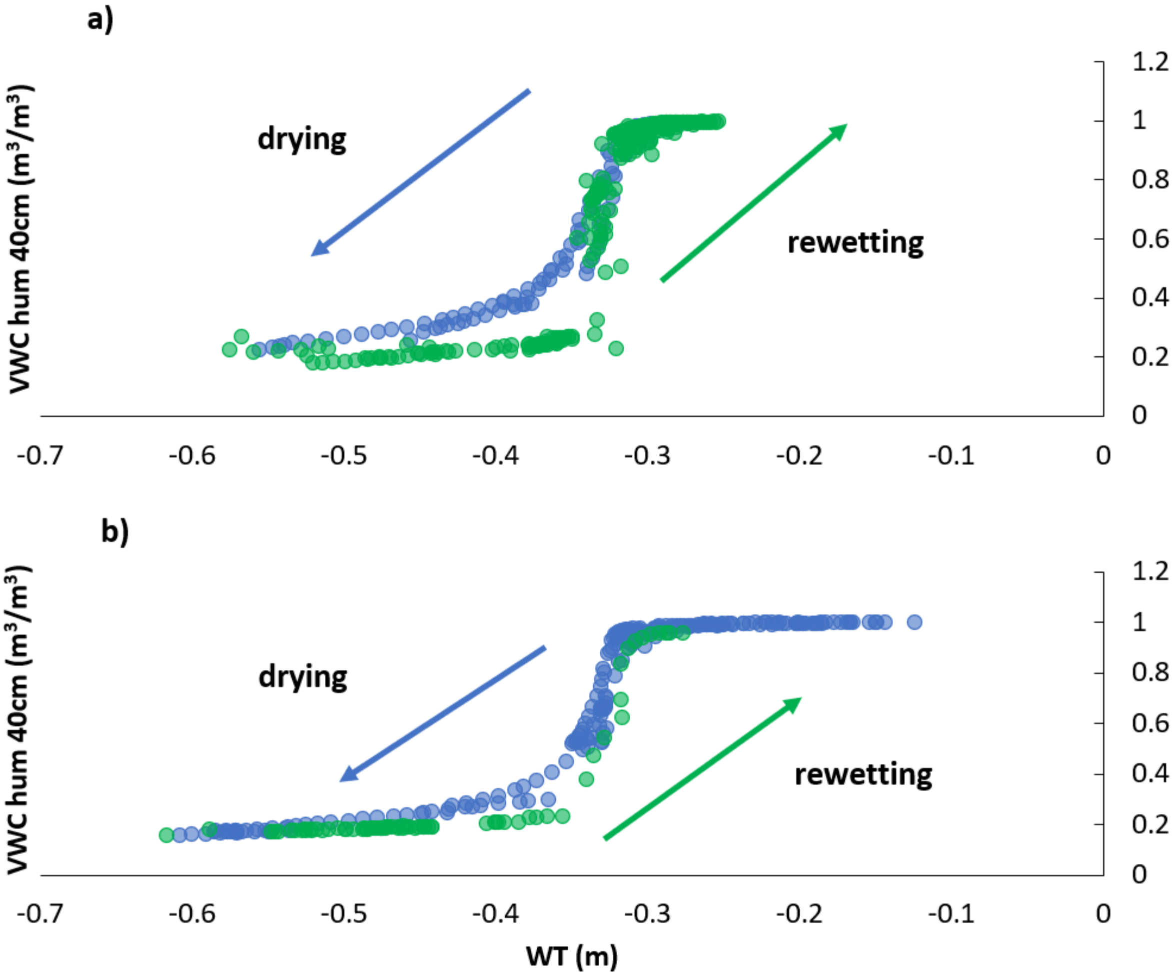


Figure 3.2 Hysteresis a) in 2018 and b) in 2019, between WT depth (m) and volumetric water content (VWC, m^3/m^3) at 40 cm depth in the hummocks.

3.4.2 CO_2 fluxes and AR contributions

In 2018, NEE and respiration values were greater for the sedges than the shrubs, but less variable (Table 3.2). shrub plot NEE averaged 461 ± 103 mg CO_2 m^{-2} hr^{-1} (± standard deviation), averaged 195 ± 81 mg CO_2 m^{-2} hr^{-1} for HR, 414 ± 154 mg CO_2 m^{-2} hr^{-1} for ER, and 250 ± 69 mg CO_2 m^{-2} hr^{-1} in the "shrub only" plots (Figure 3.3a). Sedge plot NEE averaged 827 ± 139 mg CO_2 m^{-2} hr^{-1}, 240 ± 25 mg CO_2 m^{-2} hr^{-1} for HR, 625 ± 131 mg CO_2 m^{-2} hr^{-1} for ER, and 356 ± 42 mg CO_2 m^{-2} hr^{-1} in the "sedge only" plots (Figure 3.3b). AR (derived from the difference between ER and HR measurements) in the shrubs averaged 187 ± 134 mg CO_2 m^{-2} hr^{-1}, and 385 ± 127 mg CO_2 m^{-2} hr^{-1} in the sedges (Figure B2 a, b), while AR contributions to ER averaged 47 ± 24 % for the shrubs and 61 ± 10 % for the sedges in 2018 (Figure 3.5a).

In 2019, NEE and respiration values were also greater for the sedges than the shrubs, but the variability was similar between the plant types (Table 3.2). The shrub plot NEE averaged 323 ± 120 mg CO_2 m^{-2} hr^{-1}, 309 ± 123 mg CO_2 m^{-2} hr^{-1} for HR, 611 ± 194 mg CO_2 m^{-2} hr^{-1} for ER, and 403 ± 135 mg CO_2 m^{-2} hr^{-1} in the "shrub only" plots (Figure 3.4a). Sedge plot NEE averaged 799 ± 176 mg CO_2 m^{-2} hr^{-1}, 426 ± 178 mg CO_2 m^{-2} hr^{-1} for HR, 729 ± 218 mg CO_2 m^{-2} hr^{-1} for ER, and 323 ± 107 mg CO_2 m^{-2} hr^{-1} in the "sedge only" plots (Figure 3.4b). AR fluxes in the shrubs averaged 378 ± 164 mg CO_2 m^{-2} hr^{-1}, and 343 ± 142 mg CO_2 m^{-2} hr^{-1} in the sedges (Figure B2 c, d), while AR contributions to ER averaged 62 ± 16 % for the shrubs and 55 ± 14 % for the sedges (Figure 3.5b).

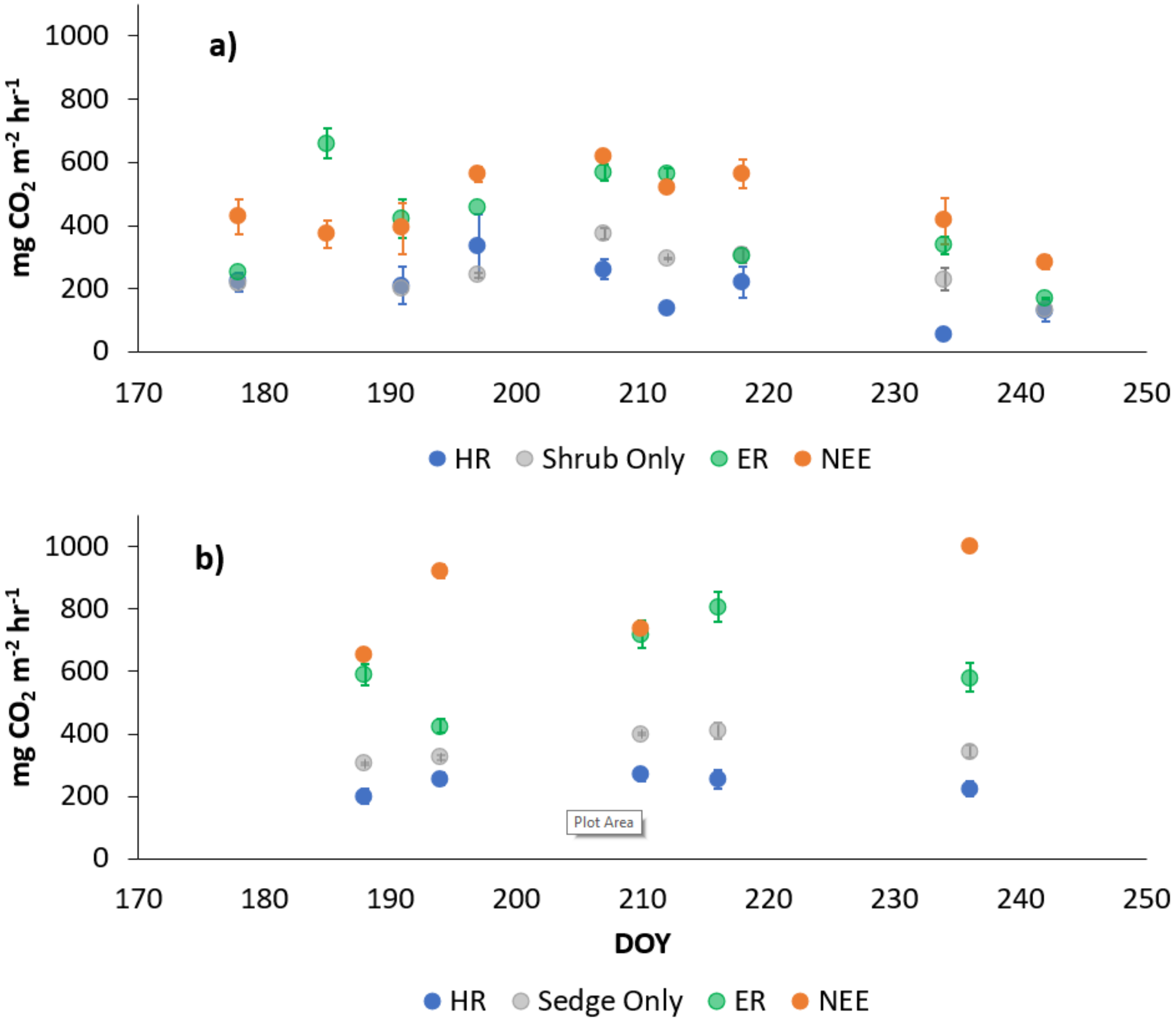


Figure 3.3 Average CO_2 fluxes in the a) shrub plots and b) sedge plots across the growing season of 2018 (± Standard Error).

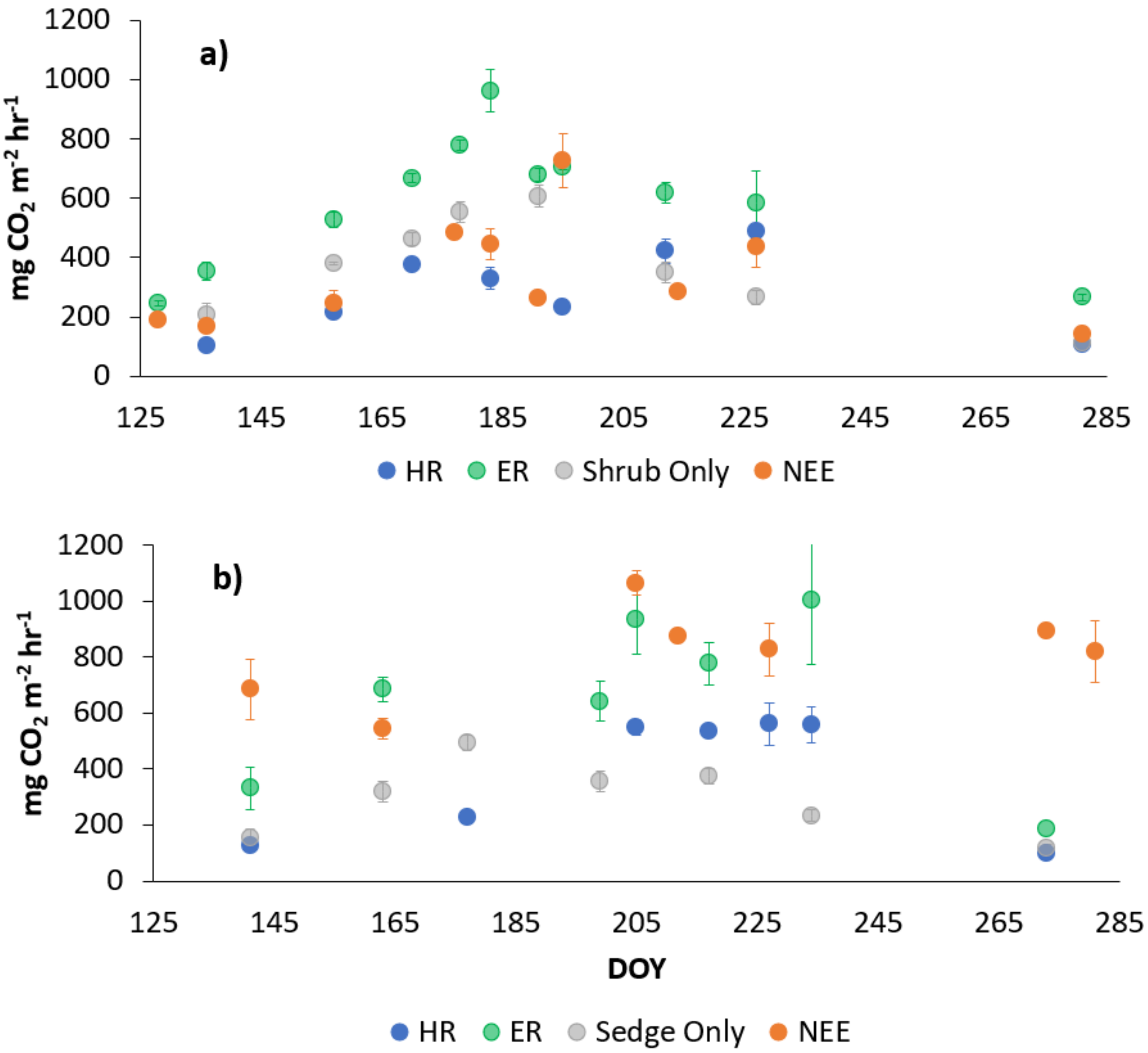


Figure 3.4 Average CO_2 fluxes in the a) shrub plots and b) sedge plots across the growing season of 2019 (± Standard Error).

Table 3.2. Annual average ecosystem respiration (ER), autotrophic respiration (AR), heterotrophic respiration (AR), and net ecosystem exchange (NEE) values for the shrubs and sedges in 2018 and 2019 (± standard deviation).

		ER	**HR**	**Shrub- and sedge- only plots**	**NEE**	**AR**
2018	**shrubs**	414 (154)	195 (81)	250 (69)	461 (103)	187 (134)
	sedges	625 (131)	240 (25)	356 (42)	827 (139)	385 (127)
2019	**shrubs**	611 (194)	309 (123)	403 (135)	323 (120)	378 (164)
	sedges	729 (218)	426 (178)	323 (107)	799 (176)	343 (142)

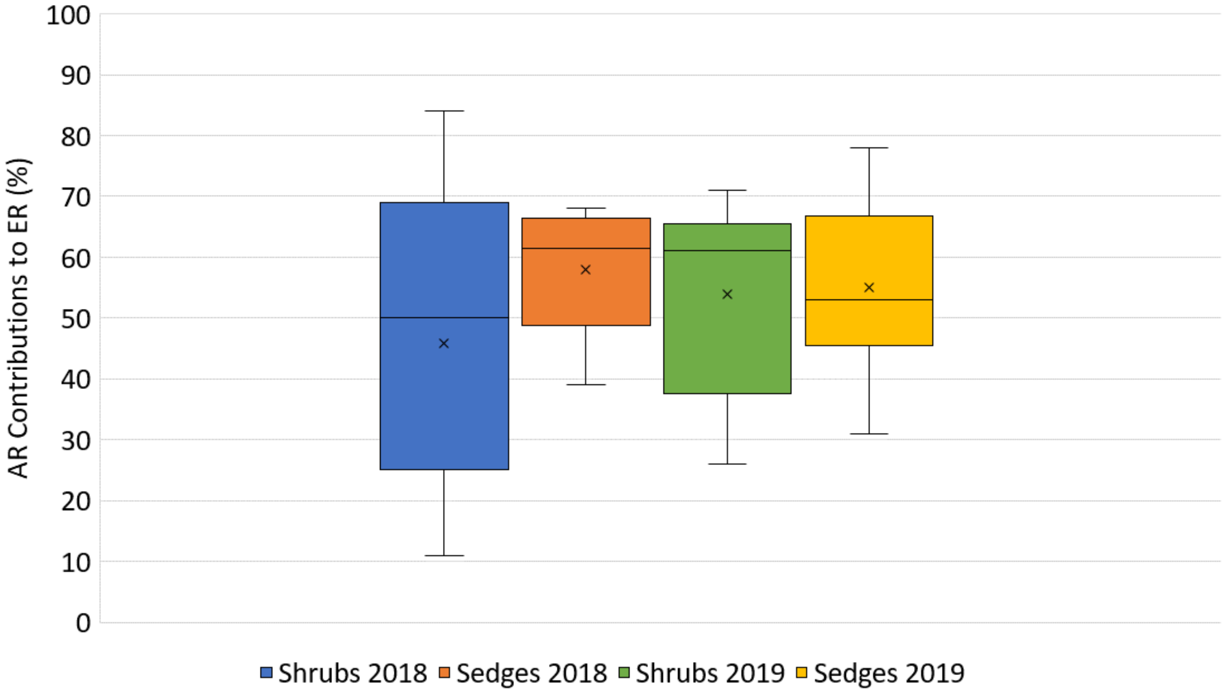


Figure 3.5 AR contributions (%) to ER across the growing seasons of 2018 and 2019.

3.4.3 Statistical analyses

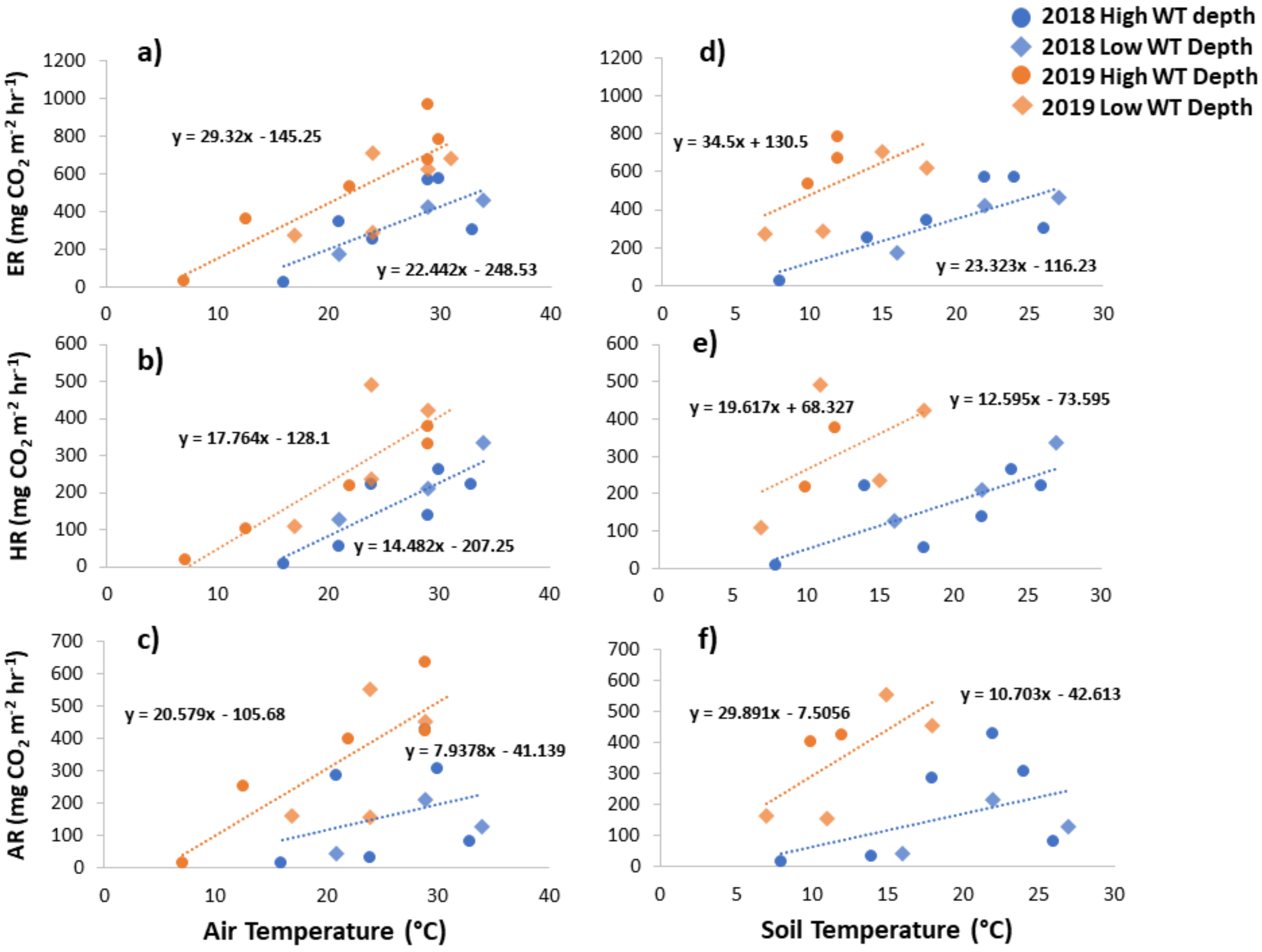
Repeated measures ANOVA show that the fluxes from the different manipulation treatments were significantly different for both the sedges (F = 24.4, P = 0.0004, DF = 13) and the shrubs (F = 6.045, P = 0.0077, DF = 23) in 2018 as well as the sedges (F = 4.9, P = 0.0180, DF = 20) and the shrubs (F = 4.57, P = 0.0210, DF = 23) in 2019. There was a significant difference in ER (t = -1.8002, P = 0.0920, DF = 15) between the sedges and the shrubs, but only for 2018, and not for 2019. Whereas, NEE was only significantly different between the sedges and the shrubs in 2019 and not 2018 (t = -2.9200, P = 0.0260, DF = 18). Subsequently, between the two years, NEE (t = -2.9500, P = 0.0181, DF = 18), ER (t = -2.0924, P= 0.0508, DF = 18) and respiration from the "shrub only" plots (t = -2.0501, P = 0.0583, DF = 15) were significantly different, but not for the "sedge only" plots.

When the environmental controls on the CO_2 fluxes were considered individually, both the variance in fluxes of ER and HR were correlated with air temperature for both plant types and in both growing seasons and with soil temperature for the shrubs in 2018. Soil temperature was also correlated with HR in 2018 and with ER in 2019 for the sedges. The variance in AR fluxes was a bit more complex. The growing season of 2018 showed no relationships with AR fluxes for any of the environmental variables, whereas for 2019, air temperature explained much of the variance in the shrubs, and air and soil temperature much of the variance in the sedges (Table 3.3). Correlation analyses revealed a positive relationship between temperature and respiration, where warmer temperature increased ER and HR (Table B1). Combining the two years of data would have allowed for more datapoints and hence increased the accuracy of the results, but since 2018 was anomalously warm, this would have produced spurious relationships, especially for the shrubs, where although the slope was similar, respiration fluxes in 2019 were higher than 2018 for the same air and soil temperature (Figures 3.6 and 3.7).

Although there seemed to be only one significant linear relationship with WT depth and HR in 2019 for the sedges (Table 3.3), a lower WT was generally associated with increased ER, AR, and HR fluxes (Table B1, Figures 3.6 and 3.7). Linear regression analyses from 2019 in the shrubs showed greater relationships between ER, AR and HR and WT depths when the water table was above 35 cm (R^2 increased to between 0.50 and 0.70 in all cases, with p-values < 0.05), whereas the relationships broke down when the water tables were below 35 cm (Figure 3.6). Although technically only the relationship between HR and WT depth in 2019 for the sedges was significant (Table 3.3), WT depth correlated well with ER and AR too (Table B1). When the water table was above 35 cm, the relationship between HR and WT depth was similar to when all the data points were considered, but the relationships with ER and AR were better correlated, with R^2 increasing to 0.71 and 0.66, respectively. While the relationships between respiration fluxes and WT depth with a low water table was worse in the sedges than when all WT depths were considered, correlations with all the WT depths considered were still greater in the sedges than in the shrubs (Figures 3.6 and 3.7). There were not enough data points in 2018 to test the difference in linear relationships with various WT ranges for either plant type, which is a limitation of our study, where more continuous measurements of the controls on respiration components (e.g., using automatic chambers) would be beneficial.

Table 3.3 Coefficient of determination (R^2) for linear regressions between respiration (ER, AR, and HR) and environmental variables in 2018 and 2019 with p-values in brackets and significant relationships ($p < 0.1$) in bold. WT is water table depth, Air T is air temperature measured at the flux tower, Soil T is soil temperature at 10 cm depth.

Environmental Variable		Shrubs			Sedges		
		ER	HR	AR	ER	HR	AR
Air T	2018	**0.57 (0.02)**	**0.74 (0.002)**	0.11 (0.380)	**0.59 (0.040)**	**0.73 (0.030)**	0.42 (0.160)
	2019	**0.72 (0.001)**	**0.74 (0.002)**	**0.62 (0.011)**	**0.63 (0.010)**	**0.44 (0.070)**	**0.65 (0.010)**
Soil T	2018	**0.64 (0.010)**	**0.58 (0.010)**	0.21 (0.220)	0.42 (0.110)	**0.63 (0.060)**	0.55 (0.255)
	2019	0.36 (0.150)	0.27 (0.280)	0.51 (0.112)	**0.55 (0.050)**	0.26 (0.290)	**0.77 (0.020)**
WT	2018	0.23 (0.180)	0.23 (0.180)	0.01 (0.740)	0.02 (0.750)	0.003 (0.910)	0.15 (0.440)
	2019	0.16 (0.220)	0.14 (0.320)	0.007 (0.860)	0.31 (0.110)	**0.64 (0.020)**	0.199 (0.270)



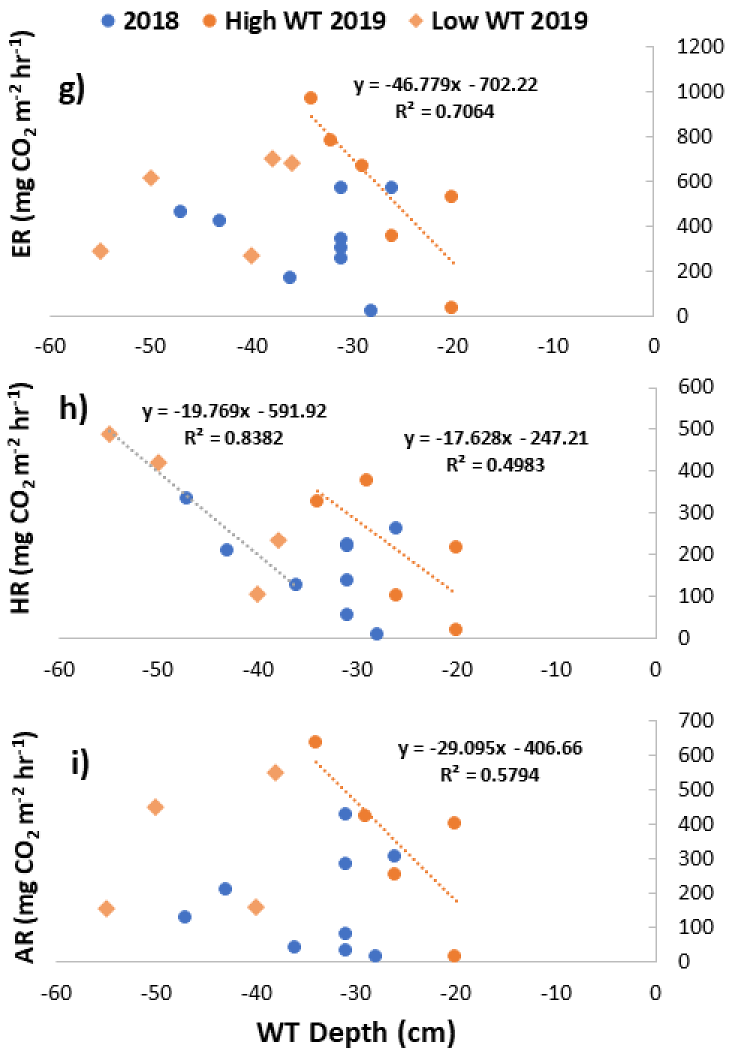
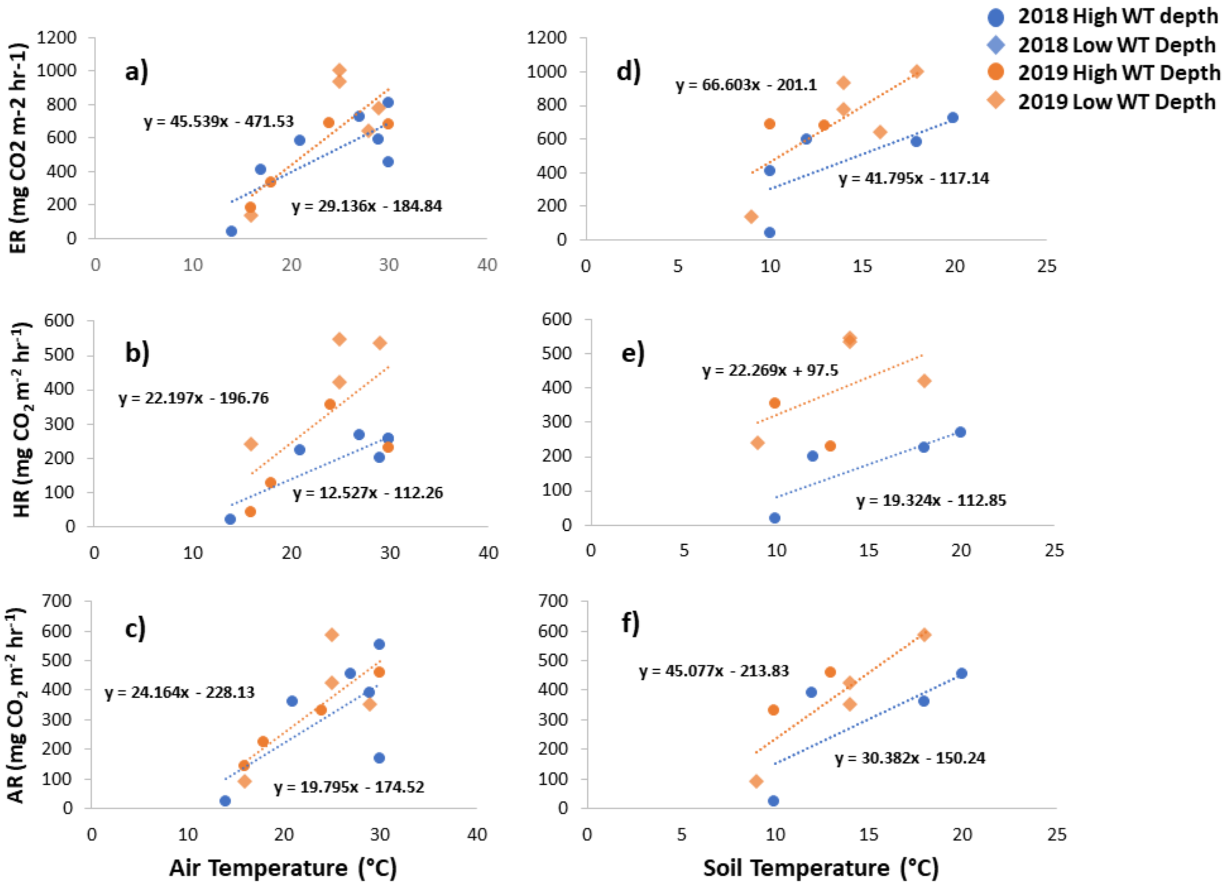


Figure 3.6 Scatterplots with trend lines of relationships between air temperature and a) ER, b) HR, and c) AR; between soil temperature and d) ER, e) HR, and f) AR; and between water table (WT) depth and g) ER, h) HR, and i) AR in the shrubs across the growing seasons of 2018 and 2019. High WT refers to water table positions from surface to 35 cm depth.


2018 High WT depth
2018 Low WT Depth
2019 High WT Depth
2019 Low WT Depth
a)
y = 45.539x - 471.53
y = 29.136x - 184.84
ER (mg CO2 m-2 hr-1)
d)
y = 66.603x - 201.1
y = 41.795x - 117.14
b)
y = 22.197x - 196.76
y = 12.527x - 112.26
HR (mg CO$_2$ m^{-2} hr^{-1})
e)
y = 22.269x + 97.5
y = 19.324x - 112.85
c)
y = 24.164x - 228.13
y = 19.795x - 174.52
AR (mg CO$_2$ m^{-2} hr^{-1})
f)
y = 45.077x - 213.83
y = 30.382x - 150.24
Air Temperature (°C)
Soil Temperature (°C)
0
10
20
30
40
5
15
25
100
200
300
400
500
600
700
800
1000
1200

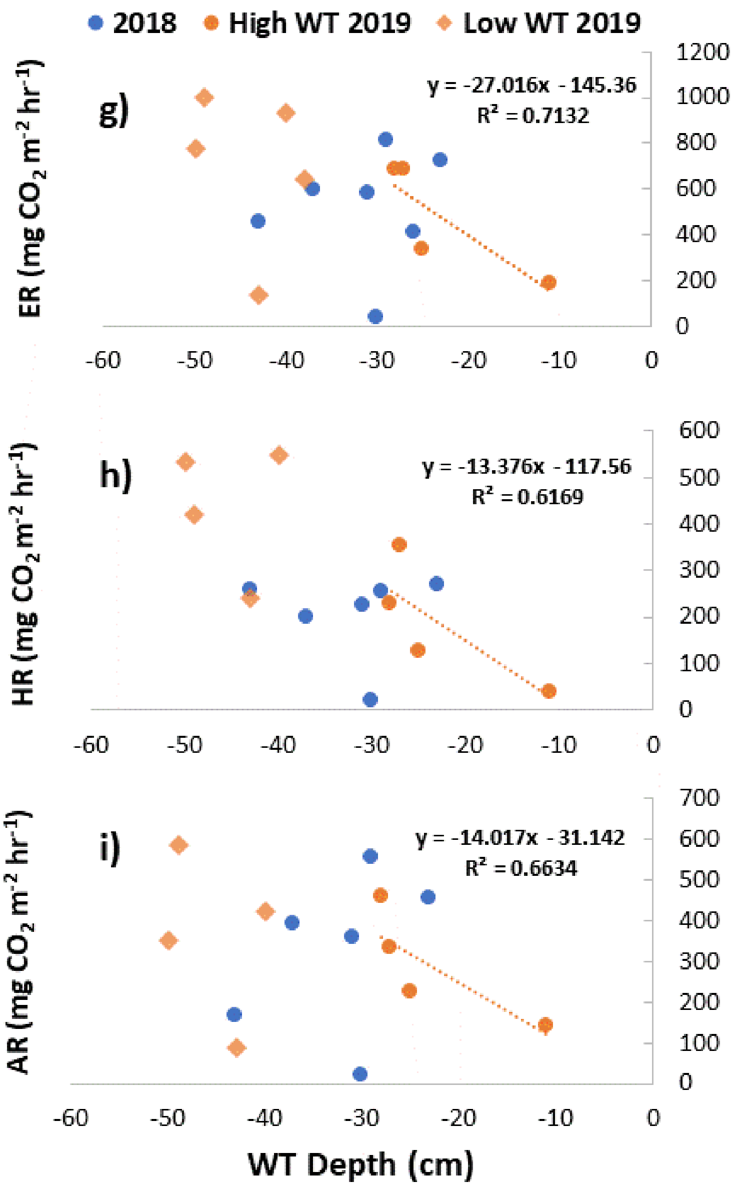
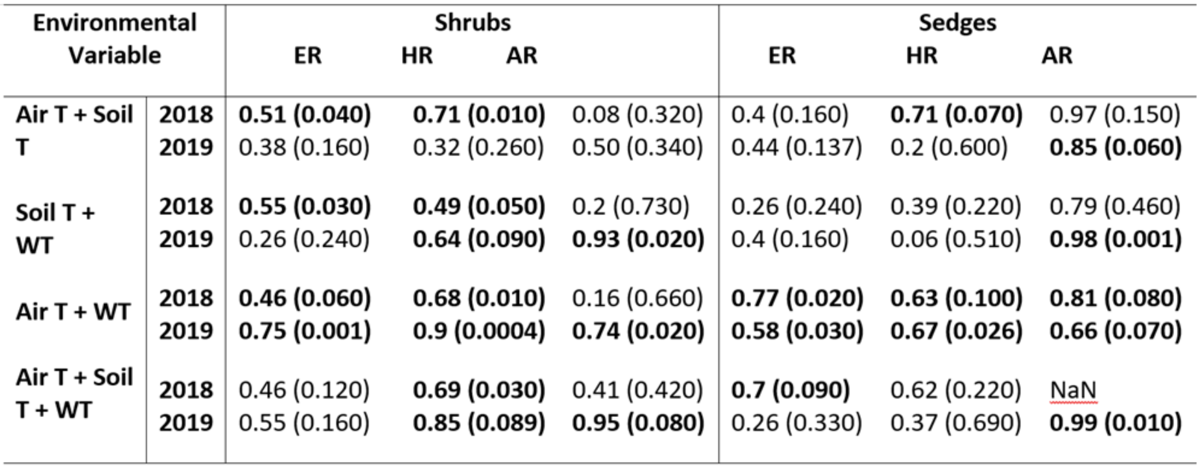


Figure 3.7 Scatterplots with trend lines of relationships between air temperature and a) ER, b) HR, and c) AR; between soil temperature and d) ER, e) HR, and f) AR; and between water table (WT) depth and g) ER, h) HR, and i) AR in the sedges across the growing seasons of 2018 and 2019. High WT refers to water table positions from surface to 35 cm depth.

Multiple regression analyses though, showed the interactive effect of both temperature *and* WT position explained much of the variance in CO_2 fluxes for ER and HR. This was true for both plant types and in both growing seasons. However, there were only strong relationships found between AR and a combination of WT depth and air and soil temperature in 2019 for both plant types and no relationships in 2018 (Table 3.4). The regression trees show that in 2018, air temperature was the factor that best predicted the CO_2 fluxes for the sedges (explained ~ 70% of the respiration response) followed by WT depth (explained ~ 30% of the respiration response), whereas soil temperature best predicted the CO_2 fluxes for the shrubs (explained ~ 50% of the respiration response) followed by air temperature (explained ~ 40% of the respiration response, for both ER and AR (all R^2 values ~ 0.70). Air and soil temperature seemed to be the best factors to predict HR for both plant types, where the combined explanation of the respiration response exceeded 80% (R^2 ~ 0.80). In contrast, the regression trees show that WT depth was a much more important factor in predicting the resulting CO_2 fluxes in 2019, where the explanation of the respiration response was ~ 40% in most cases (all R^2 values ~ 0.60). Air temperature was still the more prominent factor though, where the explanation of the respiration response was ~ 60% in most cases (R^2 ~0.70).

Table 3.4 Coefficient of determination (R^2) for multiple regressions between respiration (ER, AR and HR) and environmental variables in 2018 and 2019 with p-values in brackets and significant relationships ($p < 0.1$) in bold. WT is water table depth, Air T is air temperature measured at the flux tower, Soil T is soil temperature at 10 cm depth. “NaN” refers to there not being enough data points to determine significance.



Environmental Variable		**Shrubs**			**Sedges**		
		ER	**HR**	**AR**	**ER**	**HR**	**AR**
Air T + Soil T	**2018**	**0.51 (0.040)**	**0.71 (0.010)**	0.08 (0.320)	0.4 (0.160)	**0.71 (0.070)**	0.97 (0.150)
	2019	0.38 (0.160)	0.32 (0.260)	0.50 (0.340)	0.44 (0.137)	0.2 (0.600)	**0.85 (0.060)**
Soil T + WT	**2018**	**0.55 (0.030)**	**0.49 (0.050)**	0.2 (0.730)	0.26 (0.240)	0.39 (0.220)	0.79 (0.460)
	2019	0.26 (0.240)	**0.64 (0.090)**	**0.93 (0.020)**	0.4 (0.160)	0.06 (0.510)	**0.98 (0.001)**
Air T + WT	**2018**	**0.46 (0.060)**	**0.68 (0.010)**	0.16 (0.660)	**0.77 (0.020)**	**0.63 (0.100)**	**0.81 (0.080)**
	2019	**0.75 (0.001)**	**0.9 (0.0004)**	**0.74 (0.020)**	**0.58 (0.030)**	**0.67 (0.026)**	**0.66 (0.070)**
Air T + Soil T + WT	**2018**	0.46 (0.120)	**0.69 (0.030)**	0.41 (0.420)	**0.7 (0.090)**	0.62 (0.220)	NaN
	2019	0.55 (0.160)	**0.85 (0.089)**	**0.95 (0.080)**	0.26 (0.330)	0.37 (0.690)	**0.99 (0.010)**

Additionally, the growing season of 2018 resulted in quite variable AR contributions to ER from the shrubs, with a coefficient of variation of 54%, whereas the AR from the sedges only had a coefficient of variation of 19%. In contrast, the variation in AR contributions to ER in 2019 was much less variable for the shrubs, with a coefficient of variation of ~30% for both plants. Although, if one were to remove the one very low AR contribution value from the shrub time series, which occurred at the hottest and driest part of the season, the average AR contribution for the shrubs in 2019 would be much greater than the sedges (~70%) and even less variable.

3.5 Discussion

3.5.1 AR and HR contributions to ER and environmental controls on CO_2 fluxes

ER and NEE were similar to those found in other studies (Bubier et al., 2007; Flanagan and Syed, 2011; Humphreys et al., 2014; Sulman et al., 2010), where the sedge plots showed greater respiration and NEE fluxes than the shrubs plots (Helbig et al., 2019; Lai, 2012). We found that average AR contributions to ER at Mer Bleue, calculated from direct plot measurements, were also consistent with findings in the literature (Maier and Kress, 2000; Schuur and Trumbore, 2006). Hardie et al. (2009), for example, reported AR contributions from a blanket bog in the UK uplands to range between 41% and 54% of the total ecosystem CO_2 flux, using direct static chamber measurements as well.

The respiration fluxes varied, sometimes considerably, and our results show that the variability in ER and HR was driven by changes in temperature and WT position. For example, air and soil temperatures had the greatest influence on CO_2 fluxes, especially for measures of ER and HR when linear regressions were conducted with individual environmental variables (Table 3.3). While in some studies, it may seem as though temperature is the dominant factor driving changes in ecosystem functioning and peatland C cycling (Cai et al., 2010; Charman et al., 2013), others indicate that soil moisture (or the degree of wetness) may also play an important role (e.g. Belyea and Malmer, 2004). Von Buttlar et al. (2018) suggest that together, heat and drought events lead to the strongest C sink reduction compared to any single-factor extreme. Mäkiranta et al. (2010) similarly state that a warming climate may raise respiration from peat decomposition, but only if the decrease in moisture of the surface layers is minor, thus favouring further decomposition.

Temporal and spatial variability in respiration arise because AR and HR are affected differently with climate variability. Wang et al. (2014) suggest that both HR and AR are affected by changes in air temperature, but that HR does not acclimate as fast as AR, so we often see a shift towards higher HR/AR ratios in warming experiments. For example, Grogan and Jonasson (2005) found that newly-photosynthesized C by plants was more sensitive to changes in temperature than the C derived from older stores of soil organic matter deeper (SOM) in the peat. AR contributions to ER were highest in cooler and wetter conditions and lowest in hotter and drier conditions and varied considerably, especially in 2018 (Figure 3.5). The erratic behaviour in weather conditions throughout the growing season of 2018 may explain the lack in any detectable statistical relationship relating AR to the environmental variables, and the lack in statistical relationships with WT depth in general, especially in the shrubs. The greater hysteresis present would imply that the WT did not rebound as quickly during a rain event or drop as quickly when conditions became drier. However, the WT dropped even further towards the end of the growing season in 2019 than it did throughout the growing season of 2018. It seems that the less variable weather conditions, and increased wetness towards the beginning of the growing season, may have led to both plant types having a similar AR contribution in 2019.

Lai et al. (2014) found the relationship with temperature changed with varying moisture conditions. We found the same with an increase in the significance of the linear relationship with WT position when a certain range of WT depths were considered (Figures 3.6 and 3.7). Multiple regression analyses also showed it was the interactive effect of both temperature and water table position that explained much of the variance. This was especially true for the sedges (Table 3.4). These findings are partially explained by the change in weather conditions and the functioning of the plants themselves. Where the growing season of 2018 was characterised by a sharp rise in

WT mid-way through the season and consisted of a hotter and drier June and July than normal, the growing season of 2019 was characterised by less variable weather conditions, but more wet in May and June than normal (Figure 3.1). Considering that sedges can tap into deep water sources, it is reasonable that the respiration of the sedges would be more affected by water table depth than the shrubs; shrub roots spread out laterally and are thus more disconnected from the water table for large parts of the growing season, and most roots do not function well if they are in very saturated conditions (Iversen et al., 2018; Murphy and Moore, 2010). The HR fluxes seem to follow the same general trend as the ER fluxes for the shrubs, more so than for the sedges, in both years despite the more variable weather conditions in 2018; possibly highlighting the stronger influence of soil temperature than WT depth on respiration fluxes for the shrubs. Furthermore, ER was significantly different between the shrubs and the sedges in 2018, as well as significantly different between the two study years for the shrubs. This would further suggest that sporadic weather conditions and fluctuating WT depth has more of an effect on the respiration from the shrubs than it does on the sedges.

3.5.2 AR and HR dependence on the plant functional type

One of the keys to understanding how the vegetation responds to the surrounding environment is to determine the capacity of the plant functional types to adapt to hydrologic and temperature extremes, or hot and dry conditions (Porporato et al., 2004). The sedges have much higher productivity rates than the shrubs for this reason (Frolking et al., 1998); the vegetation not only possess roots that can survive in semi-permanent saturated conditions, but also tend to allocate a lot of their energy to aboveground leaves to increase the loss of water to the atmosphere and balance the presence of an increased water supply. Sedges have vertical root structures that can tap into the WT at deeper depths even during the drier parts of the season

(Buttler et al., 2015) and can consequently support a greater aboveground biomass when WT depth fluctuates, hence showing a higher average AR contribution to ER than the shrubs in 2018 (Murphy et al., 2009a). On the other hand, shrubs, which often dominate ecosystems like bogs that have a water table at a greater depth for longer periods of time, allocate more of their energy to belowground roots and to smaller needle like stems so they can make use of whatever water is available to the plants in the soil, while minimizing the loss of water aboveground through transpiration (Bonan, 2008; Murphy and Moore, 2010). The shrubs seem to take advantage of this, by relying on the water retained by the mosses closer to the surface (Nijp et al., 2017), and hence show a greater variability in aboveground respiration and consequently in AR contributions to ER when the WT depths fluctuate a lot like they did in 2018 (Mccarter and Price, 2014). It also possibly explains why AR contributions to ER are greater for the shrubs than the sedges in 2019, when changes in WT depth were more consistent.

The respiration dynamics depend on the mechanisms of the different plant functional types in obtaining water resources, and the relationships of the vascular plants with the mosses seem to play a vital role in how the plants respond to a change in climate. Indeed, Järveoja et al. (2018) found in a fen in northern Sweden, that it was plant phenology that drove respiration dynamics rather than abiotic factors. Our study found that in the shrubs, the CO_2 fluxes were, at times, greater for HR than they were in the “shrub only” plots. These instances seem to coincide with periods that were hot and dry (Figures 3.3 and 3.4), and in 2018, was a phenomenon only seen in the shrubs; the sedges never showed this despite measurements taken around the same time. This suggests that the shrubs are more intimately associated with the mosses around them than are the sedges, as Chiapusio et al. (2018) also found in their study. Along with a more pronounced hysteresis loop in 2018, this also supports our argument that the shrubs are more disconnected from WT dynamics than the sedges. A change in soil temperature, which affects mainly the surface would influence the shrub's response more so than WT position or soil moisture, whereas the sedges would be more affected by changes in WT depth for most of the growing season (Figures 3.6 and 3.7), due to the difference in root structure between the two plant types. In 2019, on the other hand, DOY 191 – 217 was one of the hotter parts of the growing season, where the water tables during this hot period were lower than they were for the dry period in 2018, and consisted of less sporadic rain events, indicated by the less obvious hysteresis loop. This may explain why the CO_2 fluxes were, at times, greater for HR than they were in the "shrub only" and "sedge only" plots in 2019. While a greater HR in warmer periods could suggest increased microbial activity and/or oxygen availability (Sulman et al., 2010), these findings could also indicate that both vascular plants have some sort of relationship with the mosses, as Crow and Wieder (2005) found in their study, or it could be explained by the ability of the mosses, with their "phenotypic plasticity," to cope with rising temperatures and repeated droughts (Jassey and Signarbieux, 2019).

Similar manipulations have been applied to chamber set ups to determine contributions of AR and HR by removing all of the roots belowground as well, a process known as girdling (Hahn et al., 2006; Hardie et al., 2009). However, these were done mainly in forested systems where roots are more easily removed without disturbing surrounding vegetation like the mosses surrounding the vascular plants in a bog. In peatlands, this is too invasive an approach, and we opted to remove only the aboveground vegetation, while keeping in mind that residuals of the roots left behind may contribute to the fluxes we measure. There was, at times, a difference in respiration between the light and dark rounds measured from the clipped plots, especially in 2018 (data not shown). This may be explained by the slow decomposition of the roots, especially in the sedges, where constant re-clipping throughout the growing season was necessary. Stewart (2006) suggests, for example, that the soil organic matter decomposition is 1.6 to 1.9 times greater in the hollows (where the sedges mostly reside) than in the hummocks. Although, we examined patterns of respiration mainly in the hummocks, which represent 70% of the bog (Lafleur et al. 2003), and incorporated mosses, shrubs and sedges. Marinier et al. (2004) found that re-clipping was necessary in their study, but that a root exclosure helped in minimizing the ingrowth of new roots; thus, we also included a root exclosure around our plots. This re-clipping requirement may also explain why the repeated measures ANOVA analyses between the treatments was not as significantly different in 2019 than in 2018. However, we also did not find any statistically significant difference between the HR fluxes between the plants, which one would expect if a difference in root residuals were to play a major role. This finding was promising; respiration from all the plots without vegetation were showing similar values throughout the growing season. There was also no difference in HR fluxes between the two years in our study too though, which was more surprising as the WT depths seemed to have some influence on the HR fluxes, especially when considered alongside the dominant effect of temperature. Rewcastle et al. (2020) for example, did not find significant CO_2 fluxes from residual root decomposition using root exclosure methods, yet also found rather variable HR rates which they attribute to changes in water table and soil moisture. Although, their study was conducted in a forested bog, where tree roots would have been the dominant contributor, and whose root structure is different from short woody shrubs.

While the remnants of roots in the clipped plots may partially explain why the HR fluxes were sometimes higher in these plots than the respiration values in the “shrub only” or “sedge only” plots, we cannot ignore that this phenomenon occurred mostly when it was hotter and drier. Zeh et al. (2020) for example, found a higher degree of decomposition of peat under sedges than under shrubs, particularly when temperatures were higher. It may also be possible that the mosses in these conditions are inhibiting the respiration of the microbes below, with the vascular plants providing a priming effect to respiration (Robroek et al., 2016). For example, Gavazov et al. (2018) found enhanced heterotrophic decomposition of peat carbon due to rhizosphere priming, and Basiliko et al. (2012) similarly suggest that a priming effect may occur when decomposition of soil organic matter is stimulated by rhizodeposition. In our case, the mosses may be assimilating C from the roots of the vascular plants and release that back to the atmosphere as another source of respiration in addition to that which is derived directly from photosynthesis (Turetsky and Wieder, 1999). Metcalfe et al. (2011) also suggest that the amount of C allocated belowground is governed by the total amount of C acquired by photosynthesis, which is likely to be higher for plants that have both a greater leaf area and higher photosynthetic rates. In our study, it is clear in both growing seasons that NEE was higher in the sedges than it was in the shrubs. So, when the mosses were removed, they were no longer able to benefit from this priming effect, and when weather conditions became warmer and drier, the clipped plots, which represent HR, released more CO_2 than the plots that only contained the vascular plants. This conclusion is speculative and a further look into the link with belowground processes may help support this claim. Although, Shao (2022) showed in his modelling study that when the ericoid mycorrhiza fungi around the shrub roots were removed from the model, the autotrophic respiration of the mosses increased from ~ 75 g C $m^{-2}yr^{-1}$ to ~ 125 g C $m^{-2}yr^{-1}$, highlighting the importance of shrub-moss-mycorrhizae associations to carbon cycling in peatlands.

3.6. Conclusions

ER and HR seem to be primarily related to air and soil temperature for both plant types and for AR in the sedges, however, interactive effects of environmental variables occur, with WT depth playing a significant role in some cases. Additionally, there is some plant dependence on the dynamics of respiration, with the shrubs showing more variable respiration values and potentially having a greater relationship with the mosses than do the sedges. This study provided a detailed analysis of partitioning ER, especially with regards to unveiling the presence of the intermediate form of respiration we deemed plant-associated HR and has furthered our knowledge of C cycling in peatlands.

Given the complex nature of respiration and its components, future studies should consider obtaining more continuous measurements of respiration fluxes, through an automatic chamber set up for example, and that belowground resources are seemingly quite significant to understanding respiration (e.g., root dynamics). Fenner & Freeman (2011) found in an ombrotrophic, oligotrophic *Sphagnum* peatland (i.e., a bog) that if demands for both water *and* nutrients are not met, this will lead to a higher loss of C from plants through drought-induced increases in nutrient and labile carbon levels that stimulate anaerobic decomposition. Thus, we suggest an in-depth exploration of pore water analyses, through measures of dissolved organic carbon, and nutrients, such as phosphorus and nitrogen, will be helpful. Tools such as root exudate analyses, and stable and radiocarbon isotopes of C have been used more frequently over the last few decades to determine the source of respired C (Hahn et al., 2006; Hardie et al., 2009), analyses for which we suggest this project would also benefit.

3.7 Author contributions

Tracy E. Rankin designed the experiments, with the support of Nigel T. Roulet, and carried them out. Tracy E. Rankin also prepared the manuscript with contributions from all co-authors.

3.8 Competing interests

The authors declare that they have no conflict of interest.

3.9 Acknowledgements

This study was funded through grants from the Natural Sciences and Engineering Research Council of Canada (CRD programs). The authors gratefully acknowledge the support from M. Dalva, M. Hassa, K. Hutchins, and Z. Humeau (McGill) as well as from Elyn R. Humphreys (Carleton University) for the environmental data from the eddy covariance tower.

3.10 References

Abdalla, M., Hastings, A., Bell, M. J., Smith, J. U., Richards, M., Nilsson, M. B., Peichl, M., Löfvenius, M. O., Lund, M., Helfter, C., Nemitz, E., Sutton, M. A., Aurela, M., Lohila, A., Laurila, T., Dolman, A. J., Belelli-Marchesini, L., Pogson, M., Jones, E., Drewer, J., Drosler, M. and Smith, P.: Simulation of CO_2 and attribution analysis at six european peatland sites using the ECOSSE model, Water. Air. Soil Pollut., 225(11), doi:10.1007/s11270-014-2182-8, 2014.

Abdi, Herve.: Coefficient of Variation, Encyclopeadia of Research Design, In Neil Salkind (Ed.), 2010.

Arain, M. Altaf., Xu, Bing., Brodeur, Jason J., Khomik, Myroslava., Peichl, Matthias., Beamesderfer, Eric., restrepo-Couple, Natalia. and Thorne, Robin.: Heat and Drought Impact on Carbon Exchange in an Age-Sequence of temperate pine forests., Ecological Processes., 11(7)., doi: 10.1186/s13717-021-00349-7., 2022.

Basiliko, N., Stewart, H., Roulet, N. T. and Moore, T. R.: Do Root Exudates Enhance Peat Decomposition?, Geomicrobiol. J., 29(4), 374–378, doi:10.1080/01490451.2011.568272, 2012.

Belyea, L. R. and Malmer, N.: Carbon sequestration in peatland: patterns and mechanisms of response to climate change, Glob. Chang. Biol., 10, 1043–1052, doi:10.1111/j.1365-2486.2004.00783.x, 2004.

Blodau, C.: Carbon cycling in peatlands - A review of processes and controls, Environ. Rev., 10(2), 111–134, doi:10.1139/a02-004, 2002.

Bonan, G.: Ecological Climatology, Cambridge University Press., 2008.

Brieman L., Friedman J., Olshen R., Stone C.: Classification and regression trees., Routledge., 1984.

Bubier, J. L., Moore, T. R. and Bledzki, L. A.: Effects of nutrient addition on vegetation and carbon cycling in an ombrotrophic bog, Glob. Chang. Biol., 13(6), 1168–1186, doi:10.1111/j.1365-2486.2007.01346.x, 2007.

Bunsen, M. S. and Loisel, J.: Carbon storage dynamics in peatlands: Comparing recent- and long-term accumulation histories in southern Patagonia, Glob. Chang. Biol., 26(10), 5778–5795, doi:10.1111/gcb.15262, 2020.

Von Buttlar, J., Zscheischler, J., Rammig, A., Sippel, S., Reichstein, M., Knohl, A., Jung, M., Menzer, O., Altaf Arain, M., Buchmann, N., Cescatti, A., Gianelle, D., Kiely, G., Law, B. E., Magliulo, V., Margolis, H., McCaughey, H., Merbold, L., Migliavacca, M., Montagnani, L., Oechel, W., Pavelka, M., Peichl, M., Rambal, S., Raschi, A., Scott, R. L., Vaccari, F. P., Van Gorsel, E., Varlagin, A., Wohlfahrt, G. and Mahecha, M. D.: Impacts of droughts and extreme-temperature events on gross primary production and ecosystem respiration: A systematic assessment across ecosystems and climate zones, Biogeosciences, 15(5), 1293–1318, doi:10.5194/bg-15-1293-2018, 2018.

Buttler, A., Robroek, B. J. M., Laggoun-Défarge, F., Jassey, V. E. J., Pochelon, C., Bernard, G., Delarue, F., Gogo, S., Mariotte, P., Mitchell, E. A. D. and Bragazza, L.: Experimental warming interacts with soil moisture to discriminate plant responses in an ombrotrophic peatland, J. Veg. Sci., 26(5), 964–974, doi:10.1111/jvs.12296, 2015.

Cai, T., Flanagan, L. B. and Syed, K. H.: Warmer and drier conditions stimulate respiration more than photosynthesis in a boreal peatland ecosystem: Analysis of automatic chambers and eddy covariance measurements, Plant, Cell Environ., 33(3), 394–407, doi:10.1111/j.1365-3040.2009.02089.x, 2010.

Charman, D. J., Beilman, D. W., Blaauw, M., Booth, R. K., Brewer, S., Chambers, F. M., Christen, J. A., Gallego-Sala, A., Harrison, S. P., Hughes, P. D. M., Jackson, S. T., Korhola, A., Mauquoy, D., Mitchell, F. J. G., Prentice, I. C., van der Linden, M., De Vleeschouwer, F., Yu, Z. C., Alm, J., Bauer, I. E., Corish, Y. M. C., Garneau, M., Hohl, V., Huang, Y., Karofeld, E., Le Roux, G., Loisel, J., Moschen, R., Nichols, J. E., Nieminen, T. M., MacDonald, G. M., Phadtare, N. R., Rausch, N., Sillasoo, Ü., Swindles, G. T., Tuittila, E.-S., Ukonmaanaho, L., Väliranta, M., van Bellen, S., van Geel, B., Vitt, D. H. and Zhao, Y.: Climate-related changes in peatland carbon accumulation during the last millennium, Biogeosciences, 10(2), 929–944, doi:10.5194/bg-10-929-2013, 2013.

Chiapusio, G., Jassey, V. E. J., Bellvert, F., Comte, G., Weston, L. A., Delarue, F., Buttler, A., Toussaint, M. L. and Binet, P.: Sphagnum Species Modulate their Phenolic Profiles and Mycorrhizal Colonization of Surrounding Andromeda polifolia along Peatland Microhabitats, J. Chem. Ecol., 44(12), 1146–1157, doi:10.1007/s10886-018-1023-4, 2018.

Crow, S. E. and Wieder, R. K.: Sources of CO_2 emission from a northern peatland: Root respiration, exudation, and decomposition, Ecology, 86(7), 1825–1834, doi:10.1890/04-1575, 2005.

Dorrepaal, E., Toet, S., van Logtestijn, R. S. P., Swart, E., van de Weg, M. J., Callaghan, T. V., Aerts, R., Logtestijn, V., Richard, S. P., Swart, E., Weg, V. De, Martine, J., Callaghan, T. V., Aerts, R., van Logtestijn, R. S. P., Swart, E., van de Weg, M. J., Callaghan, T. V. and Aerts, R.: Carbon respiration from subsurface peat accelerated by climate warming in the subarctic, Nature, 460, 616–619, doi:10.1038/nature08216, 2009.

Environment Canada: Historical Weather Data, Gov. Canada [online] Available from: https://climate.weather.gc.ca/historical_data/search_historic_data_e.html, 2021.

Fan, Z., David Mcguire, A., Turetsky, M. R., Harden, J. W., Michael Waddington, J. and Kane, E. S.: The response of soil organic carbon of a rich fen peatland in interior Alaska to projected climate change, Glob. Chang. Biol., 19(2), 604–620, doi:10.1111/gcb.12041, 2013.

Fenner, Nathalie., Freeman, Chris.: Drought induced carbon loss in peatlands., Nature Geoscience., 4., 895-900., doi: https://doi.org/10.1038/ngeo1323., 2011.

Flanagan, L. B. and Syed, K. H.: Stimulation of both photosynthesis and respiration in response to warmer and drier conditions in a boreal peatland ecosystem, Glob. Chang. Biol., 17(7), 2271–2287, doi:10.1111/j.1365-2486.2010.02378.x, 2011.

Frolking, S., Roulet, N. T., Moore, T. R., Lafleur, P. M., Bubier, J. L. and Crill, P. M.: Modeling seasonal to annual carbon balance of Mer Bleue Bog, Ontario, Canada, Global Biogeochem. Cycles, 16(3), doi:10.1029/2001GB001457, 2002.

Frolking, S. E., Bubier, J. ., Moore, T. R., Ball, T., Bellisario, L. M., Bhardwaj, A., Carroll, P., Crill, P. M., Lafleur, P. M., McCaughey, J. H., Roulet, N. T., Suyker, A. E., Verma, S. B., Waddington, J. M. and Whiting, G. J.: Relationship between ecosystem productivity and photosynthetically active radiation for northern peatlands, Global Biogeochem. Cycles, 12(1), 115–126, 1998.

Gavazov, K., Albrecht, R., Buttler, A., Dorrepaal, E., Garnett, M. H., Gogo, S., Hagedorn, F., Mills, R. T. E., Robroek, B. J. M. and Bragazza, L.: Vascular plant-mediated controls on atmospheric carbon assimilation and peat carbon decomposition under climate change, Glob. Chang. Biol., 24(9), 3911–3921, doi:10.1111/gcb.14140, 2018.

Griffis, T. J., Rouse, W. R. and Waddington, J. M.: Interannual variability of net ecosystem CO_2 exchange at a subarctic fen, Geography, 14(4), 1109–1121, 2000.

Grogan, P. and Jonasson, S.: Temperature and substrate controls on intra-annual variation in ecosystem respiration in two subarctic vegetation types, Glob. Chang. Biol., 11(3), 465–475, doi:10.1111/j.1365-2486.2005.00912.x, 2005.

Hahn, V., Högberg, P. and Buchmann, N.: ^{14}C - A tool for separation of autotrophic and heterotrophic soil respiration, Glob. Chang. Biol., 12(6), 972–982, doi:10.1111/j.1365-2486.2006.001143.x, 2006.

Hardie, S. M. L., Garnett, M. H., Fallick, A. E., Ostle, N. J. and Rowland, A. P.: Bomb-^{14}C analysis of ecosystem respiration reveals that peatland vegetation facilitates release of old carbon, Geoderma, 153(3–4), 393–401, 2009.

Van Hees, P. A. W., Jones, D. L., Finlay, R., Godbold, D. L. and Lundström, U. S.: The carbon we do not see - The impact of low molecular weight compounds on carbon dynamics and respiration in forest soils: A review, Soil Biol. Biochem., 37(1), 1–13, doi:10.1016/j.soilbio.2004.06.010, 2005.

Heimann, M. and Reichstein, M.: Terrestrial ecosystem carbon dynamics and climate feedbacks, Nature, 451(7176), 289–292, doi:10.1038/nature06591, 2008.

Heinemeyer, A., Croft, S., Garnett, M. H., Gloor, E., Holden, J., Lomas, M. R. and Ineson, P.: The MILLENNIA peat cohort model: Predicting past, present and future soil carbon budgets and fluxes under changing climates in peatlands, Clim. Res., 45(1), 207–226, doi:10.3354/cr00928, 2010.

Helbig, M., Humphreys, E. R. and Todd, A.: Contrasting Temperature Sensitivity of CO_2 Exchange in Peatlands of the Hudson Bay Lowlands, Canada, J. Geophys. Res. Biogeosciences, 124(7), 2126–2143, doi:10.1029/2019JG005090, 2019.

Hicks Pries, C. E., Schuur, E. A. G. and Crummer, K. G.: Thawing permafrost increases old soil and autotrophic respiration in tundra: Partitioning ecosystem respiration using ^{13}C and ^{14}C, Glob. Chang. Biol., 19(2), 649–661, doi:10.1111/gcb.12058, 2013.

Hicks Pries, C. E., Van Logtestijn, R. S. P., Schuur, E. A. G., Natali, S. M., Cornelissen, J. H. C., Aerts, R. and Dorrepaal, E.: Decadal warming causes a consistent and persistent shift from heterotrophic to autotrophic respiration in contrasting permafrost ecosystems, Glob. Chang. Biol., 21(12), 4508–4519, doi:10.1111/gcb.13032, 2015.

Humphreys, E. R., Charron, C., Brown, M. and Jones, R.: Two Bogs in the Canadian Hudson Bay Lowlands and a Temperate Bog Reveal Similar Annual Net Ecosystem Exchange of CO_2, Arctic, Antarct. Alp. Res., 46(1), 103–113, doi:10.1657/1938-4246.46.1.103, 2014.

Hungate, B. A., Holland, E. A., Jackson, R. B., FS, C., HA, M. and Cb, F.: The fate of carbon in grasslands under carbon dioxide enrichment, Nature, 388(6642), 576–579, doi:10.1038/41550, 1997.

Iversen, C. M., Childs, J., Norby, R. J., Ontl, T. A., Kolka, R. K., Brice, D. J., McFarlane, K. J. and Hanson, P. J.: Fine-root growth in a forested bog is seasonally dynamic, but shallowly distributed in nutrient-poor peat, Plant Soil, 424(1–2), 123–143, doi:10.1007/s11104-017-3231-z, 2018.

Järveoja, J., Nilsson, M. B., Gažovič, M., Crill, P. M. and Peichl, M.: Partitioning of the net CO_2 exchange using an automated chamber system reveals plant phenology as key control of production and respiration fluxes in a boreal peatland, Glob. Chang. Biol., 24(8), 3436–3451, doi:10.1111/gcb.14292, 2018.

Jassey, V. E. J. and Signarbieux, C.: Effects of climate warming on Sphagnum photosynthesis in peatlands depend on peat moisture and species-specific anatomical traits, Glob. Chang. Biol., 25(11), 3859–3870, doi:10.1111/gcb.14788, 2019.

Kalacska, M., Arroyo-Mora, J. P., de Gea, J., Snirer, E., Herzog, C. and Moore, T. R.: Videographic analysis of Eriophorum vaginatum spatial coverage in an Ombotrophic bog, Remote Sens., 5(12), 6501–6512, doi:10.3390/rs5126501, 2013.

Kuiper, J. J., Mooij, W. M., Bragazza, L. and Robroek, B. J. M.: Plant functional types define magnitude of drought response in peatland CO_2 exchange, Ecology, 95(1), 123–131, doi:10.1890/13-0270.1, 2014.

Kurbatova, J., Tatarinov, F., Molchanov, A., Varlagin, A., Avilov, V., Kozlov, D., Ivanov, D. and Valentini, R.: Partitioning of ecosystem respiration in a paludified shallow-peat spruce forest in the southern taiga of European Russia, Environ. Res. Lett., 8(4), doi:10.1088/1748-9326/8/4/045028, 2013.

Lafleur, P. M., Roulet, N. T., Bubier, J.L., Frolking, S. and Moore, T.R.: "Interannual variability in the peatland-atmosphere carbon dioxide exchange at an ombrotrophic bog.", Global Biogeochem. Cycles 17(2): 1036, doi:1010.1029/2002GB001983. 2003.

Lafleur, P. M., Moore, T. R., Roulet, N. T. and Frolking, S.: Ecosystem Respiration in a Cool Temperate Bog Depends on Peat Temperature But Not Water Table, Ecosystems, 8(6), 619–629, doi:10.1007/s10021-003-0131-2, 2005.

Lai, D. Y. F., Roulet, N. T. and Moore, T. R.: The spatial and temporal relationships between CO2 and CH4 exchange in a temperate ombrotrophic bog, Atmos. Environ., 89, 249–259, doi:10.1016/j.atmosenv.2014.02.034, 2014.

Lai, Y. F.: Spatial and Temporal Variations of Carbon Dioxide and Methane Fluxes Measured by Autochambers at the Mer Bleue Bog, McGill University., 2012.

Lavoie, C., Grosvernier, P., Girard, M. and Marcoux, K.: Spontaneous revegetation of mined peatlands : An useful restoration tool ?, Wetl. Ecol. Manag., 11, 97–107, 2003.

Lees, K.J., Artz, R.R.E., Chandler, D., Aspinall, T., Boulton, C.A., Buxton, J., Cowie, N.R., and Lenton, T.M.: Using remote sensing to assess peatland resilience by estimating soil surface moisture and drought recovery., Science of the Total Environment., 761., doi: https://doi.org/10.1016/j.scitotenv.2020.143312. 2021.

Lin, X., Tfaily, M. M., Steinweg, J. M., Chanton, P., Esson, K., Yang, Z. K., Chanton, J. P., Cooper, W., Schadt, C. W. and Kostka, J. E.: Microbial community stratification linked to utilization of carbohydrates and phosphorus limitation in a Boreal Peatland at Marcell Experimental Forest, Minnesota, USA, Appl. Environ. Microbiol., 80(11), 3518–3530, doi:10.1128/AEM.00205-14, 2014.

Loisel, J., Yu, Z., Beilman, D. W., Camill, P., Alm, J., Amesbury, M. J., Anderson, D., Andersson, S., Bochicchio, C., Barber, K., Belyea, L. R., Bunbury, J., Chambers, F. M., Charman, D. J., Vleeschouwer, F. De, Fiałkiewicz-kozieł, B., Finkelstein, S. A., Gałka, M., Garneau, M., Hammarlund, D., Hinchcliffe, W., Holmquist, J., Hughes, P., Jones, M. C., Klein, E. S., Kokfelt, U., Korhola, A., Kuhry, P., Lamarre, A., Lamentowicz, M., Large, D., Lavoie, M., Macdonald, G., Mäkilä, M., Mallon, G., Mathijssen, P., Mauquoy, D., Moore, T. R., Nichols, J., Reilly, B. O., Oksanen, P., Packalen, M., Peteet, D., Richard, P. J. H., Robinson, S., Ronkainen, T., Rundgren, M., Sannel, A. B. K., Tarnocai, C., Thom, T., Tuittila, E. S., Turetsky, M. R., Valiranta, M., van der Linden, M., van Geel, B., van Bellen, S., Vitt, D. H., Zhao, Y. and Zhou, W.: A database and synthesis of northern peatland soil properties and Holocene carbon and nitrogen accumulation, Holocene Spec. Issue, 24(9), 1028–1042, doi:10.1177/0959683614538073, 2014.

Maier, C. A. and Kress, L. W.: Soil CO_2 evolution and root respiration in 11 year-old loblolly pine (Pinus taeda) plantations as affected by moisture and nutrient availability, Can. J. For. Res., 30(3), 347–359, doi:10.1139/cjfr-30-3-347, 2000.

Mäkiranta, P., Riutta, T., Penttilä, T. and Minkkinen, K.: Dynamics of net ecosystem CO_2 exchange and heterotrophic soil respiration following clearfelling in a drained peatland forest, Agric. For. Meteorol., 150(12), 1585–1596, doi:10.1016/j.agrformet.2010.08.010, 2010.

Malhotra, A., Brice, D. J., Childs, J., Graham, J. D., Hobbie, E. A., Vander Stel, H., Feron, S. C., Hanson, P. J. and Iversen, C. M.: Peatland warming strongly increases fine-root growth, Proc. Natl. Acad. Sci. U. S. A., 117(30), 17627–17634, doi:10.1073/pnas.2003361117, 2020.

Marinier, M., Glatzel, S. and Moore, T.: The role of cotton-grass (Eriophorum vaginatum) in the exchange of CO_2 and CH_4 at two restored peatlands, eastern Canada, Ecoscience, 11(2), 141–149, 2004.

Mccarter, C. P. R. and Price, J. S.: Ecohydrology of Sphagnum moss hummocks: Mechanisms of capitula water supply and simulated effects of evaporation, Ecohydrology, 7(1), 33–44, doi:10.1002/eco.1313, 2014.

Melling, Lulie., Hatano, Ryusuke., Goh, Kah Joo.: Soil CO_2 flux from three ecosystems in tropical peatland of Sarawak, Malaysia., Tellus B: Chemical and Physical Meteorology, 57:1, 1-11, DOI: 10.3402/tellusb.v57i1.16772. 2017.

Metcalfe, D. B., Fisher, R. A. and Wardle, D. A.: Plant communities as drivers of soil respiration: Pathways, mechanisms, and significance for global change, Biogeosciences, 8(8), 2047–2061, doi:10.5194/bg-8-2047-2011, 2011.

Minkkinen, K., Laine, J., Shurpali, N. J., Makiranta, P., Alm, J. and Penttilä, T.: Heterotrophic soil respiration in forestry-drained peatlands, Boreal Environ. Res., 12(May), 115–126, 2007.

Murphy, M., Laiho, R. and Moore, T. R.: Effects of water table drawdown on root production and aboveground biomass in a boreal Bog, Ecosystems, 12(8), 1268–1282, doi:10.1007/s10021-009-9283-z, 2009a.

Murphy, M. T. and Moore, T. R.: Linking root production to aboveground plant characteristics and water table in a temperate bog, Plant Soil, 336(1), 219–231, doi:10.1007/s11104-010-0468-1, 2010.

Murphy, M. T., McKinley, A. and Moore, T. R.: Variations in above-and below-ground vascular plant biomass and water table on a temperate ombrotrophic peatland, Botany, 87(9), 845–853, doi:10.1139/B09-052, 2009b.

Nijp, J. J., Metselaar, K., Limpens, J., Teutschbein, C., Peichl, M., Nilsson, M. B., Berendse, F. and van der Zee, S. E. A. T. M.: Including hydrological self-regulating processes in peatland models: Effects on peatmoss drought projections, Sci. Total Environ., 580, 1389–1400, doi:10.1016/j.scitotenv.2016.12.104, 2017.

Ojanen, P., Minkkinen, K., Lohila, A., Badorek, T. and Penttilä, T.: Chamber measured soil respiration: A useful tool for estimating the carbon balance of peatland forest soils?, For. Ecol. Manage., 277, 132–140, doi:10.1016/j.foreco.2012.04.027, 2012.

Oke, T. A. and Hager, H. A.: Plant community dynamics and carbon sequestration in Sphagnum-dominated peatlands in the era of global change, Glob. Ecol. Biogeogr., 29(10), 1610–1620, doi:10.1111/geb.13152, 2020.

Peichl, M., Öquist, M., Ottosson Löfvenius, M., Ilstedt, U., Sagerfors, J., Grelle, A., Lindroth, A. and Nilsson, M. B.: A 12-year record reveals pre-growing season temperature and water table level threshold effects on the net carbon dioxide exchange in a boreal fen, Environ. Res. Lett., 9(5), doi:10.1088/1748-9326/9/5/055006, 2014.

Pelletier, L., Moore, T. R., Roulet, N. T., Garneau, M. and Beaulieu-Audy, V.: Carbon dioxide and methane fluxes of three peatlands in the La Grande Rivière watershed, James Bay lowland, Canada, J. Geophys. Res. Biogeosciences, 112(1), 2007.

Phillips, C. L., Bond-Lamberty, B., Desai, A. R., Lavoie, M., Risk, D., Tang, J., Todd-Brown, K. and Vargas, R.: The value of soil respiration measurements for interpreting and modeling terrestrial carbon cycling, Plant Soil, 413, 1–25, doi:10.1007/s11104-016-3084-x, 2017.

Porporato, A., Daly, E. and Rodriguez-Iturbe, I.: Soil water balance and ecosystem response to climate change, Am. Nat., 164(5), 625–632, doi:10.1086/424970, 2004.

Pouliot, R., Rochefort, L. and Karofeld, E.: Initiation of microtopography in re-vegetated cutover peatlands: Evolution of plant species composition, Appl. Veg. Sci., 15(3), 369–382, doi:10.1111/j.1654-109X.2011.01164.x, 2012.

Rewcastle K E, Moore J A M, Henning J A, Mayes M A, Patterson C M, Wang G, Metcalfe D B, Classen A T.: Investigating drivers of microbial activity and respiration in a forested bog. Pedosphere. 30(1): 135–145. doi:10.1016/S1002-0160(19)60841-6. 2020.

Robroek, B. J. M., Albrecht, R. J. H., Hamard, S., Pulgarin, A., Bragazza, L., Buttler, A. and Jassey, V. E. J.: Peatland vascular plant functional types affect dissolved organic matter chemistry, Plant Soil, 407, 135–143, doi:10.1007/s11104-015-2710-3, 2016.

Roulet, N. T., Lafleur, P. M., Richard, P. J. H., Moore, T. R., Humphreys, E. R. and Bubier, J.: Contemporary carbon balance and late Holocene carbon accumulation in a northern peatland, Glob. Chang. Biol., 13(2), 397–411, doi:10.1111/j.1365-2486.2006.01292.x, 2007.

Ryan, M. G. and Law, B. E.: Interpreting, measuring, and modeling soil respiration, Biogeochemistry, 73(1), 3–27, doi:10.1007/s10533-004-5167-7, 2005.

Schuur, E. A. G. and Trumbore, S. E.: Partitioning sources of soil respiration in boreal black spruce forest using radiocarbon, Glob. Chang. Biol., 12, 165–176, doi:10.1111/j.1365-2486.2005.01066.x, 2006.

Shao, S.: Modeling microbial dynamics and nutrient cycles in ombrotrophic peatlands, McGill University., PHD thesis., 2022.

Shao, S., Wu, J., He, H. and Roulet, N.: Integrating McGill Wetland Model (MWM) with peat cohort tracking and microbial controls, Sci. Total Environ., 806, 151223, doi:10.1016/j.scitotenv.2021.151223, 2022.

St-Hilaire, F., Wu, J., Roulet, N. T., Frolking, S., Lafleur, P. M., Humphreys, E. R. and Arora, V.: McGill wetland model: Evaluation of a peatland carbon simulator developed for global assessments, Biogeosciences Discuss., 5(2), 1689–1725 [online] Available from: https://hal.archives-ouvertes.fr/hal-00297998, 2008.

Strack, M.: Peatlands and Climate Change, edited by Dr. Maria Strack, International Peat Society., 2008.

Sulman, B. N., Desai, A. R., Saliendra, N. Z., Lafleur, P. M., Flanagan, L. B., Sonnentag, O., MacKay, D. S., Barr, A. G. and Van Der Kamp, G.: CO_2 fluxes at northern fens and bogs have opposite responses to inter-annual fluctuations in water table, Geophys. Res. Lett., 37(19), 3–7, doi:10.1029/2010GL044018, 2010.

Tarnocai, C.: The effect of climate change on carbon in Canadian peatlands, Glob. Planet. Change, 53(4), 222–232, doi:10.1016/j.gloplacha.2006.03.012, 2006.

Tarnocai, C., Kettles, I. and Ballard, M.: Peatlands of Canada, Geol. Surv. Canada open file 6561, doi:https://doi.org/10.4095/288786, 2011.

Teklemariam, T. A., Lafleur, P. M., Moore, T. R., Roulet, N. T. and Humphreys, E. R.: The direct and indirect effects of inter-annual meteorological variability on ecosystem carbon dioxide exchange at a temperate ombrotrophic bog, Agric. For. Meteorol., 150(11), 1402–1411, doi:10.1016/j.agrformet.2010.07.002, 2010.

Turetsky, M. R. and Wieder, R. K.: Boreal bog Sphagnum refixes soil-produced and respired $^{14}CO_2$, Ecoscience, 6(4), 587–591, doi:10.1080/11956860.1999.11682559, 1999.

Waddington, J. M., Strack, M. and Greenwood, M. J.: Toward restoring the net carbon sink function of degraded peatlands: Short-term response in CO_2 exchange to ecosystem-scale restoration, J. Geophys. Res., 115, G01008, doi:10.1029/2009JG001090, 2010.

Wang, X., Liu, L., Piao, S., Janssens, I. A., Tang, J., Liu, W., Chi, Y., Wang, J. and Xu, S.: Soil respiration under climate warming: Differential response of heterotrophic and autotrophic respiration, Glob. Chang. Biol., 20(10), 3229–3237, doi:10.1111/gcb.12620, 2014.

Warren, J. M., Jensen, A. M., Ward, E. J., Guha, A., Childs, J., Wullschleger, S. D. and Hanson, P. J.: Divergent species-specific impacts of whole ecosystem warming and elevated CO_2 on vegetation water relations in an ombrotrophic peatland, Glob. Chang. Biol., 27(9), 1820–1835, doi:10.1111/gcb.15543, 2021.

Zeh, L., Theresa Igel, M., Schellekens, J., Limpens, J., Bragazza, L. and Kalbitz, K.: Vascular plants affect properties and decomposition of moss-dominated peat, particularly at elevated temperatures, Biogeosciences, 17(19), 4797–4813, doi:10.5194/bg-17-4797-2020, 2020.

Chapter 4: The role of belowground processes in the respiration dynamics of an ombrotrophic bog

Bridging statement to Chapter 4

Root exudate and nutrient analyses as well as stable and radiocarbon isotopes of CO_2 (gas samples) from the Mer Bleue Bog were conducted in this chapter. These measurements were analysed against the respiration fluxes found in Chapter 3 to explore how the belowground processes in a bog affect the respiration of the shrubs and sedges at the site. We found that the respiration response of the plants to changes in climate is influenced by their different mechanisms of obtaining water and nutrient resources, and the shrubs seem to be more intimately associated with mosses than are sedges, supporting the claim in Chapter 3 that heterotrophic respiration is more related to vegetation dynamics than was previously suggested.

4.1 Abstract

Northern peatlands are globally significant carbon sinks that vary from year-to-year depending on environmental and biogeochemical conditions. These variations are due to changes in primary production and ecosystem respiration. Respiration dynamics are complex, where some plants act to mediate belowground decomposition and support heterotrophic respiration through the presence of mycorrhizal fungi, especially in sedge dominated peatlands. Currently, the role of belowground processes in peatlands, especially those that pertain to the rhizosphere, are not well documented. The objective of our study was to explore how belowground processes control respiration dynamics in an ombrotrophic bog in eastern Ontario (Mer Bleue). Root exudate and nutrient analyses were conducted to determine the effect of ecosystem nutrition on respiration, and carbon isotope analyses of CO_2 were conducted to determine the source of respired carbon. We found that the respiration response of the shrubs and sedges at the site to changes in climate is influenced by their different mechanisms of obtaining water and nutrient resources, and shrubs seem to be more intimately associated with mosses than are sedges. Our study reveals the importance of belowground processes to our understanding of peatland respiration dynamics.

4.2 Introduction

Northern peatlands play a significant role in the global carbon (C) cycle as long-term sinks of C since dead plant material in undisturbed peatlands does not decompose as rapidly as it accumulates as peat. For example, peatlands cover 12% of Canada's terrestrial surface (Tarnocai et al., 2011) yet contain ~50% of the organic carbon stored in Canadian soils (Tarnocai,, 2006). Following the last glaciation, peatlands have accumulated C at an average rate of 23-26 g m^{-2} yr^{-1} (Charman et al., 2013; Loisel et al., 2014). However, peatlands can be a source or a sink of carbon depending on the environmental and biogeochemical conditions of a given year, such as temperature and nutrient stoichiometry (Dorrepaal et al., 2009; Roulet et al., 2007; Straková et al., 2012).

Ecosystem respiration (ER) is composed of both an autotrophic component, that consists of respiration by plant parts, and a heterotrophic component, that consists of respiration by soil microorganisms (e.g., bacteria and fungi). However, respiration dynamics are complex, where different outcomes of a peatland's C cycle following a disturbance, such as a change in climate, could occur depending on which respiration source drives the response. For example, a positive feedback to climate change can occur if heterotrophic respiration (HR) of old soil C drives the increase, because greater temperatures would lead to the system losing C to the atmosphere that had been stored for hundreds to thousands of years. A negative feedback to climate change can occur if autotrophic respiration (AR) drives the increase, which is linked to enhanced primary productivity that fixes more C (Hicks Pries et al., 2013). Both peatland models and field measurements do not tease out these complexities in respiration dynamics very well though, which may lead to an overestimation of C sequestration due to unexpected allocations of C to labile pools with different turnover rates (Hungate et al., 1997; Phillips et al., 2017).

The role of belowground processes (e.g., root exudation and nutrient dynamics) in respiration dynamics is also not well documented. Although most of the variability in sink strength comes from changes in gross primary production (GPP) and AR (Blodau, 2002; Heimann and Reichstein,, 2008), the dynamics of HR is not straightforward. HR was often considered a bulk variable that is correlated with environmental and substrate variables (Minkkinen et al., 2007; St-Hilaire et al., 2008) but has recently been shown to be more intimately linked to vegetation dynamics (e.g. root dynamics and productivity) than previously thought. For example, Jacoby et al. (2017) suggest that aboveground respiration and productivity of plants are influenced by microbial - soil - plant interactions. Lin et al. (2014) also found that a plant's response to climate change is dependent on the carbon use efficiency and that shifts in microbial community composition because of a change in temperature could potentially counteract an accelerated loss of carbon. Similarly, Fan et al. (2013) suggest that long-term exposure to warmer conditions may lead to an increase in HR outpacing an increase in carbon input, and that C sequestration will weaken, which they attribute to root-soil interactions and a change in the transport of labile C. Some plant functional types may also fix the respired CO_2 from the vegetation that surrounds them rather than using atmospheric CO_2 directly in the process of photosynthesis, including *Sphagnum* mosses (Smolders et al., 2001; Turetsky and Wieder, 1999). Here, the rate of litter supply is related to plant production through root-soil interactions and belowground processes rather than through plant biomass (Gavazov et al., 2018). Similarly, Basiliko et al. (2012) highlight the difficulties in separating root respiration from HR.

Ecosystem nutrition and resource availability from various depths in the subsoil are also important factors in controlling the variability in respiration and its components (Hungate et al., 1997; Lin et al., 2014). A plant's metabolism and its allocation of carbon can be just as important though. Juszczak et al. (2013) found that the temperature response of HR depends on the chemical composition of substrates and nutrient availability, whereas Bubier et al. (2007) found that a change in nutrient availability led to a change in plant production and productivity, which affected the peatland’s ability to sequester CO_2. Similarly, Keiser et al. (2019) found that substrate type was the controlling factor of increased respiration in most cases with increasing temperatures, due to a greater photosynthesis allowing for increased decomposition and leaching of root exudates to belowground decomposers. Evidently, belowground processes, such as nutrient availability and root exudation, play an important role in better understanding peatland plant functioning and respiration dynamics (Ryan and Law, 2005). They are more connected to aboveground production than just the slow decomposition of dead organic matter, especially when root dynamics are considered (Van Hees et al., 2005). This has been seen in sedge dominated or forested peatlands (Järveoja et al., 2018; Kurbatova et al., 2013; Wang et al., 2014) and in permafrost ecosystems (Crow and Wieder, 2005; Hicks Pries et al., 2015), but it is unknown whether this same degree of vegetation influence on HR exists in shrub-dominated peatlands.

Thus, the objective of our study was to determine whether the woody shrubs at Mer Bleue, an ombrotrophic bog in eastern Ontario, also mediate belowground processes as has been found with sedges. Specifically, we explored the influence of vegetation dynamics on respiration using a variety of methods, including measurements of both stable and radio isotopes of carbon ($\delta^{13}C$ and $\Delta^{14}C$) in respired CO_2, as well as an in-depth exploration of root exudate and nutrient dynamics. Our hypotheses are two-fold: 1) the presence of roots from woody vascular plants prime the decomposition of organic matter; and 2) woody shrubs are more intimately associated with the mosses and the peat surrounding them than are sedges. Conducting analyses of both $\delta^{13}C$ and $\Delta^{14}C$ will not only supplement our understanding of respiration dynamics at the site, but they will also provide great insight into how the different plant functional types allocate carbon. The results from the root and pore water measurements will provide an indication of the biogeochemical factor(s) that best describe changes in respiration influenced by ecosystem nutrition, such as substrate and nutrient availability. Overall, this project will help improve our understanding of peatland carbon cycling, as well as peatland plant-functioning with changes in climate.

4.3 Methods

4.3.1 Study site

Mer Bleue is a 28 km^2 ombrotrophic raised bog located near Ottawa, Ontario in Canada (45.41°N, 75.52°W). The bog is situated in a cool continental climate, with a mean annual temperature of 6.4 °C ranging from -10.3 °C in January to 21.0 °C in July. Mean annual precipitation is 943 mm, 350 mm of which falls from May to August, with a mean annual snowfall of 223 cm (Environment Canada; 1981–2010 climate normals). Peat depth at the centre of the bog reaches about 5 to 6 m and gradually gets shallower as you move outwards, ending at < 0.3 m deep at the edge of the peatland. Bog development began 7100–6800 years ago, and it has a hummock-lawn microtopography (Roulet et al., 2007). The surface of the bog is covered by *Sphagnum* mosses (*Sphagnum angustifolium, Sphagnum capillifolium, Sphagnum fallax, Sphagnum magellanicum*), and the vascular plant cover is dominated by low growing ericaceous evergreen shrubs, making up about 80% of the areal coverage (mainly *Chamaedaphne calyculata,* with some *Ledum groenlandicum, Rhododendron groenlandicum,* and *Kalmia angustifolia*), with an occasional mix of sedges (*Eriophorum vaginatum*) that make up about 3-5% of the areal coverage (Humphreys et al., 2014; Lai et al., 2014).

The sedges have roots that expand vertically into the peat, sometimes up to 50 cm depth, so they can tap into water and nutrient resources at greater depths even during the drier parts of the season (Murphy et al., 2009; Pouliot et al., 2012). In contrast, the shrubs allocate much of their biomass to belowground roots, which tend to spread out laterally (within the first 15-20 cm) rather than vertically (Iversen et al., 2018), and to smaller needle like stems to make use of whatever water is available to the plants in the soil and the nutrients within (Bonan, 2008; Murphy and Moore, 2010). So, the water and nutrient resources available to shrubs are limited to what can be obtained by the plants near the surface.

The *Sphagnum* mosses are mixed with the other vegetation, so finding plots of just *Sphagnum* mosses was impossible. Therefore, the plots as described below, contained either *Eriophorum* and *Sphagnum* (which we called the sedge section) or *Chamaedaphne* and *Sphagnum* (which we called the shrub section).

4.3.2 Chamber setup (CO_2 fluxes):

We conducted CO_2 measurements at the plot level using manual chamber methods. Nine collars represented the shrub section, and nine collars represented the sedge section. The collars were sampled on a weekly to bi-weekly basis, weather depending, from May through September in the 2018 and 2019 growing seasons. Fluxes were obtained using a transparent static chamber (diameter of 26 cm and height of 50 cm) placed and sealed over permanent PVC collars inserted into the peat to a depth of 15 cm at each sampling location. The chamber contained a fan to allow for adequate mixing, and a cooling system was used to maintain ambient temperature conditions (Waddington et al., 2010).

In 2018, the CO_2 concentrations were measured every 5 seconds over a period of 5 minutes, using an ultra-portable greenhouse gas analyser (Los Gatos Research (LGR), San Jose, California). In 2019, the site was too wet to safely carry in the LGR, so a smaller portable CO_2 gas analyser (EGM-4, PP systems, Amesbury, Massachusetts) was used instead. CO_2 concentrations were measured every 10 seconds for the first minute, then every 30 seconds after that, for a total of 5 minutes.

For each collar, a period of sampling under dark conditions was conducted using a static chamber covered by an opaque bag. This represented the ecosystem respiration (ER) for that plot. In the spring of both 2018 and 2019, some of the plots were manipulated to reveal the influence of vegetation (Table 4.1). In each section, 3 plots were designated as reference plots (with full vegetation), representing ER, 3 plots had all the aboveground vegetation removed, and 3 plots had only the mosses removed (i.e., only the vascular plants remained). We assumed that the plots where all the aboveground vegetation was removed represented HR, with the acknowledgment that there may have been a residual component of AR from the decomposing roots. In the plots representing no vegetation, a root exclosure was set up and a layer of green mesh placed on top to minimize any confounding effects of temperature and moisture. We then derived AR as ER – HR. The resulting fluxes of respiration and its components are reported by Rankin et al. (2022).

Table 4.1 Manual chamber set up with descriptions of manipulations and reported measurements. All values reported are directly measured or derived from dark respiration measurements.

Measurement	**Plot Manipulation**	**Measurement method (Direct - DT, Derived - DV)**
ER / reference plots	Full vegetation: shrub + mosses and sedge + mosses	DT; average of triplicates
HR / clipped plots	All aboveground vegetation removed; both shrub and sedge sections	DT; average of triplicates
“Shrub Only” plots	All mosses removed, only shrubs remain	DT; average of triplicates
“Sedge Only” plots	All mosses removed, only sedges remain	DT; average of triplicates
“Moss only” plots	Only mosses remain, both shrub and sedge sections	DT; only based on one plot
AR	N/A	DV; ER - HR of averaged triplicates

4.3.3 Quality control

Statistical analyses showed that the fluxes from the different manipulation treatments were significantly different (using repeated measures ANOVA) for both the sedges (F = 24.4, Pr = 0.00039) and the shrubs (F = 6.045, Pr = 0.0077) in 2018 as well as the sedges (F = 4.9, Pr = 0.018) and the shrubs (F = 4.57, Pr = 0.021) in 2019 (Rankin et al., 2022). Notably, a different greenhouse gas analyser was used in 2018 than in 2019, but with the same manual chamber method: both gas analysers were calibrated beforehand, and measurements started when stabilized ambient concentrations of CO_2 were reached. Statistical analysis showed that there was no significant difference between the fluxes measured with the two gas analysers (T = 1.59, P-value = 0.13). In both years, regression equations of concentrations over time were used to calculate a flux for CO_2 for each 5-minute period. Only regressions with R^2 values over 0.8 were kept, which resulted in less than 10% of the values being removed.

4.3.4 Environmental variables

At the time of respiration flux sampling, water table (WT) depth was determined manually using a permanently installed perforated PVC beside each set of 3 collars. Soil temperatures were obtained using a temperature probe inserted to depths of 0, 5 and 10 cm, roughly in the same location each time just outside of each collar. Daily air temperatures were obtained from the Ottawa International Airport weather station located about 18 km southwest of the site (Environment Canada, 2020).

4.3.5 Nutrient and root exudate analyses

Porewater samples were obtained at 20, 45, and 60 cm depths for each of the set of three collars in both 2018 and 2019 growing seasons. We attempted to obtain porewater samples at 75 cm depth as well, but unfortunately, the peat was very compacted, and we were only able to obtain 2 samples at this depth in the shrub section in 2018. So, additional samples were taken in August of 2020 at 20, 45, 60 and 75 cm depths in both sections. Additionally, some destructive sampling of roots from the two species were collected periodically through the growing seasons, wrapped in mosses from the site to keep the roots moist with field-like conditions, and placed in deionized water for 4 hours, as explained in Edwards et al. (2018). The liquid solution obtained from the roots and the porewater samples were then analysed for nutrients (inorganic phosphate, PO_4 and sulphate, SO_4) as well as low molecular weight compounds (lactate, acetate, citric acid, and pyruvate), using high pressure ion chromatography (Dionex ICS-6000 HPIC system, Thermo Fisher Scientific Inc., USA) at Lund University in Sweden.

Further analyses of inorganic PO_4 concentrations were conducted on the porewater samples from 2018 and 2019 as well as on additional root *and* porewater samples collected in August of 2020, using malachite green (Ohno and Zibilske, 1991) on a spectrophotometer at McGill University (Epoch Microplate Spectrophotometer, BioTek Instruments Inc., Winooski, Vermont). This allowed for a more in-depth, and a more accurate, analysis of PO_4 concentrations.

All values were determined based on a set of standard curves with R^2 values of at least 0.95 for quality control purposes. Further, deionized water samples were also analysed for nutrient and root exudate concentrations as a control. Only the concentration values that were statistically higher than those found in the deionized water samples were reported in this study.

4.3.6 Stable and radiocarbon isotopes of C

We sampled $\delta^{13}C$ and $\Delta^{14}C$ from respired CO_2 at the plot level using manual chamber methods and a soil corer, similar to the methods explained in (Hicks Pries et al., 2013). Measures of $\delta^{13}C$ values were obtained in 2019 as well as in 2020 to determine whether our observations were replicable on an interannual basis. $\Delta^{14}C$ was measured in 2018 only, due to the cost of the analyses.

Peat samples were obtained using a soil corer from 25 cm and 80 cm depth under the three dominant vegetation types (sedges, shrubs, and mosses) in August of 2019 and 2020, placed into mason jars and incubated for 2 hours at room temperature (allowing CO_2 gas to build up inside the jars). The CO_2 gas obtained through the incubations was placed in previously evacuated 12 mL exetainers (2 vials were used for each sample containing about 40 mL total when the exetainers are over-pressurized) and run within 24 hours through a cavity ringdown laser spectroscopy isotope analyser (G2201-I Isotope Analyzer, Picarro, Santa Clara, CA), which measures $\delta^{13}C$ of CO_2 in the gas sample. The Picarro was calibrated using CO_2 cylinders with known isotopic composition (Christiansen et al., 2015). For quality control purposes, a standard gas with a known $\delta^{13}C$ value of -28.5 ‰ was put through the Picarro each time the machine was used, and three readings were conducted that measured ~ -26 +/- 0.5 ‰ every time with CO_2 concentrations ~ 850 ppm. Air samples from the room were also inserted into the Picarro each time the machine was used, and three readings were conducted that measured ~ -11.5 +/- 0.5 ‰ every time with CO_2 concentrations ~ 450 ppm.

Gas samples for $\delta^{13}C$ signatures were also obtained using the manual chamber. Sample periods were run for 30 minutes, with CO_2 concentrations obtained using a portable CO_2 gas analyser (EGM-4, PP systems, Amesbury, Massachussetts), and gas samples obtained using syringes every 6 minutes. The gas samples were placed in previously evacuated 12 mL exetainers (2 vials were used for each sample containing about 40 mL total when the exetainers are over-pressurized) and analysed within 24 hours in the lab for $\delta^{13}C$ signatures using the Picarro mass spectrometer.

For all gas samples, $\delta^{13}C$ was plotted against $1/[CO_2]$, which is commonly known as a Keeling curve, where a linear regression curve is fitted to the data, and the intercept of the best-fit line represents the $\delta^{13}C$ of the source (Pataki et al., 2003). All Keeling curves had R^2 values over 0.90, thus all values were included in the results section below, although some Keeling curves were derived from only 5 sample points instead of 6, where a sample point was removed due to the seal on the exetainer being compromised.

$\Delta^{14}C$ for the reference and clipped plots were measured in August 2018 as described by Hardie et al. (2009). Similar to the gas samples obtained for the $\delta^{13}C$ analyses, chambers were placed over the reference and clipped plots for an hour each to allow enough CO_2 gas to build up. Roughly 800 mL of gas was extracted from each plot and placed in previously evacuated jars. Peat samples were obtained using a soil corer under both vascular plant species and separated in two sections: the first from the surface to 25 cm depth, and the second from 25-50 cm depth. The peat samples were incubated, and CO_2 allowed to build up in the mason jars. 800 mL of gas was obtained from the mason jars and placed in previously evacuated jars.

All the gas samples were sent to the University of Ottawa within 48 hours to be processed for $\Delta^{14}C$ analysis. Samples were purified cryogenically, reduced to graphite and then analysed (Crann et al., 2017; St-Jean et al., 2017). Only samples with a yield above 0.15 mg C after processing were kept. Small yields were inevitable given the finite amount of gas extractable from the chamber without inducing a suction, thus only 75% of the samples were analyzed for $\Delta^{14}C$, and of those samples some resulted in relatively large analytical uncertainties.

Radiocarbon analyses were performed using an Accelerator Mass Spectrometer (Multi-element 3MV Tandem Accelerator, AEL AMS Laboratory, University of Ottawa, Ontario). $^{12,13,14}C+3$ ions were measured at 2.5 MV terminal voltage with Ar stripping. The fraction of modern carbon, $F^{14}C$, was calculated according to (Reimer et al., 2013) as the ratio of the sample $^{14}C/^{12}C$ to the standard $^{14}C/^{12}C$ (Ox-II) measured in the same data block. $^{14}C/^{12}C$ ratios were background-corrected and the result was corrected for spectrometer and preparation fractionation using the AMS measured $^{13}C/^{12}C$ ratio and is normalized to $\delta^{13}C$ (PDB). $D^{14}C$ (defined as per mil Depletion or Enrichment Relative to Standard Normalized for Isotope Fractionation) was calculated as $(F^{14}C - 1) \cdot 1000$.

4.4 Results

4.4.1 Environmental variables and CO_2 fluxes

The growing season of 2018 was characterised by variable (more sporadic) weather conditions based on the manual measurements of WT depth and soil temperatures at 10 cm depth (Soil T), and the mean daily air temperatures (Air T) taken from the weather station nearby (Figure 4.1a; Environment Canada 2019). Air temperatures ranged from 21 °C to 35 °C, soil temperatures (at 10cm depth) ranged between 12 °C and 27 °C, and WT depth ranged between 23 cm and 47 cm depth (June – August mean WT = 34 cm depth). It was an anomalously hot year compared to the normal averages, where the mean annual temperature for July, for example, is 21.0 °C (Environment Canada; 1981–2010 climate normals). There was also a dryer start to the growing season than normal for June, and July, but generally a wetter August and September than normal

(Teklemariam et al., 2010), with a significant rise in WT depth following a series of large rain events.

In contrast, the growing season of 2019 had less variable weather than 2018, despite a greater range in WT depth. It was wetter in May and June compared to the normal averages and consistently became warmer and drier as the growing season progressed (Figure 4.1b), with WT depth similar to normal averages in July and August (Teklemariam et al., 2010). Mean daily air temperatures (23 °C to 31 °C) and soil temperatures at 10 cm depth (10 °C and 18 °C) had a much smaller range than in 2018, and WT depth ranged between 20 cm and 55 cm depth (May – August mean WT = 36.5 cm depth).

Additional samples were taken in late August instead of mid-July in 2020, which would have been peak growing season and the preferable time to obtain samples, but our field campaign was delayed because of COVID restrictions. At that point, temperatures had already started to cool down, with an average of 19 °C, and there were sporadic rain events much like the growing season of 2018 (Environment Canada Historical Weather Data).

Directly measured dark respiration (HR) in 2018 averaged 195 ± 81 mg CO_2 m^{-2} hr^{-1}, 414 ± 154 mg CO_2 m^{-2} hr^{-1} for ER, and 187 ± 134 mg CO_2 m^{-2} hr^{-1} for AR in the shrubs (Figure 4.2a). CO_2 fluxes from the sedges in 2018 averaged 240 ± 25 mg CO_2 m^{-2} hr^{-1} for HR, 625 ± 131 mg CO_2 m^{-2} hr^{-1} for ER, and 385 ± 127 mg CO_2 m^{-2} hr^{-1} for AR (Figure 4.2b). In contrast, CO_2 flux measurements from 2019 show that the shrubs averaged 309 ± 123 mg CO_2 m^{-2} hr^{-1} for HR, 611 ± 194 mg CO_2 m^{-2} hr^{-1} for ER, and 378 ± 164 mg CO_2 m^{-2} hr^{-1} for AR (Figure 4.2c). CO_2 fluxes from the sedges averaged 426 ± 178 mg CO_2 m^{-2} hr^{-1} for HR, 729 ± 218 mg CO_2 m^{-2} hr^{-1} for ER, and 343 ± 142 mg CO_2 m^{-2} hr^{-1} for AR (Figure 4.2d).

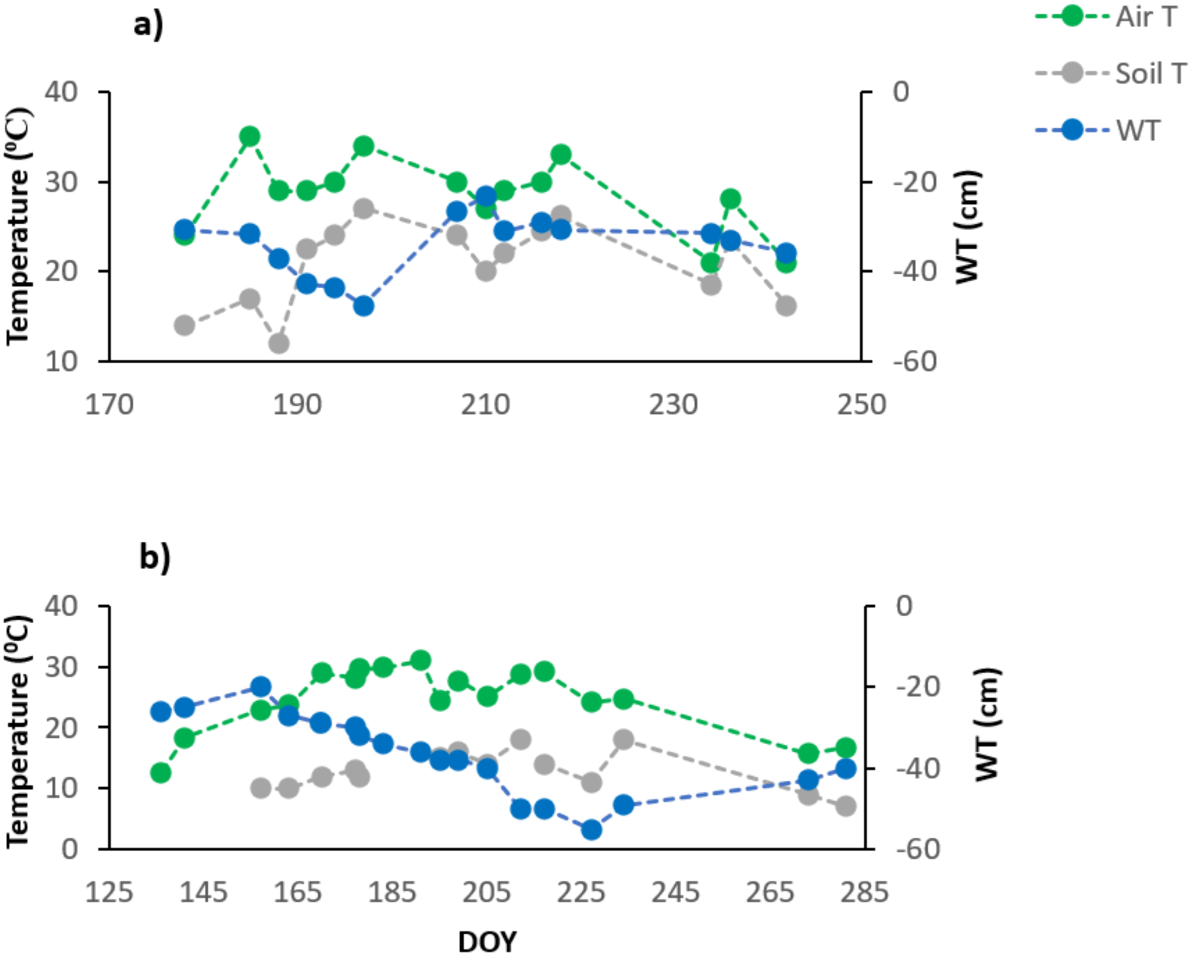


Figure 4.1 Environmental variables taken on the same day as flux measurements for the growing seasons of a) 2018 and b) 2019. Soil T is soil temperature at 10 cm depth, taken manually along with water table (WT) depth, while the mean daily air temperatures (Air T) were taken from the weather station nearby.

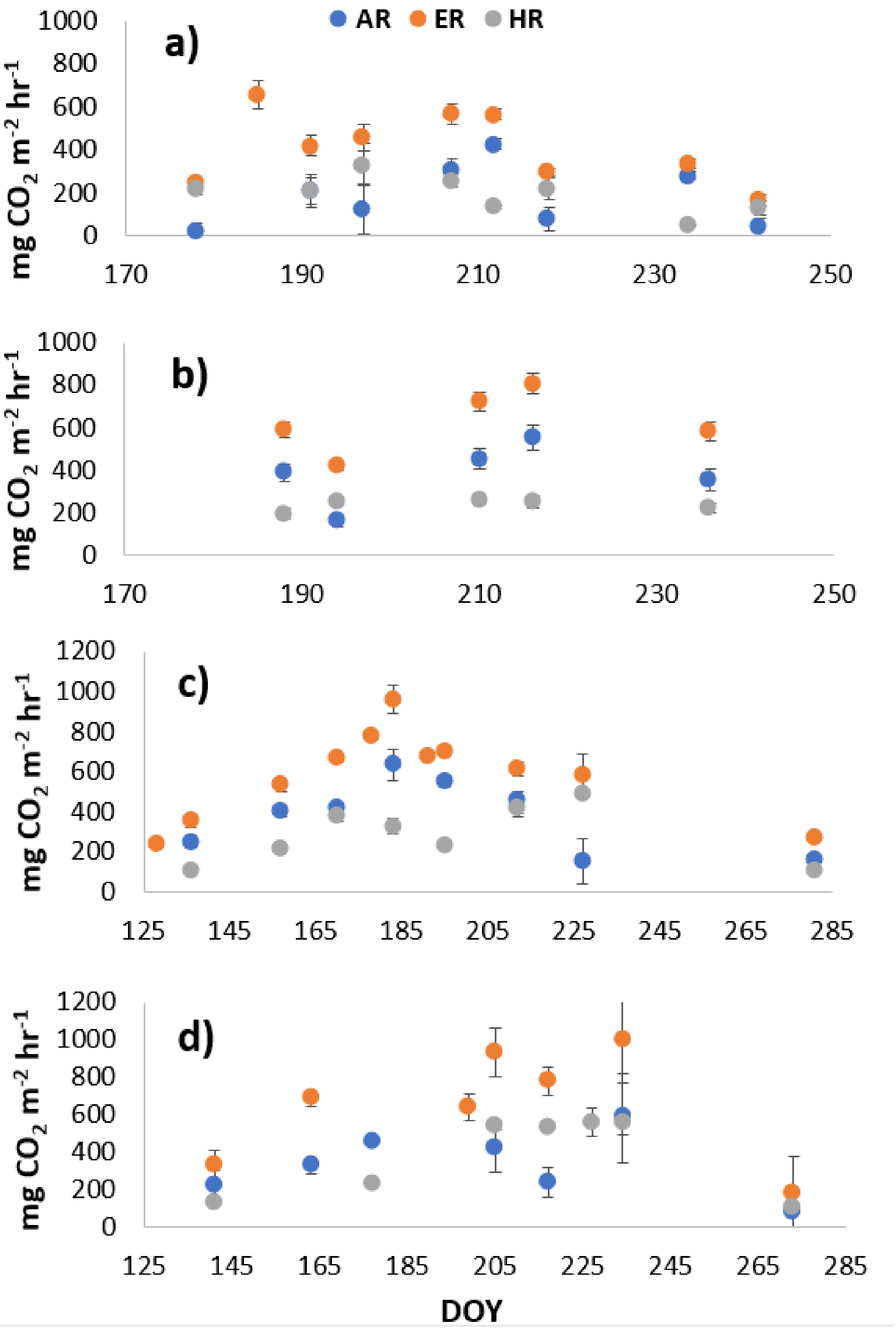


Figure 4.2 CO$_2$ fluxes from the a) shrub plots and b) sedge plots in 2018, and from the c) shrub plots and d) sedge plots in 2019.

4.4.2 Root exudate and nutrient analyses

The root exudates of the shrubs show high concentrations of citric acid and pyruvate, especially towards the end of the growing season in 2018 when water tables were closer to the surface (Figure 4.3a). These organic acids were also seen in higher abundance from the roots of the shrubs in 2019 when water tables were closer to the surface (Figure 4.3b). No significant concentrations of pyruvate or citric acid were found in the pore water nor from the roots of the sedges. In both the 2018 and 2019 growing seasons, an increase in citric acid and pyruvate was associated with an increase in AR (Figures 4.2 and 4.3).

Lactate and acetate both increased towards the end of the growing season in 2018 as well, but both were present in higher abundance in the root exudates of the shrubs (Figure 4.4 a, b), with a similar trend to citric acid and pyruvate. In 2019, on the other hand, lactate and acetate concentrations were highest towards the beginning of the season, and again found in greater abundance in the root exudates of the shrubs, but a significant amount was found in the sedge roots (Figure 4.4 c, d). Changes in respiration associated with changes in lactate and acetate are similar to those found for citric acid and pyruvate; In the 2018 growing season, an increase in lactate and acetate was associated with an increase in AR (Figures 4.2 and 4.4). For example, a small jump from 80 mg CO_2 $m^{-2}hr^{-1}$ in AR from the shrubs to ~ 335 mg CO_2 $m^{-2}hr^{-1}$ was found with an increase of 50 µmol/L in lactate concentrations and an increase of 80 µmol/L in acetate concentrations during the time when there was a large rain event in early August (Environment Canada, 2019).

The root exudates from the sedges, on the other hand, did not contain any significant amount of lactate and acetate concentrations, but rather, they showed high concentrations (> 50 µmol/L) of both inorganic sulphate and inorganic phosphate (SO_4 and PO_4), once again trending upward toward the end of the growing season in 2018 (Figure 4.5a). The growing season of 2019 also showed high concentrations of PO_4 and SO_4 exuded from the roots of the sedges (> 100 µmol/L), but highest concentrations were found in May and August and no temporal trend was observed (Figure 4.5b). Neither growing season showed statistically significant nutrient concentrations in the root exudates of the shrubs. Some PO_4 and SO_4 were found at times in the pore water, but very sporadically and mostly below the root zone (not shown). However, a re-analysis conducted in 2020 of the 2018 and 2019 pore water samples suggests a segregation of higher PO_4 concentrations around 60 cm depth, with values ranging from 7 to 12 µmol/L in 2018 and from 4 to 7 µmol/L in 2019. In 2019, reanalysed values were also between 6.5 and 13 µmol/L at 45 cm depth in September (which were samples taken after the analyses completed in Sweden). Samples from August 2020 showed even higher concentrations of PO_4 at 60 cm depth between 33 and 50 µmol/L (Figure 4.6).

AR was influenced by nutrient concentrations in both 2018 and 2019 growing seasons, where higher concentrations of PO_4 from the sedge roots were, at times, associated with increased respiration from the sedge plots. However, HR was also influenced by nutrient concentrations in 2019. For example, an increase in PO_4 concentration between mid-July and the beginning of August 2019 (~ 60 µmol/L) was associated with a jump in HR from 228 mg CO_2 $m^{-2}hr^{-1}$ to 547 mg CO_2 $m^{-2}hr^{-1}$, but a decrease of ~ 40 µmol/L in PO_4 concentrations directly after this was associated with a decrease in AR from 420 mg CO_2 $m^{-2}hr^{-1}$ to 240 mg CO_2 $m^{-2}hr^{-1}$.

We found spatial variability in PO_4 concentrations from the sedge roots as well (Figure 4.7). In 2018, the greatest PO_4 concentrations were found in the clipped plots and those where the mosses were removed, while the reference plots showed relatively low values. In contrast, the growing season of 2019 showed higher values towards the beginning of the growing season also from the manipulated plots, but the high values towards the end of the growing season in both 2019 were from the reference plots. Results from the extended nutrient analyses from August 2020 support the finding of high PO_4 concentrations extracted from the roots of the sedges (ranging between 29 and 45 µmol/L) and not as much from the roots of the shrubs (ranging between 3.5 and 9 µmol/L). Like the end of the growing season in 2019, samples from the sedge roots showed highest PO_4 concentrations from the reference plots (45 µmol/L), with slightly lower concentrations from the manipulated plots (35 and 29 µmol/L from the clipped and sedge only plots, respectively).

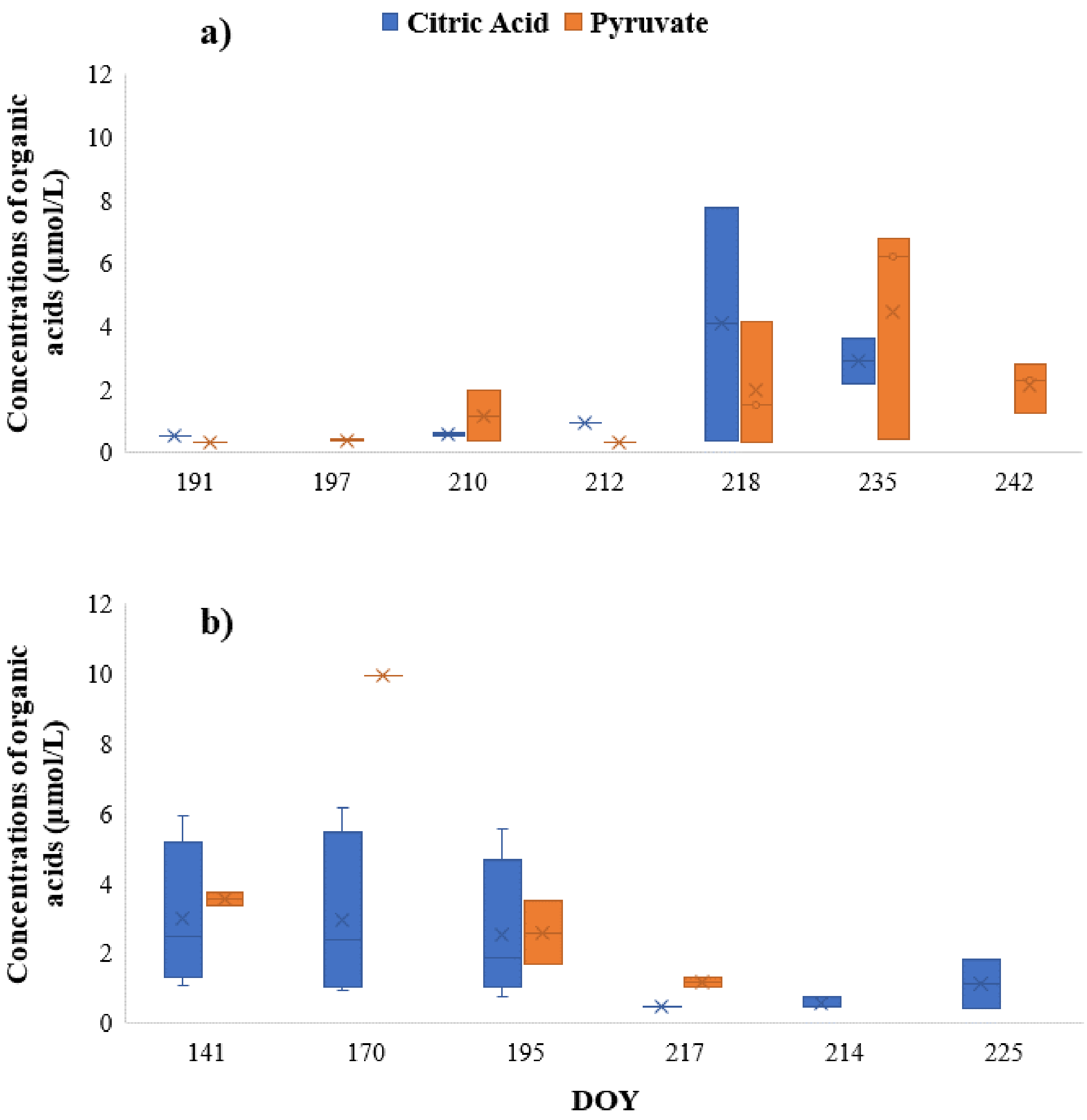


Figure 4.3 Concentrations (µmol/L) of citric acid and pyruvate from the roots of the shrubs in a) 2018 and b) 2019

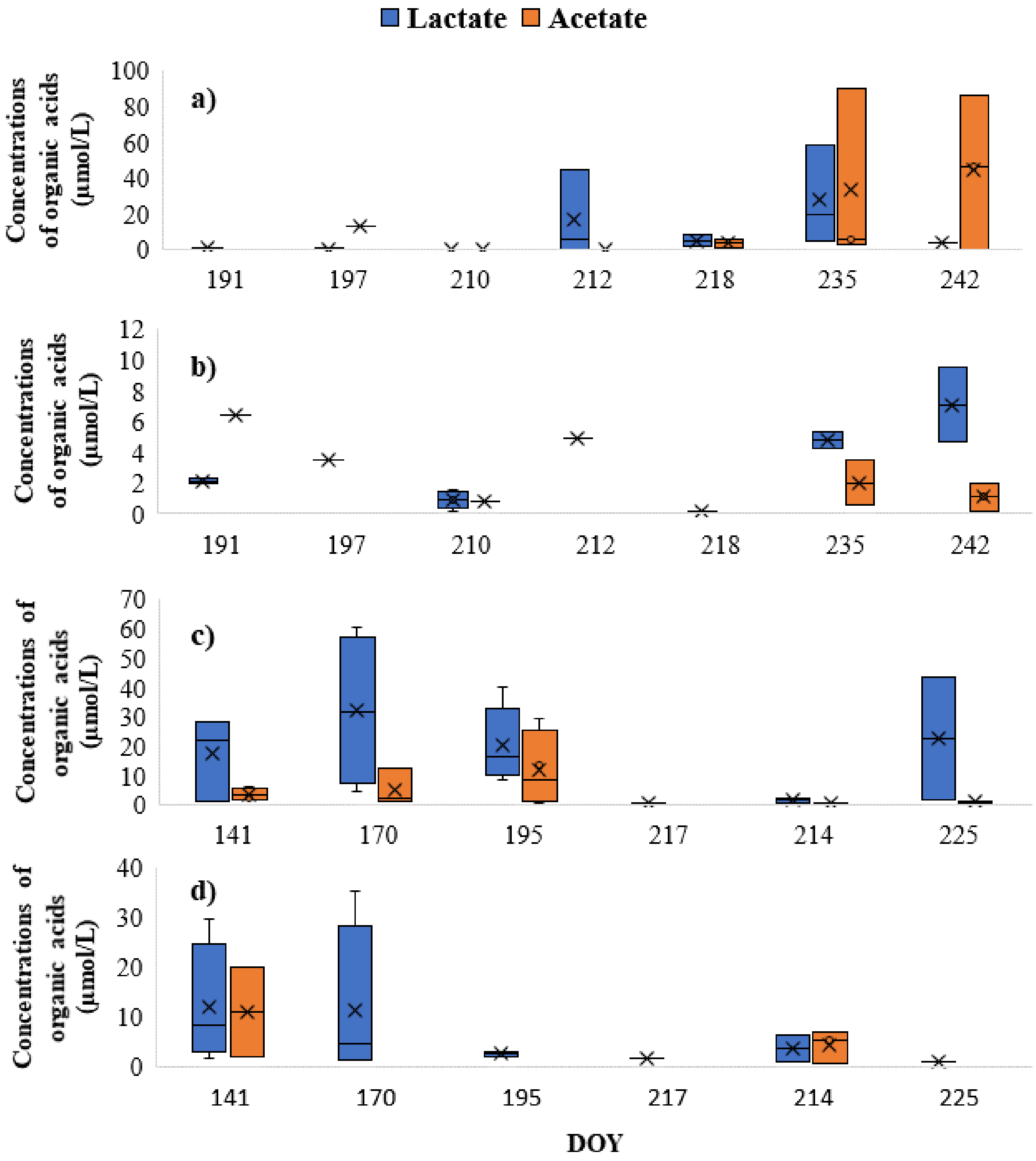


Figure 4.4 Lactate and acetate concentrations (µmol/L) from the roots of a) the shrubs in 2018, b) the sedges in 2018, c) the shrubs in 2019, and d) the sedges in 2019.

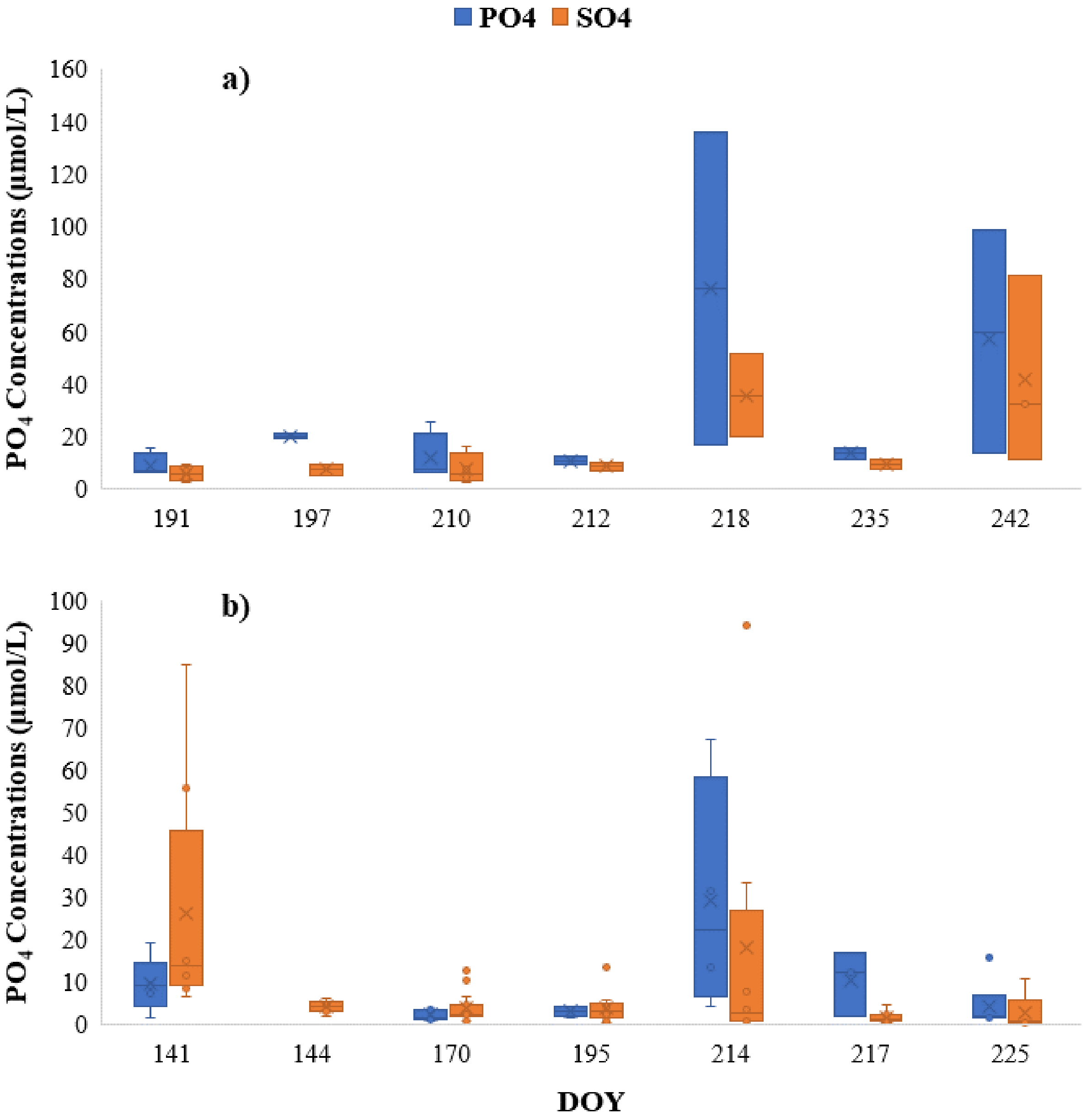


Figure 4.5 PO_4 and SO_4 concentrations (µmol/L) from the roots of the sedges in a) 2018 and b) 2019.

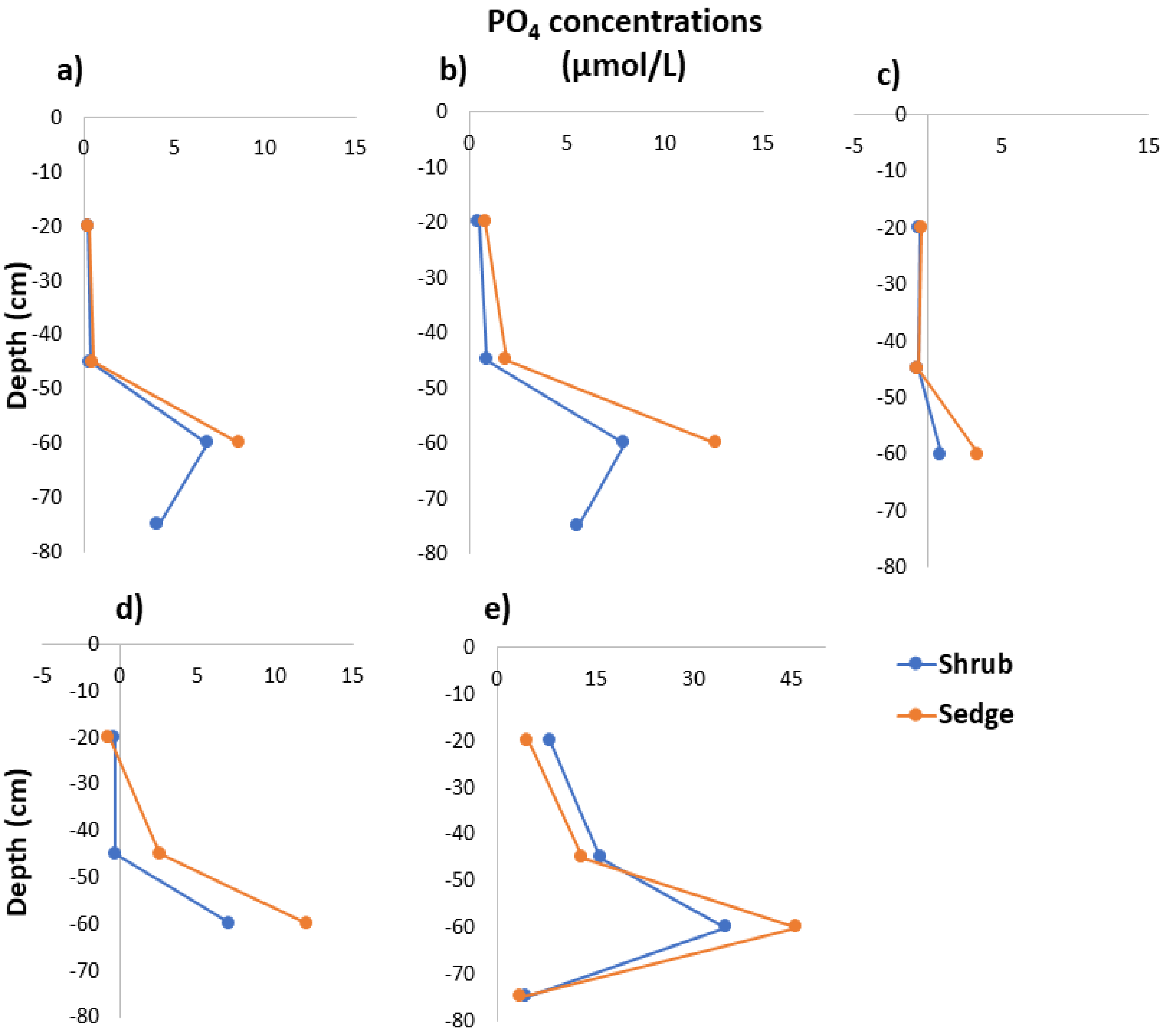


Figure 4.6 Depth profiles of pore water PO$_4$ concentrations at a) the end of July and b) end of August in 2018, at c) the middle of June and d) beginning of August in 2019, and at e) the end of August 2020.

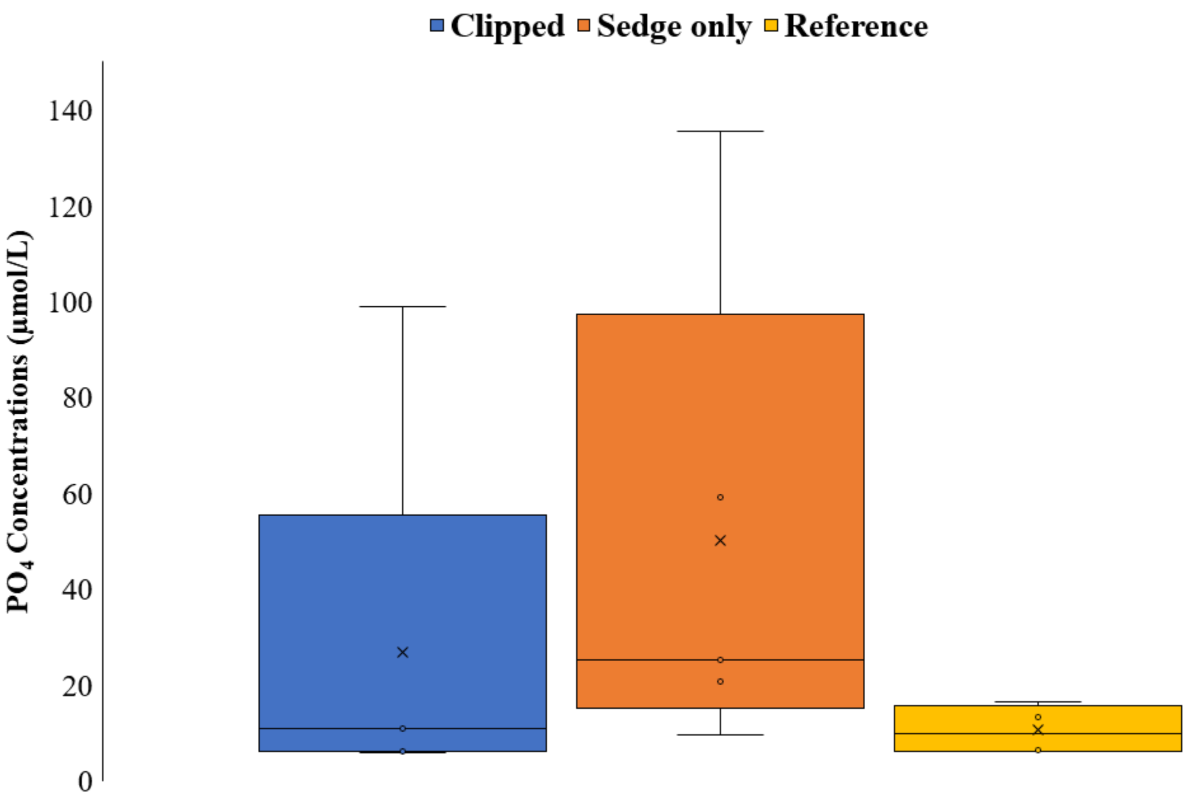


Figure 4.7 PO_4 concentrations extracted from the sedge roots in 2018 by manipulation type.

4.4.3 Stable and radiocarbon isotopes of C

We found that $\delta^{13}C$-CO_2 values were not distinguishable between the reference plots of the shrubs and sedges, nor between the clipped plots (+/- 1‰). However, the CO_2 in the moss plot was relatively depleted in ^{13}C compared to the vascular plant plots (~ 4 ‰ difference). We also found a greater difference in $\delta^{13}C$ values between the reference plots and the shrub only plots (reference plots ~ 3 ‰ more depleted), despite the smaller difference in $\delta^{13}C$ values between the mosses and the vascular plants in this section (Figure 4.8). Furthermore, we found higher $\delta^{13}C$ values with depth for both plant types and in both growing seasons (i.e., more enriched values at 80 cm depth than at 25 cm depth), with a greater depth gradient in 2019 than

2020 for both plant types, but also with a consistently greater enrichment in the sedge section than the shrub section (Figure 4.8). The $\delta^{13}C$ values between the two years are generally within the analytical error of 1 ‰ for most of the plots, except the difference in $\delta^{13}C$ values at 80 cm depth in the shrub section, where the $\delta^{13}C$ values in 2020 was ~ 5 ‰ more depleted than in 2019.

For both plant types, ^{14}C-CO_2 in the reference plots was similar to the amount of ^{14}C-CO_2 in the ambient samples and that found in the peat at 0- 25 cm depth (~ 0 ‰). ^{14}C-CO_2 in the clipped plots was higher than in the reference plots and ambient samples (~25 ‰) and similar to that found in the peat at 25-50 cm depth, for both plant types as well (Figure 4.9).

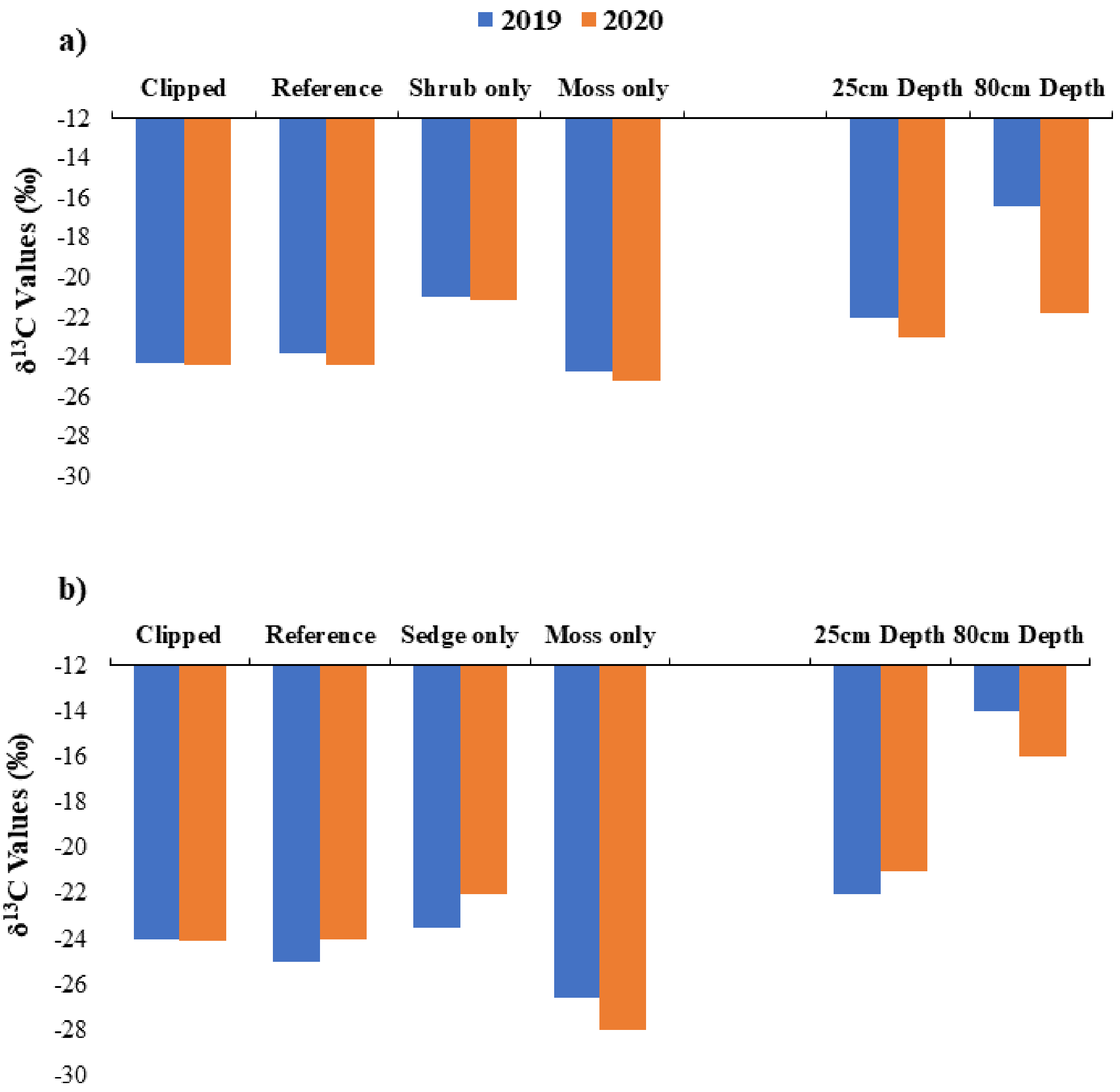


Figure 4.8 δ^{13}C values from the various plots in the a) shrub and b) sedge sections (all values have an analytical error of +/- 1 ‰). The cluster of values on the left side of the graphs correspond to the δ^{13}C values in the manual chamber plots, and the cluster of values on the right side of graphs correspond to the incubations of peat at 25 and 80 cm depths.

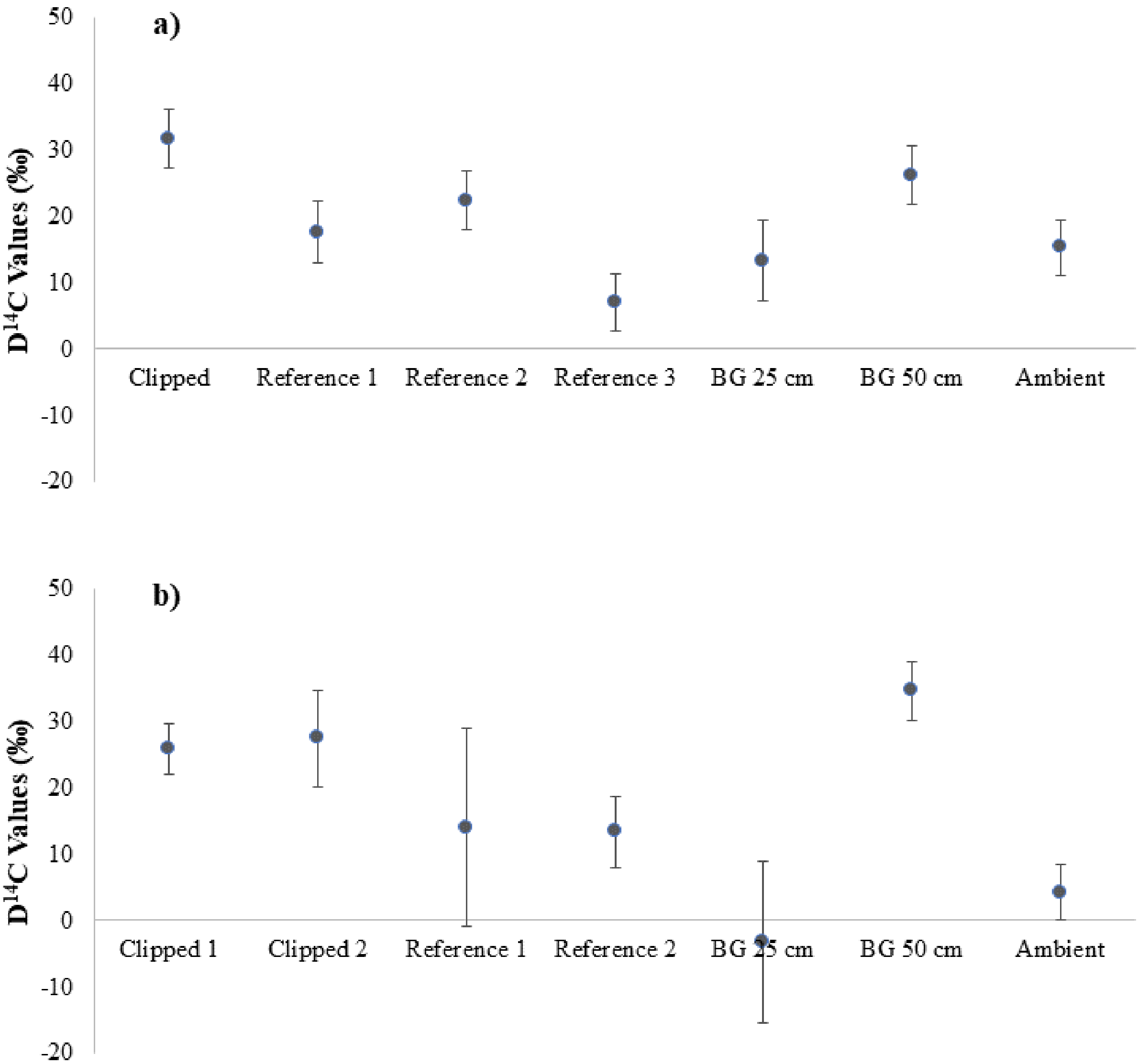


Figure 4.9 $D^{14}C$ for plots in the a) shrub and b) sedge in 2018. Reported as ‰ enrichment or depletion relative to standard normalized for isotopic fractionation.

4.5 Discussion

4.5.1 Nutrient and root exudate analyses

Pyruvate and citric acid are typically found in drier ecosystems and from mycorrhizal fungi that tend to be present around shrub species with faster turnover rates and greater biodegradability (Edwards et al., 2018; Robroek et al., 2016). Shrubs are the dominant plant species found at Mer Bleue, which explains the high values of pyruvate and citric acid that we observed. Greater root exudate concentrations from the shrubs (pyruvate, citric acid, lactate and acetate) were found during the warmer periods of the growing season. This is in line with the findings by Keiser et al. (2019), who found that temperature generally had a greater influence on substrate availability than other environmental variables. They attributed this finding to microbes allocating labile C as an additional source of energy to meet nutrient demands, dampening the carbon lost through respiration; at least until very high temperatures are surpassed. Similarly, (Dieleman et al., 2016) found that both decomposition rates and pore water dissolved organic carbon increased with rising temperatures.

However, Dieleman et al. (2016) also found that high water tables prompted greater pore water dissolved organic carbon and lability. This may explain why organic acid concentrations were generally greater in 2019 than 2018; it was wetter in 2019 than 2018 at the beginning of the growing season. Although microbial activity and decomposition rates decrease once a system is saturated (Dieleman et al., 2016), microbial activity and decomposition rates generally increase with wetness (Keller and Bridgham, 2007; Straková et al., 2012). We also found that an increase in the organic acids from shrubs seemed to coincide with an increase in respiration in times that were relatively wet. Similarly, Robroek et al. (2016) found that an increase in low molecular weight compounds led to increased carbon losses due to greater destabilization of organic matter and increased microbial activity. Edwards et al. (2018) associate this with a decrease in the cost of maintaining the mycorrhizal symbiotic relationship with increasing wetness and potentially increased nutrient availability within the moist mosses during wetter periods. This may also explain why AR was more influenced by a change in organic acids in 2018, while HR was more influenced by a change in organic acids in 2019. For example, the small jump in AR from the shrub plots in 2018 with an increase in organic acid concentrations occurred during the time when there was a large rain event in early August (Environment Canada, 2020).

One of the keys to understanding how the vegetation responds to their surrounding environment is through exploring the mechanisms by which plants obtain water and nutrients. Ecosystem nutrition and availability of nutrients at various levels in the subsoil have a major influence on a plant's metabolism and functioning (Larmola et al., 2013; Lin et al., 2014; Lu et al., 2022). Bogs have a water table that resides at a greater depth than fens for most, if not all, of the growing season (Bonan, 2008). The shrubs in this study, which often dominate ecosystems like bogs, have roots that spread out laterally, and small needle-like stems so they can make use of whatever water is available to the plants in the soil (Murphy et al., 2009). The shrubs at Mer Bleue appear to also rely on the water and nutrients retained by the mosses closer to the surface (Mccarter and Price, 2014). In contrast, the sedges at Mer Bleue have roots that grow vertically to depths of 50 cm and below and can therefore tap into the water and nutrient supply at greater depths even during the drier parts of the season (Buttler et al., 2015). Since the deeper root structures of the sedges allow for nutrients to turnover less quickly than they do for the shrubs (Edwards et al., 2018), we believe this to be one of the reasons for higher PO_4 amounts exuded from the roots of the sedges (Figure 4.4). However, high P concentrations of the sedge roots are more likely due to their uptake efficiency (Cornwell et al., 2001), a lack in competition for deeper subsoil P (Iversen et al., 2022), and translocation of P from leaves to the roots towards the end of the growing season (Jonasson and Chapin, 1985). It is possible that the length of the growing season differs between the shrubs and the sedges (Bubier et al., 2003), but the average growing season for Mer Bleue is beginning of May through end of September (Wang et al., 2014; Rafat et al., 2022), for which the reported results do not go beyond. Herndon et al. (2019) suggest that iron desorption under reducing conditions can also play a role in the high PO_4 concentration below the water table. However, iron concentrations, which may lead to higher desorption rates in peatlands, were not significant in our study (~ 0.015 mg/L).

We also found a spatial trend in PO_4 extracted from roots of the sedges, where concentrations were higher in the "sedge only" and clipped plots than in the reference plots (Figure 4.7), which were about 30 meters away. Some plots showed highest concentrations in the wetter periods while other plots showed highest concentrations in the drier periods. The roots sampled for PO_4 concentrations were not directly from the manipulated plots though, and visual inspection did not show any difference between the health of the individual roots of the plants. Thus, the spatial difference was likely related to localized moisture dynamics and a change in water flow throughout the growing seasons, which would alter the accessibility of the nutrients below and how they are used. Such water flow reversals were seen at Mer Bleue in the past, especially following large rain events (Fraser, 1999; Lu, 2019).

The results from the porewater samples helped determine the factors leading to increased PO_4 concentrations. In fact, the highest concentrations were found in both the roots and porewater in September 2019 and August 2020, where temperatures were already cooler than the rest of the growing season and the fall rains seem to have already started (Environment Canada Historical Weather). Additionally, PO_4 could have been segregated near 60 cm or 45 cm depths because this is right beneath the root zone of the sedges, indicating a high P uptake efficiency by the sedge root system, hence P is depleted in their rooting zone, with higher concentrations below. In addition, the depths between 45 cm - 60 cm is a zone with the most fluctuating water tables (e.g., 8 mm and 16 mm rain fell 2 days prior to sampling for PO_4 analyses in August 2020), hence, around 60 cm depth is a more active zone biogeochemically than other depths that are consistently above or below the water table surface (Morris et al., 2011; Waddington et al., 2015). This 45 - 60 cm depth range is also where either aerobic or anaerobic processes are dominant as the redox potential changes (Bridgham et al., 1998; Inisheva et al., 2016). Bridgham et al. (1998) also suggest the assumption that ombrotrophic bogs are inherently nutrient-limiting may be outdated and low nutrient availability, as seen in a bog, does not necessarily mean nutrient limitation (Chapin et al., 2004).

In contrast, we found very little PO_4 in the roots of the shrubs and very little in the porewater in and around the roots of the shrubs. The shrubs in Mer Bleue are colonized by mycorrhizal fungi (Larmola et al., 2017), which promote the uptake of P and other nutrients by the dense and widespread network of mycorrhizal hyphae in return for carbohydrates supplied by the shrubs (He et al., 2021). This symbiosis indicates P limiting conditions in the topsoil of Mer Bleue, likely fostered by competition with microorganisms and mosses, which explains why we observe only small PO_4 concentrations in and around the roots of the shrubs (Wang et al., 2016). Organisms under limiting conditions have lower P concentrations in their plant tissues and therefore recycle P much faster (McGill and Cole, 1981). Acidic soils low in plant-available P tend to desorb fixed soil P for the plants to use, increasing the efflux of organic acids from the roots (Edwards et al., 2018; Jacoby et al., 2017), which may explain why we also see higher organic acids exuded from the shrubs than the sedges.

Both nutrients and root exudates correlated with respiration, with AR being more influenced by increased PO_4 concentrations in 2018 and HR being more influenced by increased

PO_4 concentrations in 2019. Jacoby et al. (2017) suggest that aboveground respiration and productivity of plants are influenced by microbial - soil - plant interactions. As more PO_4 was made available to the sedges, respiration increased, but these times were also associated with lower water tables (at least during the growing season months between May and August), highlighting the importance of both water and nutrient supply influencing a plant's response to changes in their environment. Similarly, Hungate et al. (1997) suggest that if demands for both nutrient *and* water resources are not met or if the growth of the plants is constrained, this will lead to a higher loss of C from plants through root turnover and respiration; partially explaining why AR was more influenced by changes in root exudates and nutrient concentrations in 2018. Minkkinen et al. (2007) suggest that HR increases from nutrient poor to nutrient rich sites but is also dependent on temperature acclimatisation of the plants. Fan et al. (2013) though, suggest that HR is affected by both temperature and moisture changes, where HR increases as WT depths increase and may be equally responsive to temperature as AR (St-Hilaire et al., 2008). This partially explains why HR was more influenced by nutrient and root exudate changes in 2019; the increase in PO_4 concentrations towards the end of the growing season in 2019 occurred in the driest and warmest conditions of that year. Bunsen and Loisel (2020) agree that the response of peatlands to climate is a function of temperature, moisture, and nutrient conditions.

4.5.2 Stable and radiocarbon isotopes of C

Where the nutrient and root exudate analyses provide insight into the role of root dynamics and plant functioning in describing changes in respiration, analyses of both $\delta^{13}C$ and $\Delta^{14}C$ provide insight into how the different species allocate carbon and where the respired CO_2 is coming from. Indeed, isotope analyses determine the portion of respired CO_2 that comes from either recently fixed plant C and that which is derived from older C sources in the soil, providing valuable insight into the processes that control the storage and release of C in terrestrial ecosystems (Hahn et al., 2006; Werner et al., 2012).

δ^{13}C values differ across plant types due to different photosynthetic strategies, relationships to water table and soil moisture (Ehleringer et al., 2000; Flanagan et al., 1999). δ^{13}C values from the plants and the peat in our study fall within the typical values reported in the literature (Hardie et al., 2009; Yang et al., 2015). Firstly, others have found a similar depletion in δ^{13}C values from mosses relative to those found in vascular plants. For example, Loader et al. (2016) found δ^{13}C values in *Sphagnum* mosses to range between -24.6 and -27.5‰. But they found increasingly more negative values with an increase in depth to the water table, which they attribute to changes in the ease with which CO_2 diffuses to the site of photosynthesis. This is contrary to what we found in this study (Figure 4.8). Loader et al. (2007) imply instead that we are simply detecting δ^{13}C values from different parts of the mosses between the two sections. They found that the branches of *Sphagnum* mosses were more enriched in δ^{13}C values (mean ~ -25.5 ‰) than the stems (mean ~ -27.0 ‰) slightly deeper in the peat. They attribute this to a difference in assimilation, bulk composition, or the timing in their formation.

However, we expect that since the mosses at Mer Bleue do not have any noticeable root structures, they may be fixing respired CO_2 from the plants around them, analogous to a heterotroph, rather than autotrophically fixing atmospheric CO_2 as most plants do (Turetsky and Wieder, 1999). Price et al. (1996) found similar results to those found in our study (Figure 4.8), with more depleted δ^{13}C values in the hollows (where sedges generally reside) and in wetter conditions. They suggest that if the mosses create a continuous cover across the region, then CO_2 diffusion out of the bog would be higher, resulting in heavier isotopic values. Smolders et al. (2001) also found that mosses refixed more CO_2 in wetter conditions if they are dependent on substrate-derived CO_2 for their growth. We believe this may be the main explanation of our findings. As August in 2019 was quite dry and hot, the mosses were refixing less of the carbon exuded from the roots of the shrubs around them than in August 2020, which had more sporadic rain events like August in 2018 (Environment Canada, 2020). Consequently, $\delta^{13}C$ signatures showed more depleted amounts of ^{13}C from the mosses in 2020, especially in the sedge section.

Price et al. (1996)'s findings also suggest that the vascular plants in the sedge plots would be recycling more respired CO_2 than the shrub plots. However, despite there being more sedges present in the hollows than in the hummocks, an abundant number of shrubs are still found in the hollows of our site, it being the dominant plant type. Thus, the shrubs have a more closer relationship with mosses than do the sedges; they are not disconnected from the dynamics closer to the surface as the sedges are and there is a strong relationship between the mycorrhizae around the roots of the woody shrubs and the mosses (Hogberg and Read, 2006). The fact that the difference in $\delta^{13}C$ values between the reference plots and the plots where mosses were removed was greater in the shrub section than the difference in these plots in the sedge section, seems to also highlight a more intimate relationship between the shrubs and mosses. The higher $\delta^{13}C$ values in the "shrub only" plots depict a removal of the process whereby mosses refix CO_2 from the roots of the vascular plants around them (Norby et al., 2019; Smolders et al., 2001; Turetsky and Wieder, 1999). Where the plants in sedge-dominated ecosystems prime microbial decomposition with carbon from their roots, in shrub-dominated ecosystems, where water and nutrient availability is limited to what can be obtained at the surface, a mutually beneficial relationship with the mosses seems to be a better adaptive strategy of the plants. Here, the shrubs provide carbon that gets refixed by the mosses as well as facilitate the formation of microtopography, preventing the mosses from drying out through mitigating evapotranspiration rates (Oke and Hager, 2020), and in turn, the shrubs use the water retained by the upward capillary movement of mosses as well as the nutrients found within (Warren et al., 2021). Chiapusio et al. (2018) found similar results in their study, where mosses were shown to have a strong association with mycorrhizal roots of the shrubs, affecting the microbial community composition and enzymatic activities around them. Additionally, it has been found that mycorrhizal colonization increases in drier sites, and that mycorrhizae can benefit many plants in sites that are water stressed or have a low water table (Cornwell et al., 2001). For example, Kohn (2010) found that more enriched values of $\delta^{13}C$ are typically found in drier ecosystems. Since bogs are relatively drier peatlands due to their raised-dome topography, this would suggest that species more commonly found in bogs, like shrubs, would have more enriched $\delta^{13}C$ values than from sedges that tend to dominate more fen-like ecosystems. However, the $\delta^{13}C$ values differed more between the vascular plants than between the two years, suggesting our results are more consistent with a species effect rather than a hydrological effect.

Others have proposed alternative hypotheses. Larmola et al. (2010) suggest we may be removing the process of CH_4 oxidation to CO_2 by methanogenic bacteria associated with the mosses. Chen and Murrell (2010) suggest CH_4 oxidation can contribute up to 35% of the C respired. However, it seems that CH_4 oxidation occurs more frequently in relatively wetter sites than Mer Bleue. Liebner et al. (2011) found CH_4 oxidation to be the dominating process of respired CO_2, but from aquatic and brown mosses and promoted by submerged conditions. Similarly, Kip et al. (2010) found greatest oxidation in submerged mosses and lowest in hummocks and lawn moss species. However, Kox et al. (2020) suggest oxidation rates are influenced by increases in incoming solar radiation or nutrient addition, which may suggest that CH_4 oxidation is the process detected in the sedges at Mer Bleue, with the higher PO_4 concentrations found from their roots as compared to the shrubs. It may also explain why the reference plots of the sedges are slightly more depleted on average. Glatzel et al. (2004) found an increase in CH_4 oxidation rates in fens as compared to bogs. Similarly, Knorr et al. (2008) also found that drought suppressed methanogenic activity and can be attributed to a shift in acetate being commonly used as a substrate instead. The higher concentrations of acetate we found in the root and pore water surrounding the shrubs would also support this claim.

Secondly, we found $\delta^{13}C$ values from peat to be larger (more enriched) with depth (Figure 4.8), which seems in line with what others have found as well. It is not well understood why this is the case though, and researchers have postulated various reasons. $\delta^{13}C$ values become larger with depth in the soil as deeper soils allow for more microbial-derived ^{13}C enriched carbon relative to the ^{13}C depleted plant derived carbon near the surface (Hicks Pries et al., 2013). This is because Microbes are decomposing a different set of substrates than what is being respired by plants (Dorrepaal et al., 2009). Clymo and Bryant (2008) for example, found $\delta^{13}C$ values to range between -20 ‰ and -10 ‰ at 80-100 cm depth. Similarly, Aravena et al. (1993) found an average $\delta^{13}C$ values of -12.7 ‰ at 65-80 cm depth, where $\delta^{13}C$ profiles were controlled by methanogenesis and a lack of mixing of gases between shallow and deeper layers. Methanogenesis can lead to major enrichment in CO_2 ^{13}C and is a definite possibility for why we see an enrichment with depth at Mer Bleue (Lai et al., 2014). Another suggestion as to why there is an enrichment with depth is that oxygen delivered by the roots to deeper depths promote CO_2 production (Corbett et al., 2013), while others suggest decomposers preferentially use ^{12}C for respiration, so the heavier ^{13}C accumulates in the organic matter below (Krüger et al., 2014). Many suggest though that the enrichment is due to the Suess effect, whereby changes in the $\delta^{13}C$

values in the atmosphere have led to more depleted amounts of ^{13}C at the surface relative to deeper depths (Jones et al., 2010; Krohn et al., 2017).

The change in $\delta^{13}C$ values with depth does not seem to be consistent; some studies have found an enrichment with depth up to a certain point after which the $\delta^{13}C$ values become more depleted, what is referred to the turning point (Krüger et al., 2014). This has been attributed to there being different processes at play in the aerobic layer versus the anaerobic layer (Drollinger et al., 2019). Oxidation of CH_4 to CO_2 is an aerobic process that occurs in the drier part of a soil column above the water table, whereas methanogenesis is an anaerobic process that occurs below the water table that contains little to no oxygen. For example, Hobbie et al. (2017) found that the turning point occurs at a lower depth in forested bogs as opposed to wetter ecosystems, whose aerobic layer would be smaller. This may explain the greater enrichment with depth in the sedge section than the shrub section (sedges were found in areas with slightly lower elevation than the shrubs leading to the aerobic layer being smaller). Although, we measured $\delta^{13}C$ values at two distinct depths, so future studies will have to conduct profile measurements of $\delta^{13}C$ values to confirm the depth of the turning point. Nonetheless, the clipped plots have the same $\delta\ ^{13}C$, essentially, as the reference plots. This suggests that HR has essentially the same isotopic composition as AR. This is not what you would expect, since as discussed above, microbial decomposition is often expected to have a different isotope value.

Results of the ^{14}C measurements provide further information about what is occurring belowground at Mer Bleue. ^{14}C isotope measurements act like a timestamp; after fractionation effects have been accounted for, they can help separate respiration sources by providing information about the “ecosystem age” (Hardie et al., 2009; Gaudinski et al., 2000). There was an increase in ^{14}C content in atmospheric CO_2 that peaked around 1963 (‘bomb peak’) because of nuclear bomb testing in the atmosphere that occurred during the 1950s. A treaty was created because of these tests, so that since then, ^{14}C in atmospheric CO_2 has been steadily decreasing. The release of fossil fuels since this time has added to the decrease in ^{14}C in atmospheric CO_2 as well (Hahn et al., 2006; Hicks Pries et al., 2015). Our findings suggest that AR consists of younger, more labile carbon, whereas HR seems to consist of older, more recalcitrant carbon from deeper depths, as was suggested in Hicks Pries et al. (2015).

However, the presence of the bomb peak suggests that old carbon should have a lower 14 C content, whereas our findings show HR to be enriched in ^{14}C compared with current atmospheric CO_2, whereas the ^{14}C content of AR corresponds to current atmospheric CO_2. Hahn et al. (2006)'s study showed similar results as well. This seems to be especially true in plants that contain aerenchyma, where newly fixed carbon transferred by the aerenchyma belowground stimulates microbial breakdown of old carbon, and then transfers old gases directly back to the atmosphere (Garnett et al., 2020). Hardie et al. (2009) found that plant-mediated transport of CO_2 (through aerenchyma) produced in the catotelm accounted for ~ 10-23 %, a considerable component, of total ER. The slightly greater enrichment in ^{14}C from the deeper peat samples in the sedges at Mer Bleue seems to support that aerenchyma play a role in the fate of carbon released to the atmosphere. Hahn et al. (2006) state though, that there may be younger ^{14}C than what is reflected by true HR; as fine roots may die off to feed young C to the heterotrophs, the positive effect of root exudates on decomposition is lost, highlighting the importance of the priming effect of vascular plants in peatlands and the influence of plant-mediated HR.

Gavazov et al. (2018) also found higher ^{14}C values at lower elevations, which was associated with a greater ecosystem respiration, most probably due to a greater HR as well as greater decomposition of roots (Crow and Wieder, 2005). We see this when comparing the sedges against the shrubs. This may also be due to residual root decomposition in the clipped plots though (Hanson et al., 2000). We chose to assume that the roots would have been decomposed by the end of the 2018 growing season, which was 4-5 months after the clipping and trenching of the roots was conducted. It would have been much too invasive to conduct a girdling experiment, whereby all the roots are also pulled up out of the plots. To minimize the roots' contribution, we periodically clipped the aboveground plants and retrenched the plots throughout the growing season. However, it is possible that remnant roots were still present in the clipped plots.

Essentially, the clipped plots clearly show a sign of 'old' carbon, but don't show a sign of enriched $\delta^{13}C$. The difference between the clipped plots and the vegetated plots suggests HR consists of carbon that is a few decades old but is essentially the same as the plants in terms of $\delta^{13}C$, whereas AR is releasing carbon that is fixed within the past few years. But we also see enriched $\delta^{13}C$ at depth, which implies that the clipped plots are releasing C respired at depth, but this is not consistent with the $\delta^{13}C$ data. So, there must be a distinct carbon pool at depth that we don't see contributing to HR.

4.6 Summary and future considerations

In conclusion, our findings support the respiration results previously reported from the site. Root exudate and nutrient concentrations varied between the study years and across the growing season with changes in environmental conditions, but both parameters showed a positive qualitative relationship with respiration, albeit varied in the influence on HR and AR. We also found a plant's response to a change in climate is influenced by their different mechanisms of obtaining water and nutrient resources. It was inferred from the results that the shrubs are more intimately associated with the mosses than are the sedges, where the mosses obtain and recycle carbon from the roots of the shrubs, and in turn, the shrubs utilize the water and nutrient sources provided by the mosses, acting to mediate heterotrophic respiration through the presence of mycorrhizal fungi around their roots. This was shown by the more enriched $\delta^{13}C$ values in the "shrub only" plots as compared to the $\delta^{13}C$ values from the plots that contained both shrubs and mosses. The difference in $\delta^{13}C$ values between the same plots in the sedges was not as great. Instead, the sedges, with their more expansive vertical root structures, obtain their water and nutrient sources from deeper depths than the shrubs as was shown by the greater abundance of PO_4 in and around the roots of sedges.

Although the simple explanation for the high PO_4 concentrations we see at 60 cm depth is that the sedge roots do not take up P at this depth, further exploration into the higher exudation of P by the sedge roots would be useful to better understand the influence of nutrient availability on respiration dynamics. Future studies should also explore $\delta^{18}O$ signatures of CO_2 to get a better understanding of the water use efficiency and flow. Since water resources and other environmental variables can also alter $\delta^{13}C$ signatures (Flanagan et al., 1999; Leith et al., 2014), obtaining more continuous measurements of stable isotopes across growing seasons would be beneficial. Finally, conducting depth profiles of $\delta^{13}C$ signatures to detect the differences between the various plant types will also help gain a better understanding of carbon allocation in peatland plants.

4.7 References

Aravena, R., Warner, B. G., Charman, D. J., Belyea, L. R., Mathur, S. P. and Dinel, H.: Carbon isotopic composition of deep carbon gases in an ombrogenous peatland, northwestern Ontario, Canada, Radiocarbon, 35(2), 271–276, 1993.

Basiliko, N., Stewart, H., Roulet, N. T. and Moore, T. R.: Do Root Exudates Enhance Peat Decomposition?, Geomicrobiol. J., 29(4), 374–378, doi:10.1080/01490451.2011.568272, 2012.

Blodau, C.: Carbon cycling in peatlands - A review of processes and controls, Environ. Rev., 10(2), 111–134, doi:10.1139/a02-004, 2002.

Bonan, G.: Ecological Climatology, Cambridge University Press., 2008.

Bridgham, S. D., Updegraff, K. and Pastor, J.: Carbon, nitrogen, and phosphorus mineralization in northern wetlands, Ecology, 79(5), 1545–1561, doi:10.1890/0012-9658(1998)079[1545:CNAPMI]2.0.CO;2, 1998.

Bubier, J. L., Moore, T. R. and Bledzki, L. A.: Effects of nutrient addition on vegetation and carbon cycling in an ombrotrophic bog, Glob. Chang. Biol., 13(6), 1168–1186, doi:10.1111/j.1365-2486.2007.01346.x, 2007.

Bunsen, M. S. and Loisel, J.: Carbon storage dynamics in peatlands: Comparing recent- and long-term accumulation histories in southern Patagonia, Glob. Chang. Biol., 26(10), 5778–5795, doi:10.1111/gcb.15262, 2020.

Buttler, A., Robroek, B. J. M., Laggoun-Défarge, F., Jassey, V. E. J., Pochelon, C., Bernard, G., Delarue, F., Gogo, S., Mariotte, P., Mitchell, E. A. D. and Bragazza, L.: Experimental warming interacts with soil moisture to discriminate plant responses in an ombrotrophic peatland, J. Veg. Sci., 26(5), 964–974, doi:10.1111/jvs.12296, 2015.

Chapin, C. T., Bridgham, S. D. and Pastor, J.: pH and nutrient effects on above-ground net primary production in a Minnesota, USA bog and fen, Wetlands, 24(1), 186–201, doi:10.1672/0277-5212(2004)024[0186:PANEOA]2.0.CO;2, 2004.

Charman, D. J., Beilman, D. W., Blaauw, M., Booth, R. K., Brewer, S., Chambers, F. M., Christen, J. A., Gallego-Sala, A., Harrison, S. P., Hughes, P. D. M., Jackson, S. T., Korhola, A., Mauquoy, D., Mitchell, F. J. G., Prentice, I. C., van der Linden, M., De Vleeschouwer, F., Yu, Z. C., Alm, J., Bauer, I. E., Corish, Y. M. C., Garneau, M., Hohl, V., Huang, Y., Karofeld, E., Le Roux, G., Loisel, J., Moschen, R., Nichols, J. E., Nieminen, T. M., MacDonald, G. M., Phadtare, N. R., Rausch, N., Sillasoo, Ü., Swindles, G. T., Tuittila, E.-S., Ukonmaanaho, L., Väliranta, M., van Bellen, S., van Geel, B., Vitt, D. H. and Zhao, Y.: Climate-related changes in peatland carbon accumulation during the last millennium, Biogeosciences, 10(2), 929–944, doi:10.5194/bg-10-929-2013, 2013.

Chen, Y. and Murrell, C. J.: methanotrophs in moss Ice-sheet uncertainty, Geomicrobiol. J., 3(September 2010), doi:10.1099/ijs.0.020149-0, 2010.

Chiapusio, G., Jassey, V. E. J., Bellvert, F., Comte, G., Weston, L. A., Delarue, F., Buttler, A., Toussaint, M. L. and Binet, P.: Sphagnum Species Modulate their Phenolic Profiles and Mycorrhizal Colonization of Surrounding Andromeda polifolia along Peatland Microhabitats, J. Chem. Ecol., 44(12), 1146–1157, doi:10.1007/s10886-018-1023-4, 2018.

Christiansen, J. R., Outhwaite, J., & Smukler, S.: Comparison of CO_2, CH_4 and N^2O soil-atmosphere exchange measured in static chambers with cavity ring-down spectroscopy and gas chromatography, Agricultural and Forest Meteorology, 211–212, 48–57. https://doi.org/10.1016/j.agrformet.2015.06.004, 2015.

Clymo, R. S. and Bryant, C. L.: Diffusion and mass flow of dissolved carbon dioxide, methane, and dissolved organic carbon in a 7-m deep raised peat bog, Geochimica et Cosmochimica Acta, 72, 2048–2066, doi:10.1016/j.gca.2008.01.032, 2008.

Cornwell, W. K., Bedford, B. L. and Chapin, C. T.: Occurrence of arbuscular mycorrhizal fungi in a phosphorus-poor wetland and mycorrhizal response to phosphorus fertilization, Am. J. Bot., 88(10), 1824–1829, doi:10.2307/3558359, 2001.

Crann, C. A., Murseli, S., St-Jean, G., Zhao, X., Clark, I. D. and Kieser, W. E.: First Status Report on Radiocarbon Sample Preparation Techniques at the A.E. Lalonde AMS Laboratory (Ottawa, Canada), Radiocarbon, 59(3), 695–704, doi:10.1017/RDC.2016.55, 2017.

Crow, S. E. and Wieder, R. K.: Sources of CO_2 emission from a northern peatland: Root respiration, exudation, and decomposition, Ecology, 86(7), 1825–1834, doi:10.1890/04-1575, 2005.

Dieleman, C. M., Lindo, Z., Mclaughlin, J. W., Craig, A. E. and Branfireun, B. A.: Climate change effects on peatland decomposition and porewater dissolved organic carbon biogeochemistry, Biogeochemistry, 128, 385–396, doi:10.1007/s10533-016-0214-8, 2016.

Dorrepaal, E., Toet, S., van Logtestijn, R. S. P., Swart, E., van de Weg, M. J., Callaghan, T. V., Aerts, R., Logtestijn, V., Richard, S. P., Swart, E., Weg, V. De, Martine, J., Callaghan, T. V., Aerts, R., van Logtestijn, R. S. P., Swart, E., van de Weg, M. J., Callaghan, T. V. and Aerts, R.: Carbon respiration from subsurface peat accelerated by climate warming in the subarctic, Nature, 460, 616–619, doi:10.1038/nature08216, 2009.

Drollinger, S., Kuzyakov, Y. and Glatzel, S.: Catena Effects of peat decomposition on $\delta^{13}C$ and $\delta^{15}N$ depth profiles of Alpine bogs, Catena, 178(March), 1–10, doi:10.1016/j.catena.2019.02.027, 2019.

Edwards, K. R., Kaštovská, E., Borovec, J., Šantrůčková, H. and Picek, T.: Species effects and seasonal trends on plant efflux quantity and quality in a spruce swamp forest, Plant Soil, 426(1–2), 179–196, doi:10.1007/s11104-018-3610-0, 2018.

Ehleringer, J. R., Buchmann, N. and Flabagan, L. B.: Carbon Isotope Ratios in Belowground Carbon Cycle Processes, Ecol. Appl., 10(2), 412–422, 2000.

Environment Canada: Historical Weather Data, Gov. Canada [online] Available from: https://climate.weather.gc.ca/historical_data/search_historic_data_e.html, 2021.

Fan, Z., David Mcguire, A., Turetsky, M. R., Harden, J. W., Michael Waddington, J. and Kane, E. S.: The response of soil organic carbon of a rich fen peatland in interior Alaska to projected climate change, Glob. Chang. Biol., 19(2), 604–620, doi:10.1111/gcb.12041, 2013.

Flanagan, L. B., Kubien, D. S. and Ehleringer, J. R.: Spatial and temporal variation in the carbon and oxygen stable isotope ratio of respired CO_2 in a boreal forest ecosystem, Tellus, Ser. B Chem. Phys. Meteorol., 51(2), 367–384, doi:10.3402/tellusb.v51i2.16306, 1999.

Fraser, C.: The hydrology and dissolved organic carbon (DOC) biogeochemistry in a boreal peatland, McGill University., 1999.

Garnett, M. H., Hardie, S. M. L. and Murray, C.: Radiocarbon analysis reveals that vegetation facilitates the release of old methane in a temperate raised bog, Biogeochemistry, 148(1), 1–17, doi:10.1007/s10533-020-00638-x, 2020.

Gavazov, K., Albrecht, R., Buttler, A., Dorrepaal, E., Garnett, M. H., Gogo, S., Hagedorn, F., Mills, R. T. E., Robroek, B. J. M. and Bragazza, L.: Vascular plant-mediated controls on atmospheric carbon assimilation and peat carbon decomposition under climate change, Glob. Chang. Biol., 24(9), 3911–3921, doi:10.1111/gcb.14140, 2018.

Glatzel, S., Basiliko, N. and Moore, T.: Carbon dioxide and methane production potentials of peats from natural, harvested and restored sites, eastern Quebec, Canada, Wetlands, 24(2), 261–267, 2004.

Hahn, V., Högberg, P. and Buchmann, N.: ^{14}C - A tool for separation of autotrophic and heterotrophic soil respiration, Glob. Chang. Biol., 12(6), 972–982, doi:10.1111/j.1365-2486.2006.001143.x, 2006.

Hanson, P. J., Edwards, N. T., Garrten, C. T. and Andrews, J. A.: Separating Root and Soil Microbial Contributions to Soil Respiration: A Review of Methods and Observations, Biogeochemistry, 48, 115–146, doi:10.1023/A:1006244819642, 2000.

Hardie, S. M. L., Garnett, M. H., Fallick, A. E., Ostle, N. J. and Rowland, A. P.: Bomb-^{14}C analysis of ecosystem respiration reveals that peatland vegetation facilitates release of old carbon, Geoderma, 153(3–4), 393–401, 2009.

He, H., Meyer, A., Svensson, M., Rütting, T. and Klemedtsson, L.: Simulating ectomycorrhiza in boreal forests: Implementing ectomycorrhizal fungi model MYCOFON in CoupModel (v5), Geosci. Model Dev., 11(2), 725–751, doi:10.5194/gmd-11-725-2018, 2018.

He, H., Jansson, P. E. and Gärdenäs, A. I.: CoupModel (v6.0): An ecosystem model for coupled phosphorus, nitrogen, and carbon dynamics - Evaluated against empirical data from a climatic and fertility gradient in Sweden, Geosci. Model Dev., 14(2), 735–761, doi:10.5194/gmd-14-735-2021, 2021.

Van Hees, P. A. W., Jones, D. L., Finlay, R., Godbold, D. L. and Lundström, U. S.: The carbon we do not see - The impact of low molecular weight compounds on carbon dynamics and respiration in forest soils: A review, Soil Biol. Biochem., 37(1), 1–13, doi:10.1016/j.soilbio.2004.06.010, 2005.

Heimann, M. and Reichstein, M.: Terrestrial ecosystem carbon dynamics and climate feedbacks, Nature, 451(7176), 289–292, doi:10.1038/nature06591, 2008.

Herndon, E. M., Costello, L. K., Duroe, K. A., Mills, J., Kane, E. S., Sebestyen, S. D., Thompson, A. A. and Wullschleger, S. D.: Iron (Oxyhydr) Oxides Serve as Phosphate Traps in Tundra and Boreal Peat Soils, Journal of geophysical Research, Biogeosciences., 227–246, doi:10.1029/2018JG004776, 2019.

Hicks Pries, C. E., Schuur, E. A. G. and Crummer, K. G.: Thawing permafrost increases old soil and autotrophic respiration in tundra: Partitioning ecosystem respiration using ^{13}C and ^{14}C, Glob. Chang. Biol., 19(2), 649–661, doi:10.1111/gcb.12058, 2013.

Hicks Pries, C. E., Van Logtestijn, R. S. P., Schuur, E. A. G., Natali, S. M., Cornelissen, J. H. C., Aerts, R. and Dorrepaal, E.: Decadal warming causes a consistent and persistent shift from heterotrophic to autotrophic respiration in contrasting permafrost ecosystems, Glob. Chang. Biol., 21(12), 4508–4519, doi:10.1111/gcb.13032, 2015.

Hobbie, E. A., Chen, J., Hanson, P. J., Iversen, C. M., Mcfarlane, K. J., Thorp, N. R. and Hofmockel, K. S.: Long-term carbon and nitrogen dynamics at SPRUCE revealed through stable isotopes in peat profiles, 2481–2494, doi:10.5194/bg-14-2481-2017, 2017.

Hogberg, P. and Read, D. J.: Towards a more plant physiological perspective on soil ecology, Trends Ecol. Evol., 21(10), doi:10.1016/j.tree.2006.06.004, 2006.

Humphreys, E. R., Charron, C., Brown, M. and Jones, R.: Two Bogs in the Canadian Hudson Bay Lowlands and a Temperate Bog Reveal Similar Annual Net Ecosystem Exchange of CO_2, Arctic, Antarct. Alp. Res., 46(1), 103–113, doi:10.1657/1938-4246.46.1.103, 2014.

Hungate, B. A., Holland, E. A., Jackson, R. B., FS, C., HA, M. and Cb, F.: The fate of carbon in grasslands under carbon dioxide enrichment, Nature, 388(6642), 576–579, doi:10.1038/41550, 1997.

Inisheva, L. I., Szajdak, L. and Sergeeva, M. A.: Dynamics of biochemical processes and redox conditions in geochemically linked landscapes of oligotrophic bogs, Eurasian Soil Sci., 49(4), 466–474, doi:10.1134/S1064229316040050, 2016.

Iversen, C. M., Childs, J., Norby, R. J., Ontl, T. A., Kolka, R. K., Brice, D. J., McFarlane, K. J. and Hanson, P. J.: Fine-root growth in a forested bog is seasonally dynamic, but shallowly distributed in nutrient-poor peat, Plant Soil, 424(1–2), 123–143, doi:10.1007/s11104-017-3231-z, 2018.

Iversen, C. M., Latimer, J., Brice, D. J., Childs, J., Vander Stel, H. M., Defrenne, C. E., Graham, J., Griffiths, N. A., Malhotra, A., Norby, R. J., Oleheiser, K. C., Phillips, J. R., Salmon, V. G., Sebestyen, S. D., Yang, X. and Hanson, P. J.: Whole-Ecosystem Warming Increases Plant-Available Nitrogen and Phosphorus in an Ombrotrophic Bog, Ecosystems, doi:10.1007/s10021-022-00744-x, 2022.

Jacoby, R., Peukert, M., Succurro, A., Koprivova, A. and Kopriva, S.: The role of soil microorganisms in plant mineral nutrition—current knowledge and future directions, Front. Plant Sci., 8(September), 1–19, doi:10.3389/fpls.2017.01617, 2017.

Järveoja, J., Nilsson, M. B., Gažovič, M., Crill, P. M. and Peichl, M.: Partitioning of the net CO_2 exchange using an automated chamber system reveals plant phenology as key control of production and respiration fluxes in a boreal peatland, Glob. Chang. Biol., 24(8), 3436–3451, doi:10.1111/gcb.14292, 2018.

Jonasson, S. and Stuart Chapin, F.: Significance of sequential leaf development for nutrient balance of the cotton sedge, Eriophorum vaginatum L., Oecologia, 67(4), 511–518, doi:10.1007/BF00790022, 1985.

Jones, M. C., Peteet, D. M. and Sambrotto, R.: Late-glacial and Holocene $\delta^{15}N$ and $\delta^{13}C$ variation from a Kenai Peninsula, Alaska peatland, Palaeogeogr. Palaeoclimatol. Palaeoecol., 293(1–2), 132–143, doi:10.1016/j.palaeo.2010.05.007, 2010.

Juszczak, R., Humphreys, E., Acosta, M., Michalak-Galczewska, M., Kayzer, D. and Olejnik, J.: Ecosystem respiration in a heterogeneous temperate peatland and its sensitivity to peat temperature and water table depth, Plant Soil, 366, 505–520, doi:10.1007/s11104-012-1441-y, 2013.

Keiser, A. D., Smith, M., Bell, S. and Hofmockel, K. S.: Peatland microbial community response to altered climate tempered by nutrient availability, Soil Biol. Biochem., 137(December 2018), 107561, doi:10.1016/j.soilbio.2019.107561, 2019.

Keller, J. K. and Bridgham, S. D.: Pathways of anaerobic carbon cycling across an ombrotrophic – minerotrophic peatland gradient, Limnol. Oceanogr., 52(1), 96–107, 2007.

Knorr K.-H., Glaser, B. and Blodau, C.: Fluxes and ^{13}C isotopic composition of dissolved carbon and pathways of methanogenesis in a fen soil exposed to experimental drought, Biogeosciences, 5, 1457–1473, 2008.

Kohn, M. J.: Carbon isotope compositions of terrestrial C3 plants as indicators of (paleo) ecology and (paleo) climate, PNAS., 107(46), 19691–19695, doi:10.1073/pnas.1004933107, 2010.

Kox, M. A. R., Elzen, E. Van Den, Lamers, L. P. M., Jetten, M. S. M. and Kessel, M. A. H. J. Van: Microbial nitrogen fixation and methane oxidation are strongly enhanced by light in Sphagnum mosses, AMB Express, doi:10.1186/s13568-020-00994-9, 2020.

Krohn, J., Lozanovska, I., Kuzyakov, Y., Parvin, S. and Dorodnikov, M.: Science of the Total Environment CH_4 and CO_2 production below two contrasting peatland micro-relief forms: An inhibitor and $\delta^{13}C$ study, Sci. Total Environ., 586, 142–151, doi:10.1016/j.scitotenv.2017.01.192, 2017.

Krüger, J. P., Leifeld, J. and Alewell, C.: Degradation changes stable carbon isotope depth profiles in palsa peatlands, 3369–3380, doi:10.5194/bg-11-3369-2014, 2014.

Kurbatova, J., Tatarinov, F., Molchanov, A., Varlagin, A., Avilov, V., Kozlov, D., Ivanov, D. and Valentini, R.: Partitioning of ecosystem respiration in a paludified shallow-peat spruce forest in the southern taiga of European Russia, Environ. Res. Lett., 8(4), doi:10.1088/1748-9326/8/4/045028, 2013.

Lai, D. Y. F., Roulet, N. T. and Moore, T. R.: The spatial and temporal relationships between CO_2 and CH_4 exchange in a temperate ombrotrophic bog, Atmos. Environ., 89, 249–259, doi:10.1016/j.atmosenv.2014.02.034, 2014.

Larmola, T., Tuittila, E.-S., Tiirola, M., Nykanen, H., Martikainen, P. J., Yrjala, K., Tuomivirta, T. and Fritze, H.: The role of Sphagnum mosses in the methane cycling of a boreal mire, Ecology, 91(8), 2356–2365, 2010.

Larmola, T., Kiheri, H., Bubier, J. L., Dijk, N. Van, Dise, N. and Fritze, H.: Impact of simulated atmospheric nitrogen deposition on nutrient cycling and carbon sink via mycorrhizal fungi in two nutrient-poor peatlands, Geophsical Research Abstracts, 19, 3179, 2017.

Leith, F. I., Garnett, M. H., Dinsmore, K. J., Billett, M. F. and Heal, K. V: Source and age of dissolved and gaseous carbon in a peatland – riparian – stream continuum: a dual isotope (^{14}C and $d^{13}C$) analysis, Biogeochemistry, 415–433, doi:10.1007/s10533-014-9977-y, 2014.

Liebner, S., Zeyer, J., Wagner, D., Schubert, C., Pfeiffer, E. and Knoblauch, C.: Methane oxidation associated with submerged brown mosses reduces methane emissions from Siberian polygonal tundra, Journal of Ecology., 914–922, doi:10.1111/j.1365-2745.2011.01823.x, 2011.

Lin, X., Tfaily, M. M., Steinweg, J. M., Chanton, P., Esson, K., Yang, Z. K., Chanton, J. P., Cooper, W., Schadt, C. W. and Kostka, J. E.: Microbial community stratification linked to utilization of carbohydrates and phosphorus limitation in a Boreal Peatland at Marcell Experimental Forest, Minnesota, USA, Appl. Environ. Microbiol., 80(11), 3518–3530, doi:10.1128/AEM.00205-14, 2014.

Loader, N. J., Mccarroll, D., Knaap, W. O. Van Der, Robertson, I. and Gagen, M.: Characterizing carbon isotopic variability in Sphagnum, The Holocene., 3, 403–410, 2007.

Loader, N. J., Mauquoy, D., Roland, T. P., Bellen, S. V. A. N., Daley, T. J., Davies, D., Hughes, P. D. M., Pancotto, V. O., Young, G. H. F., Amesbury, M. J., Charman, D. J. and Mallon, G.: Measurements of hydrogen , oxygen and carbon isotope variability in Sphagnum moss along a micro-topographical gradient in a southern Patagonian peatland, Journal of Quaternary Science., 31, 426–435, doi:10.1002/jqs.2871, 2016.

Loisel, J., Yu, Z., Beilman, D. W., Camill, P., Alm, J., Amesbury, M. J., Anderson, D., Andersson, S., Bochicchio, C., Barber, K., Belyea, L. R., Bunbury, J., Chambers, F. M., Charman, D. J., Vleeschouwer, F. De, Fiałkiewicz-kozieł, B., Finkelstein, S. A., Gałka, M., Garneau, M., Hammarlund, D., Hinchcliffe, W., Holmquist, J., Hughes, P., Jones, M. C., Klein, E. S., Kokfelt, U., Korhola, A., Kuhry, P., Lamarre, A., Lamentowicz, M., Large, D., Lavoie, M., Macdonald, G., Mäkilä, M., Mallon, G., Mathijssen, P., Mauquoy, D., Moore, T. R., Nichols, J., Reilly, B. O., Oksanen, P., Packalen, M., Peteet, D., Richard, P. J. H., Robinson, S., Ronkainen, T., Rundgren, M., Sannel, A. B. K., Tarnocai, C., Thom, T., Tuittila, E. S., Turetsky, M. R., Valiranta, M., van der Linden, M., van Geel, B., van Bellen, S., Vitt, D. H., Zhao, Y. and Zhou, W.: A database and synthesis of northern peatland soil properties and Holocene carbon and nitrogen accumulation, Holocene Spec. Issue, 24(9), 1028–1042, doi:10.1177/0959683614538073, 2014.

Lu, L.: The cascade of Dissolved Organic Matter Through an Ombrotrophic Bog, McGill University., Master’s Thesis., 2019.

Mccarter, C. P. R. and Price, J. S.: Ecohydrology of Sphagnum moss hummocks: Mechanisms of capitula water supply and simulated effects of evaporation, Ecohydrology, 7(1), 33–44, doi:10.1002/eco.1313, 2014.

McGill, W. B. and Cole, C. V.: Comparative aspects of cycling of organic C, N, S an P through soil organic matter, Geoderma, 26, 267–286 [online] Available from: papers2://publication/uuid/C9FDF338-7106-4C1A-AE5B-64CC25970798, 1981.

Minkkinen, K., Laine, J., Shurpali, N. J., Makiranta, P., Alm, J. and Penttilä, T.: Heterotrophic soil respiration in forestry-drained peatlands, Boreal Environ. Res., 12(May), 115–126, 2007.

Morris, P. J., Belyea, L. R. and Baird, A. J.: Ecohydrological feedbacks in peatland development: a theoretical modelling study, 1190–1201, doi:10.1111/j.1365-2745.2011.01842.x, 2011.

Murphy, M., Laiho, R. and Moore, T. R.: Effects of water table drawdown on root production and aboveground biomass in a boreal Bog, Ecosystems, 12(8), 1268–1282, doi:10.1007/s10021-009-9283-z, 2009.

Murphy, M. T. and Moore, T. R.: Linking root production to aboveground plant characteristics and water table in a temperate bog, Plant Soil, 336(1), 219–231, doi:10.1007/s11104-010-0468-1, 2010.

Norby, R. J., Childs, J., Hanson, P. J. and Warren, J. M.: Rapid loss of an ecosystem engineer: Sphagnum decline in an experimentally warmed bog, Ecology and Evolution., (September), 12571–12585, doi:10.1002/ece3.5722, 2019.

Ohno, T. and Zibilske, L. M.: Determination of Low Concentrations of Phosphorus in Soil Extracts Using Malachite Green, Soil Sci. Soc. Am. J., 55(3), 892–895, doi:10.2136/sssaj1991.03615995005500030046x, 1991.

Oke, T. A. and Hager, H. A.: Plant community dynamics and carbon sequestration in Sphagnum-dominated peatlands in the era of global change, Glob. Ecol. Biogeogr., 29(10), 1610–1620, doi:10.1111/geb.13152, 2020.

Pataki, D. E., Ehleringer, J. R., Flanagan, L. B., Yakir, D., Bowling, D. R., Still, C. J., Buchmann, N., Kaplan, J. O. and Berry, J. A.: The application and interpretation of Keeling plots in terrestrial carbon cycle research, Global Biogeochem. Cycles, 17(1), doi:10.1029/2001GB001850, 2003.

Phillips, C. L., Bond-Lamberty, B., Desai, A. R., Lavoie, M., Risk, D., Tang, J., Todd-Brown, K. and Vargas, R.: The value of soil respiration measurements for interpreting and modeling terrestrial carbon cycling, Plant Soil, 413, 1–25, doi:10.1007/s11104-016-3084-x, 2017.

Pouliot, R., Rochefort, L. and Karofeld, E.: Initiation of microtopography in re-vegetated cutover peatlands: Evolution of plant species composition, Appl. Veg. Sci., 15(3), 369–382, doi:10.1111/j.1654-109X.2011.01164.x, 2012.

Price, G. D., Hoper, T., Mckenzie, J. E. and Pilcher, J. R.: Carbon-isotope variation in Sphagnum from hummock-hollow complexes: implications for Holocene climate reconstruction, The Holocene., 229–233, 1996.

Rankin, T. E., Roulet, N. T. and Moore, T. R.: Controls on autotrophic and heterotrophic respiration in an ombrotrophic bog, Biogeosciences, 19, 3285-3303, https://doi.org/10.5194/bg-19-3285-2022, 2022.

Reimer, P., Bard, E., Bayliss, A., Beck, J. W., Blackwell, P., Ramsey, C. B., Buck, C., Cheng, H., Edwards, R. L., Friedrich, and Blackwell, P.: IntCal13 and Marine13 Radiocarbon Age Calibration Curves 0 – 50 , 000 Years cal BP To cite this version : HAL Id : hal-02470111, Radiocarbon, 55(4), 1869–1887, 2013.

Robroek, B. J. M., Albrecht, R. J. H., Hamard, S., Pulgarin, A., Bragazza, L., Buttler, A. and Jassey, V. E. J.: Peatland vascular plant functional types affect dissolved organic matter chemistry, Plant Soil, 407, 135–143, doi:10.1007/s11104-015-2710-3, 2016.

Roulet, N. T., Lafleur, P. M., Richard, P. J. H., Moore, T. R., Humphreys, E. R. and Bubier, J.: Contemporary carbon balance and late Holocene carbon accumulation in a northern peatland, Glob. Chang. Biol., 13(2), 397–411, doi:10.1111/j.1365-2486.2006.01292.x, 2007.

Ryan, M. G. and Law, B. E.: Interpreting, measuring, and modeling soil respiration, Biogeochemistry, 73(1), 3–27, doi:10.1007/s10533-004-5167-7, 2005.

Smolders, A. J. P., Tomassen, H. B. M., Pijnappel, H. W., Lamers, L. P. M. and Roelofs, J. G. M.: Substrate-derived CO_2 is important in the development of Sphagnum spp., New Phytol., 152(2), 325–332, doi:10.1046/j.0028-646X.2001.00261.x, 2001.

St-Hilaire, F., Wu, J., Roulet, N. T., Frolking, S., Lafleur, P. M., Humphreys, E. R. and Arora, V.: McGill wetland model: Evaluation of a peatland carbon simulator developed for global assessments, Biogeosciences Discuss., 5(2), 1689–1725 [online] Available from: https://hal.archives-ouvertes.fr/hal-00297998, 2008.

St-Jean, G., Kieser, W. E., Crann, C. A. and Murseli, S.: Semi-Automated Equipment for CO_2 Purification and Graphitization at the A.E. Lalonde AMS Laboratory (Ottawa, Canada), Radiocarbon, 59(3), 941–956, doi:10.1017/RDC.2016.57, 2017.

Straková, P., Penttilä, T., Laine, J. and Laiho, R.: Disentangling direct and indirect effects of water table drawdown on above- and belowground plant litter decomposition: Consequences for accumulation of organic matter in boreal peatlands, Glob. Chang. Biol., 18(1), 322–335, doi:10.1111/j.1365-2486.2011.02503.x, 2012.

Tarnocai, C.: The effect of climate change on carbon in Canadian peatlands, Glob. Planet. Change, 53(4), 222–232, doi:10.1016/j.gloplacha.2006.03.012, 2006.

Tarnocai, C., Kettles, I. and Ballard, M.: Peatlands of Canada, Geol. Surv. Canada open file 6561, doi:https://doi.org/10.4095/288786, 2011.

Teklemariam, T. A., Lafleur, P. M., Moore, T. R., Roulet, N. T. and Humphreys, E. R.: The direct and indirect effects of inter-annual meteorological variability on ecosystem carbon dioxide exchange at a temperate ombrotrophic bog, Agric. For. Meteorol., 150(11), 1402–1411, doi:10.1016/j.agrformet.2010.07.002, 2010.

Turetsky, M. R. and Wieder, R. K.: Boreal bog Sphagnum refixes soil-produced and respired $^{14}CO_2$, Ecoscience, 6(4), 587–591, doi:10.1080/11956860.1999.11682559, 1999.

Waddington, J. M., Strack, M. and Greenwood, M. J.: Toward restoring the net carbon sink function of degraded peatlands: Short-term response in CO_2 exchange to ecosystem-scale restoration, J. Geophys. Res., 115(G1), G01008, doi:10.1029/2009JG001090, 2010.

Waddington, J. M., Morris, P. J., Kettridge, N., Granath, G., Thompson, D. K. and Moore, P.: Hydrological feedbacks in northern peatlands, Ecohydrology, 8(1), 113–127, doi:10.1002/eco.1493, 2015.

Wang, M., Larmola, T., Murphy, M. T., Moore, T. R. and Bubier, J. L.: Stoichiometric response of shrubs and mosses to long-term nutrient (N, P and K) addition in an ombrotrophic peatland, 403–416, doi:10.1007/s11104-015-2744-6, 2016.

Wang, X., Liu, L., Piao, S., Janssens, I. A., Tang, J., Liu, W., Chi, Y., Wang, J. and Xu, S.: Soil respiration under climate warming: Differential response of heterotrophic and autotrophic respiration, Glob. Chang. Biol., 20(10), 3229–3237, doi:10.1111/gcb.12620, 2014.

Warren, J. M., Jensen, A. M., Ward, E. J., Guha, A., Childs, J., Wullschleger, S. D. and Hanson, P. J.: Divergent species-specific impacts of whole ecosystem warming and elevated CO_2 on vegetation water relations in an ombrotrophic peatland, Glob. Chang. Biol., 27(9), 1820–1835, doi:10.1111/gcb.15543, 2021.

Werner, C., Schnyder, H., Cuntz, M., Keitel, C., Zeeman, M. J., Dawson, T. E., Badeck, F. and Brugnoli, E.: Progress and challenges in using stable isotopes to trace plant carbon and water relations across scales, Biogeosciences, 3083–3111, doi:10.5194/bg-9-3083-2012, 2012.

Yang, Y., Siegwolf, R. T. W. and Körner, C.: Species specific and environment induced variation of $\delta^{13}C$ and $\delta^{15}N$ in alpine plants, Frontiers in Plant Science., 6(June), 1–14, doi:10.3389/fpls.2015.00423, 2015.

Chapter 5: Partitioning autotrophic and heterotrophic respiration in an ombrotrophic bog

Bridging statement to Chapter 5

Like Chapter 3, this chapter addresses the main objective of my thesis; partition autotrophic (AR) and heterotrophic respiration (HR) at Mer Bleue, an ombrotrophic bog. In Chapter 3, we suggest that continuous measurements of CO_2 fluxes, and the environmental variables used to determine the controls on respiration, are needed to better understand the carbon dynamics in peatlands. So, we used automatic chamber methods in this chapter. Chapter 4 indicates that belowground processes play a major role in the respiration dynamics of an ecosystem. This chapter builds on that claim, shows that the relative magnitude of ecosystem respiration (ER) changed depending on the plant biomass, and shows that AR contributions to ER differed between bogs and fens because of a difference in HR; highlighting the greater importance of vegetation dynamics to changes in HR than has been previously suggested.

5.1 Abstract

Northern peatlands are globally significant carbon stores, but the sink strength varies from year to year due to changes in environmental and biogeochemical conditions. Ecosystem respiration is composed of both an autotrophic respiration component (AR) that consists of respiration by plant parts, and a heterotrophic respiration component (HR) that consists of respiration by microbial bacteria in the soil, fungi, etc. Manual measurements only crudely partition AR and HR, which may lead to erroneous estimates if a change favours one form of respiration over another and alters allocations of carbon to labile pools with different turnover rates. Heterotrophic respiration has also been shown to be more linked to vegetation dynamics than previously thought, particularly in wetter, sedge-dominated ecosystems like fens. It is unknown whether such plant-soil-root interactions influence HR in peatlands dominated by woody shrubs whose water table is located further below the surface. The objectives of this study were to 1) determine the contributions of autotrophic and heterotrophic respiration at Mer Bleue, an ombrotrophic bog near Ottawa, Ontario, 2) explore how the environmental conditions influence respiration and its components, 3) determine how different methodological approaches can influence our interpretation in the magnitude of respiration, and 4) compare the respiration dynamics with those found in the literature for other ecosystems. Automatic chamber measurements on plots where the vegetation was manipulated were used to partition respiration during the growing season, and controls on respiration were explored by measuring a variety of environmental variables and using multiple methodological approaches. Our results revealed differences in AR and HR contributions to ER compared to other peatland types reported in the literature. AR contributions were ~ 75% at our study bog, which is generally higher than AR contributions from fens, but also decreased substantially during extended periods of drought. HR contributions were a function of temperature and water table depth. The AR/HR ratio of 3.0 at our study bog is larger than the ratio for fens. Directly measured ER was smaller than when ER was estimated using night-time relationships with temperature, and the relative magnitude of ER changed depending on the plant biomass. The results will improve our understanding of peatland carbon cycling as well as improve the conceptualization of HR.

5.2 Introduction

Northern peatlands play a significant role in the global carbon (C) cycle as long-term sinks of C since primary production exceeds decomposition. For example, peatlands cover 12% of Canada’s terrestrial surface (Tarnocai et al., 2011) yet contain up to 56% of the organic carbon stored in Canadian soils (Tarnocai, 2006). Following the last glaciation, peatlands have accumulated C at an average rate of 23-26 g m^{-2} yr^{-1} (Charman et al., 2013; Loisel et al., 2014). However, on shorter time scales, a peatland may end up being a source or a sink of carbon depending on the environmental conditions of a given year (Dorrepaal et al., 2009; Roulet et al., 2007). Ecosystem respiration (ER) is composed of both an autotrophic component that consists of respiration by plant parts, and a heterotrophic component that consists of respiration by microbial bacteria in the soil, fungi, etc. Most studies only crudely partition respiration into its autotrophic and heterotrophic components using constant ratios and assuming growth respiration is a fixed proportion of the decomposition rates of soil organic matter (Manzoni and Porporato, 2009). This can potentially cause an overestimation of C sequestration depending on which respiration source controls the response (Hungate et al., 1997; Phillips et al., 2017). For example, heterotrophic respiration (HR) of old soil C may control the response to climate change, because the system could lose C to the atmosphere that had been stored for hundreds to thousands of years. In contrast, if autotrophic respiration (AR) controls the response to climate change, the system may fix more C (Hicks Pries et al., 2013).

Although most of the variability in CO_2 exchange comes from changes in gross primary production and AR (Blodau, 2002; Heimann and Reichstein, 2008), the dynamics of HR is more complicated than previously thought. Traditionally, HR is defined as respiration by microbial bacteria communities that is correlated with environmental and substrate variables, such as litter quality and moisture (Minkkinen et al., 2007; St-Hilaire et al., 2008), More recently, however, HR has been shown to be more linked to vegetation dynamics than previously thought, where root-soil interactions play major role. Furthermore, Bond-Lamberty et al. (2004) suggest that there is no standard practice on whether to include rhizosphere respiration (peat respiration in the vicinity of plant roots) with AR or HR. This may be due to the difficulty in separating their impact on the C balance from other root functions (Chapin et al., 2006), but it is also difficult to distinguish between what was traditionally defined as HR (respiration by microbial bacteria communities), and root respiration itself. Similarly, Basiliko et al. (2012) highlight the difficulties in separating root respiration from HR.

Some plants are more intimately associated with other plants, where they fix the respired CO_2 from the vegetation that surrounds them rather than using the CO_2 directly from the atmosphere in the process of photosynthesis, which is the case for *Sphagnum* mosses (Kuiper et al., 2014; Turetsky and Wieder, 1999). Thus, we cannot simply partition AR and HR when there may also be a possible contribution of a plant-associated component to HR, where the rate of litter supply is related to plant production through root-soil interactions and belowground processes rather than through plant biomass (Shao et al., 2022). As *Spha*gnum mosses are sensitive to changes in CO_2 concentrations (Serk and Schleucher, 2021), vascular plant coverage (i.e., shrub biomass) may also influence ER and possibly the magnitude of HR if the presence of shrubs that provides C to be fixed by the mosses is altered (Shao, 2022).

Consequently, belowground processes are more connected to aboveground production than just the slow decomposition of dead organic matter (Ryan and Law, 2005; Van Hees et al., 2005), which has been seen in sedge-dominated (Järveoja et al., 2018; Kurbatova et al., 2013; Wang et al., 2014) and in permafrost ecosystems (Crow and Wieder 2005; Hicks Pries et al., 2015). It is unknown whether this same level of vegetation influence on HR exists in shrub-dominated bogs. Where fens make up a greater proportion of peatlands in European and Scandinavian countries (Janska et al., 2017; Jimenez-Alfaro, 2018), bogs make up about 70% of peatlands in Canada (Tarnocai et al., 2011). This distinction is very important when considering respiration dynamics of peatlands as future changes in climate could have an impact on Canada's overall greenhouse gas emissions.

Considering the contributions of AR and HR to total respiration depend on environmental and biogeochemical conditions (Griffis et al., 2000; Ojanen et al., 2012), the resulting in HR/AR ratios can differ among ecosystems (Schuur and Trumbore, 2006). Moore et al. (2002) estimated that HR contributed about 46% to total ER at Mer Bleue. Hicks Pries et al. (2013), on the other hand, found that HR contributed only 6-18% to total ER at a tundra site in Alaska underlain by permafrost using direct methods. Hicks Pries et al. (2013) also state that the C losses were compensated by an increase in net productivity as the permafrost thaw deepened with increased warming, but that HR may increase substantially if the respiration of older soil eventually outpaces productivity. This statement contradicted the authors' later study, where long-term warming experiments did not lead to an increase in HR, but rather to an increase in both AR/HR ratios and the contribution of AR to total ER (Hicks Pries et al., 2015). It would be reasonable to assume that sites not underlain with permafrost, and perhaps not as sensitive to changes in temperature, would show greater AR contributions. Many studies that look at the partitioning of AR and HR are done in forests, where root structures expand further in both the horizontal and vertical directions than in peatland ecosystems (Hahn et al., 2006; Kurbatova et al., 2013). Provided that roots are associated with AR (Shao, 2022), bogs with low-lying shrubs, which do not have as expansive roots as found in trees, would show a lower contribution of AR to total ER than forested ecosystems.

A plant’s response to a change in environmental conditions or following a disturbance can also be explained by the various mechanisms by which the plants obtain water resources. Malhotra et al. (2020) suggest that environmental changes (e.g., warming) can alter fine root production, affecting water and nutrient uptake and hence ER and C storage. Oke & Hager (2020) suggest that a plant’s distribution depends on physiological tolerances and ecological strategies. Where bogs receive their water source from precipitation, fens receive water inputs from precipitation, surface runoff from adjacent land, and from the groundwater below, which causes environmental constraints on the growth of mosses through increased oxygenation of the organic substrate and enhanced decomposition (Baldwin and Batzer, 2012). A 50/50 split in AR and HR contributions to ER was found at the Degero Stormyr, a fen in northern Sweden (Järveoja et al., 2018). However, fens consist of water tables that remain high for most of a growing season, which may not be a valid assumption in bogs, where the water tables are mainly below the surface, leading to more aerobic conditions (Mitsch and Gosselink, 2007; Moore, 2008). Bogs, in this case, may show a greater contribution of HR than fens.

Finally, ER measurements may be influenced by the methods used. The typical way of measuring respiration during the day is by using relationships between respiration measured at night with eddy covariance towers, and temperature (Humphreys et al., 2014; Peichl et al., 2014). But this method can lead to an overestimation of respiration. For example, at a treed fen in Alberta (Cai et al., 2010), they found that direct measurements made with dark chambers during the day resulted in smaller ER fluxes than when the ER during the day was estimated by night-time relationships with temperature. Photorespiration may be the cause of this discrepancy, as photorespiration tends to be reduced in dark respiration measurements (Pirk et al., 2016). But environmental variables may play a role as well since photorespiration has also been shown to be stimulated in high temperature and water stress conditions (Dusenge et al., 2019; Lloyd, 2006). Consequently, the difference between the two measurement methods may not be the same across the entire growing season or even across years either. Using a standardized definition of HR and measuring dark respiration directly will be key to a better understanding of peatland C cycling.

The objectives of this study are to partition autotrophic and heterotrophic respiration at Mer Bleue, an ombrotrophic bog, using continuous automatic chamber plot measurements. Specifically, this project aims to 1) determine the contributions of autotrophic and heterotrophic respiration at Mer Bleue, an ombrotrophic bog near Ottawa, Ontario, 2) explore how the environmental conditions influence respiration and its components, 3) determine how different methodological approaches can influence our interpretation in the magnitude of respiration, and 4) compare the respiration dynamics with those found in the literature for other ecosystems.

5.3 Methods

5.3.1 Study site

Mer Bleue is a 28 km^2 ombrotrophic raised bog located near Ottawa, Ontario (45.41°N, 75.52°W). The region has a cool continental climate, with a mean annual temperature of 6.4 °C ranging from -10.3 °C in January to 21.0 °C in July. Mean annual precipitation is 943 mm, 350 mm of which falls from May to August, with a mean annual snowfall of 223 cm (Environment Canada; 1981–2010 climate normals). Peat depth reaches about 5 to 6 m near the centre of the bog and is < 0.3 m near the edge of the peatland. Bog development began 7100–6800 years ago, and consists of a hummock-lawn microtopography (Roulet et al., 2007). The surface of the bog is covered by *Sphagnum* mosses (*Sphagnum angustifolium, Sphagnum capillifolium, Sphagnum fallax, Sphagnum magellanicum*), and although there is an occasional mix of sedges (*Eriophorum vaginatum*) that make up about 3-5% of the areal coverage, Mer Bleue is dominated by low growing ericaceous evergreen shrubs that make up about 80% of the areal coverage (mainly *Chamaedaphne calyculata*, with some *Ledum groenlandicum, Rhododendron groenlandicum,* and *Kalmia angustifolia*) (Humphreys et al., 2014; Lai, 2012).

5.3.2 Automatic chamber setup (CO_2 fluxes)

CO_2 fluxes were calculated using an automatic chamber set up and separated into two clusters based on the CO_2 exchange from baseline measurements conducted in 2017 (not shown). Even though the plots all contained a mixture of *Sphagnum* mosses and the dominant shrub species at the site, *Chamaedaphne calyculata*, one cluster had ~ 30 % lower aboveground vascular plant biomass and a slightly higher presence of the *Ledum groenlandicum* shrub species than the other (data not shown).

In June 2018, we manipulated the vegetation in some of the plots. One chamber from each cluster was darkened with aluminum foil to mimic dark respiration. All the aboveground vegetation was removed in these plots (i.e., only peat remained), with a layer of green mesh placed on top to account for temperature differences. These plots were also trenched and root exclosures installed. We assumed these chambers give a measurement of HR, with the understanding that the roots may not have been completely decomposed. A chamber in Cluster 1 was only darkened, which we assume represents a direct measurement of ER during the day, and one clear chamber in each cluster was used as a reference, which we also assume to be a direct measurement of ER, but where respiration during the day was derived from a relationship of night-time respiration and temperature. Autotrophic respiration was then derived as the difference between ER and HR in the respective cluster (Table 5.1). In Cluster 1, two separate measures of AR were determined: one was the difference between ER in the reference plot and HR from the clipped plot, and the other was the difference between ER from the darkened plot and HR from the clipped plot.

The calculation of CO_2 fluxes from the automatic chambers has been previously described in Lai (2012). The collars were covered at set intervals by plastic domes with a height of 20 cm, a diameter of 52 cm and a thickness of 1 cm. The automatic chamber system is controlled by a datalogger, including chamber selection, measurement timing and data acquisition. The automatic chambers were programmed to close sequentially to measure gas concentrations for 2 minutes during the day and 15 minutes at night. Concentrations of CO_2 were measured with a closed-path infrared gas analyser. Using regression equations of concentrations over time, one measured flux was obtained for each chamber every 30 minutes, providing CO_2 fluxes on an hourly timescale. Unfortunately, the measurements of 2018 were not usable due to an issue with the pressure in the pumps that circulate the air through the chambers, which resulted in air escaping to the atmosphere. Thus, we only show the 2019 growing season results from the automatic chambers, expressed as daily averages of CO_2 fluxes.

Others have performed similar manipulations to their chamber set ups to determine contributions of AR and HR by removing all the roots belowground as well, a process known as girdling (Hahn et al., 2006; Hardie et al., 2009). However, this was done mainly in forested systems where roots are more easily removed without disturbing surrounding vegetation like the mosses surrounding the vascular plants in a bog. Hence, we felt that this was too invasive an approach, and opted to remove only the aboveground vegetation, while keeping in mind that residuals of the roots left behind may contribute to the fluxes we measure. A root exclosure was installed though to minimize the need for re-clipping of the plots, as suggested by (Marinier et al., 2004).

Table 5.1 Automatic chamber set up with descriptions of manipulations and reported measurements

Cluster #	Plot Manipulation	Measurement method
1	Full vegetation, Darkened chamber	ER, direct daytime measurement
	Darkened chamber, all aboveground vegetation removed	HR, direct daytime measurement
	Full vegetation, clear reference chamber	Daytime ER assumed from night-time relationship with temperature
2	Full vegetation, clear reference chamber	Daytime ER assumed from night-time relationship with temperature
	Darkened chamber, all aboveground vegetation removed	HR, direct daytime measurement

5.3.3 Environmental variables

Water table (WT) depth and soil temperature were monitored throughout the same sampling period as the automatic chambers, on a continual basis. Thermocouples were previously installed next to the automatic chambers that measured continuous soil temperatures at 10 and 40 cm depths. Continuous 30-minute records of water table position were also obtained with capacitance water level probes that were placed inside PVC tubes previously inserted in the peat beside each of the automatic chambers (Lai et al., 2014). Manual measurements of WT depth were taken periodically beside each automatic chamber to match against the values obtained by the capacitance probes and the continuous measurements of WT depth were constructed from these interpolations. Air temperature and photosynthetically active radiation (PAR) were measured at the meteorological station attached to the eddy covariance tower at the site, approximately 30 meters away from the automatic chamber set up (Lafleur et al., 2005).

5.3.4 Biomass estimates

The non-destructive point intercept method (Bonham, 2013) was used to estimate biomass from the automatic chamber plots. Square grids with legs were constructed using PVC pipes for the frame and legs, and string for the grid. The grid was about 55 cm wide, with grid intersections every 5 cm. The legs were about 2 feet in height. The grid was placed above the plots. The exact placement of the grid was random each sampling day, but the grid covered the whole collar. A plastic rod with a diameter of about 1 cm was stuck down vertically at a grid intersection point until it touched the peat surface. The number of leaves, shoots and flowers of each plant species touching the rod was recorded, where every other grid point in each column was sampled. Measurements were taken either six or seven times between June 27th and August 30th, 2018.

Destructive sampling was carried out about 30 m away from the automatic chamber set up. A 25 cm diameter collar was randomly placed on a hummock. The biomass was sampled non-destructively using the same point intercept method, as outlined above. The above ground vascular biomass in the plot was then clipped and bagged. In the lab, the samples were sorted by organ and species, dried at 70 degrees Celsius for 30 hours, and then weighted. Ten measurements were made between July 13th and July 30th in 2018. The number of hits of plant organs was normalized using the number of grid points in that sample. Linear regressions were generated to relate the number of hits per grid point of a plant organ to biomass. R^2 values were also generated and were all above 0.97 with a p-value < 0.001. These equations were then used to estimate the biomass in each of the 4 automatic chambers before manipulations to the plots were conducted.

5.3.5 Statistical analyses

Statistical analyses were performed using the R statistical software (RStudio, version 4.0.2). First, simple linear and multiple regressions were conducted among the respiration fluxes (ER, HR, and AR) and the various environmental variables using the “stats” package in R. Second, coefficients of variation (standard deviation / mean of population) were conducted to determine the degree of variability in AR contributions to ER and in the AR/HR ratios, as described in Abdi (2010). Third, repeated measures Analysis of Variance (ANOVA) tests were conducted using the “car” package in R to determine if the fluxes from the different treatments were significantly different. Finally, two sample t-tests were conducted using the “stats” package to determine whether the fluxes of ER as measured by the darkened chamber were significantly different from the ER measured by a temperature relationship with night-time respiration in the reference plots. We consider individual p-values less than or equal to 0.10 as significant.

5.4 Results

5.4.1 Environmental variables

The growing season of 2019 was wetter in May and June compared to the normal averages, then consistently became warmer and drier as the growing season progressed (Figure 5.1), with WT depth similar to normal averages in July and August (Teklemariam et al.,, 2010), albeit a bit drier than those measured in previous years (Humphreys et al., 2014). Mean daily air temperatures from the eddy covariance tower nearby ranged between 23 °C and 31 °C (May - August), soil temperatures at 10 cm depth ranged between 12 °C and 22 °C, and the average WT ranged between 10 cm and 53 cm depth (May – August mean WT = 36.5 cm depth). Although, the local WT depth varied slightly depending on the location of the automatic chamber (Figure 5.2).

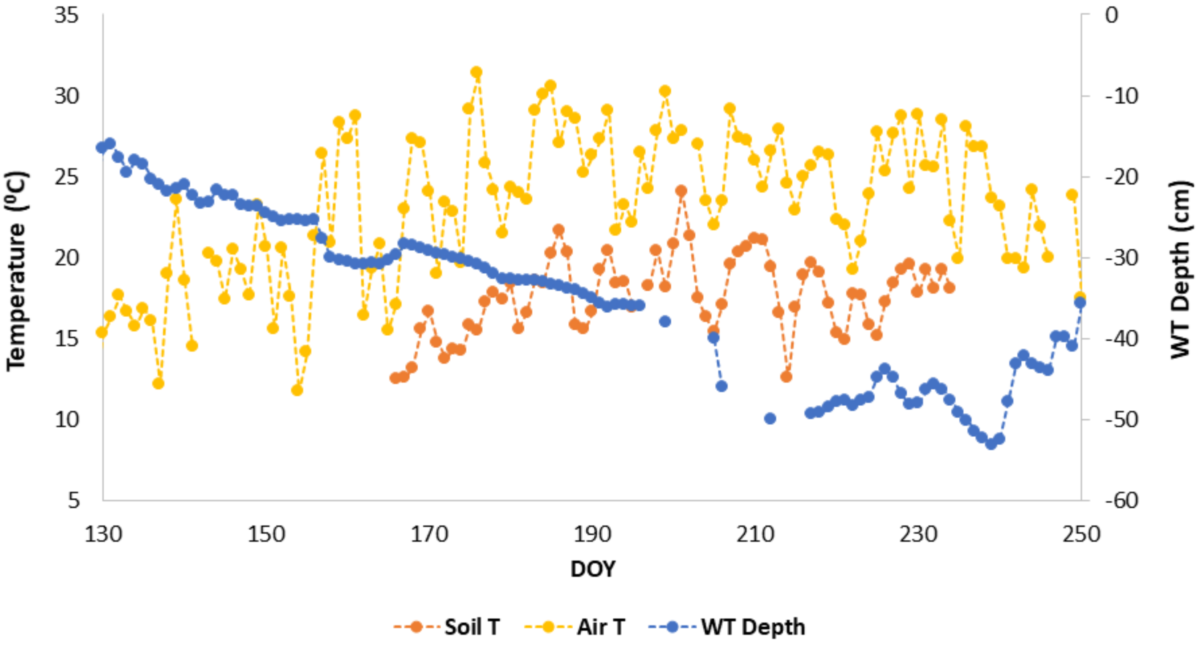


Figure 5.1 Environmental Variables across the growing season of 2019, derived from the eddy covariance tower near the automatic chamber set up. Soil T is soil temperature at 10 cm depth.

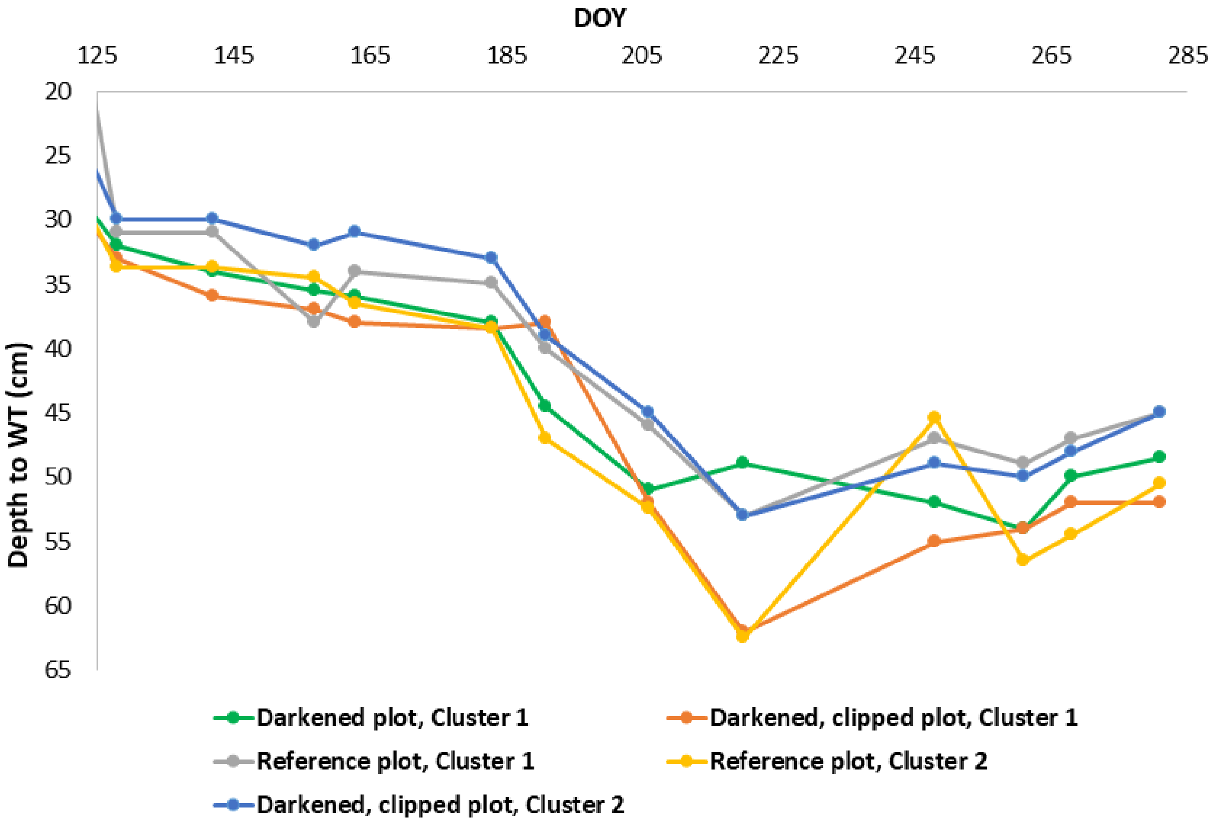


Figure 5.2 Depth to water table (WT) taken from manual measurements in 2019.

5.4.2 Biomass estimates

Although all the automatic chamber plots had *Chamaedaphne* as the dominant shrub species, the automatic chambers in Cluster 2 had a greater contribution of *Ledum* and roughly 27% lower overall shrub biomass than Cluster 1. The automatic chambers in Cluster 1 had an average estimated shrub biomass of 372 ± 10 g m^{-2} and the automatic chambers in Cluster 2 had an average estimated shrub biomass of 272 ± 42 g m^{-2}, with ~ 23% contribution from *Ledum* to overall shrub biomass in Cluster 2, and ~ 13% contribution from *Ledum* to overall shrub biomass in Cluster 1. Biomass measurements were similar to those found previously from the site using similar sampling techniques (Humphreys et al., 2014; Moore et al., 2002).

5.4.3 CO_2 fluxes

The magnitude of the ER fluxes was consistent with those found in other studies (Bubier et al,. 2007; Flanagan and Syed, 2011; Lai et al., 2014; Sulman et al., 2010). ER measured during the day from the darkened chamber in Cluster 1 ranged between 240 and 1200 mg CO_2 m^{-2} hr^{-1}, whereas ER estimated from the reference chamber, based on the temperature relationship with night-time respiration, ranged between 50 and 1250 mg CO_2 m^{-2} hr^{-1}. HR in Cluster 1 ranged between 0 and 390 mg CO_2 m^{-2} hr^{-1} (Figure 5.3). In contrast, ER estimated from the reference chamber in Cluster 2, based on the temperature relationship with night-time respiration, ranged between 100 and 475 mg CO_2 m^{-2} hr^{-1}, and HR ranged between 0 and 250 mg CO_2 m^{-2} hr^{-1} (Figure 5.4).

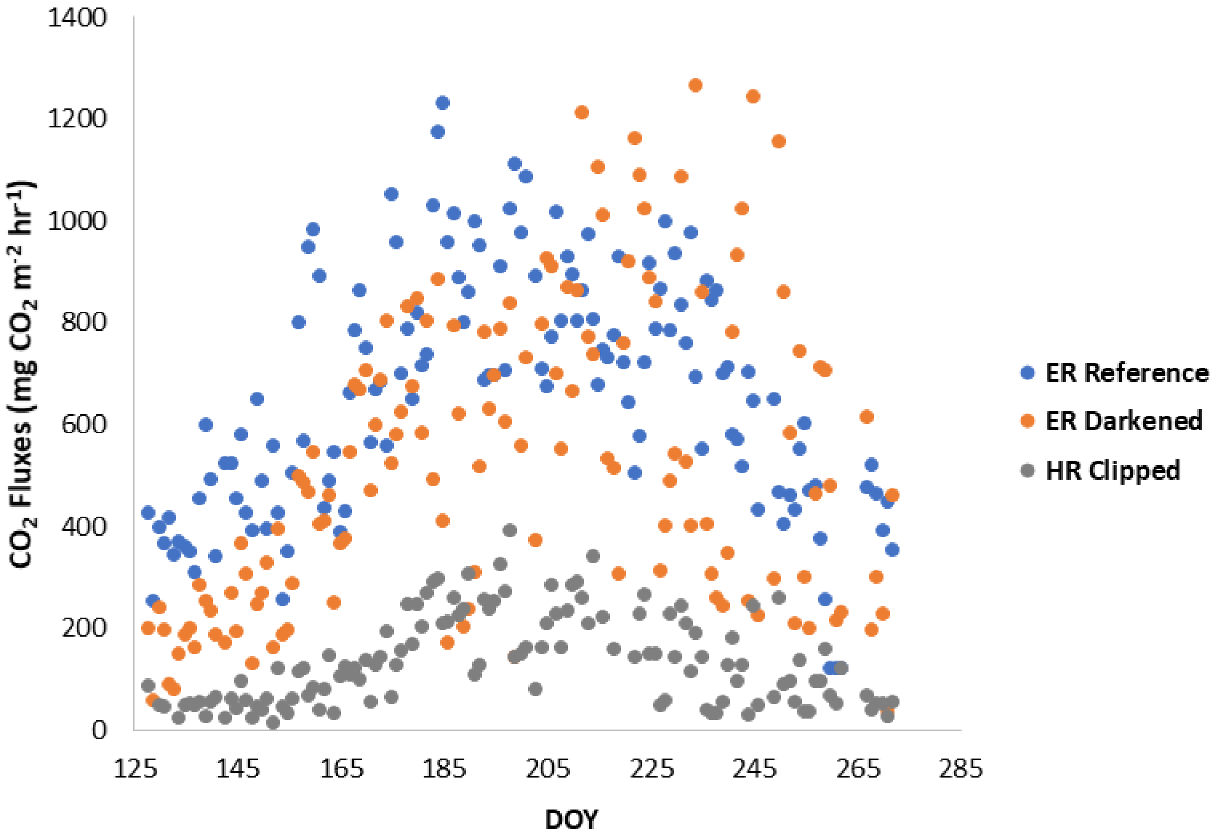


Figure 5.3 ER fluxes estimated in the reference plot based on temperature relationship with night-time respiration values, ER fluxes measured in the darkened plot, and HR fluxes measured in the clipped plot, across the growing season of 2019 in Cluster 1.

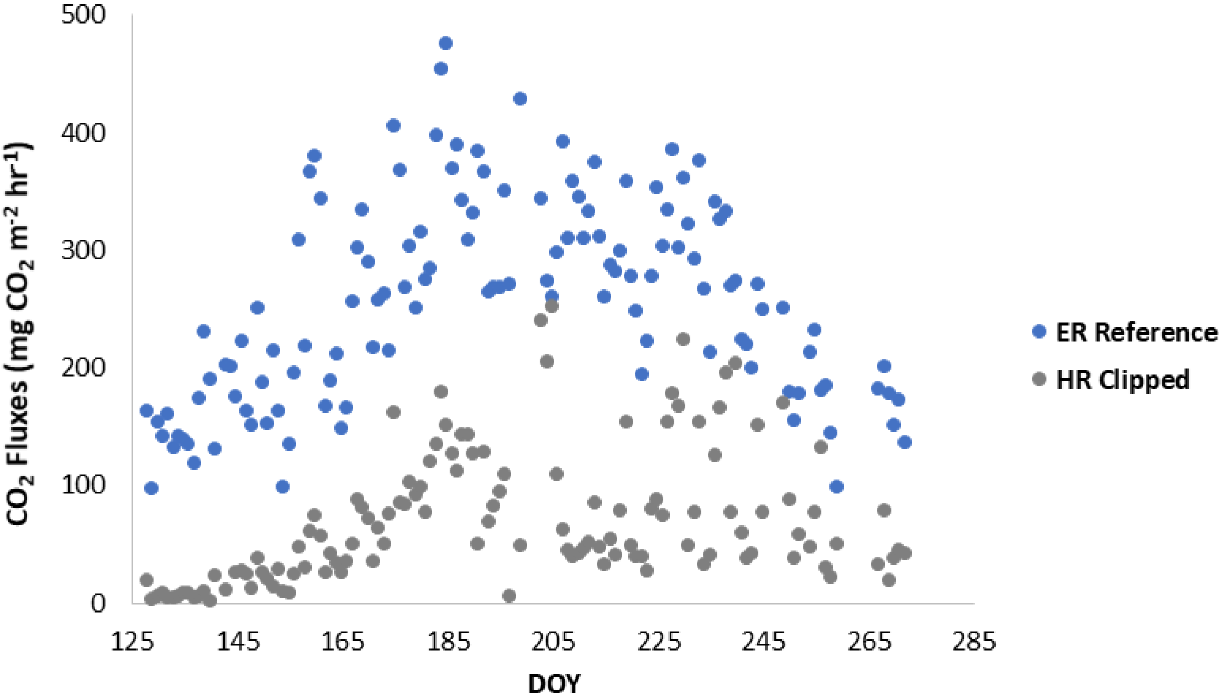


Figure 5.4 ER fluxes estimated in the reference plot, based on temperature relationship with night-time respiration values, and HR fluxes measured in the clipped plot across the growing season of 2019 in Cluster 2.

5.4.4 Derived AR contributions

Derived AR fluxes ranged from 200 to 1000 mg CO_2 m^{-2} hr^{-1}, 300 to 1100 mg CO_2 m^{-2} hr^{-1}, and 100 to 400 mg CO_2 m^{-2} hr^{-1} for the darkened and reference plot in Cluster 1 and reference plot in Cluster 2, respectively (Figure C1). Consequently, the AR contributions to ER were quite high (76.5 +/- 11.2%, 79.0 +/- 11.4% and 75.1 +/- 21.4%). The coefficients of variation in AR contributions were all quite low (15%, 14% and 22%) for the darkened and reference plot in Cluster 1 and reference plot in Cluster 2, respectively (Figure 5.5).

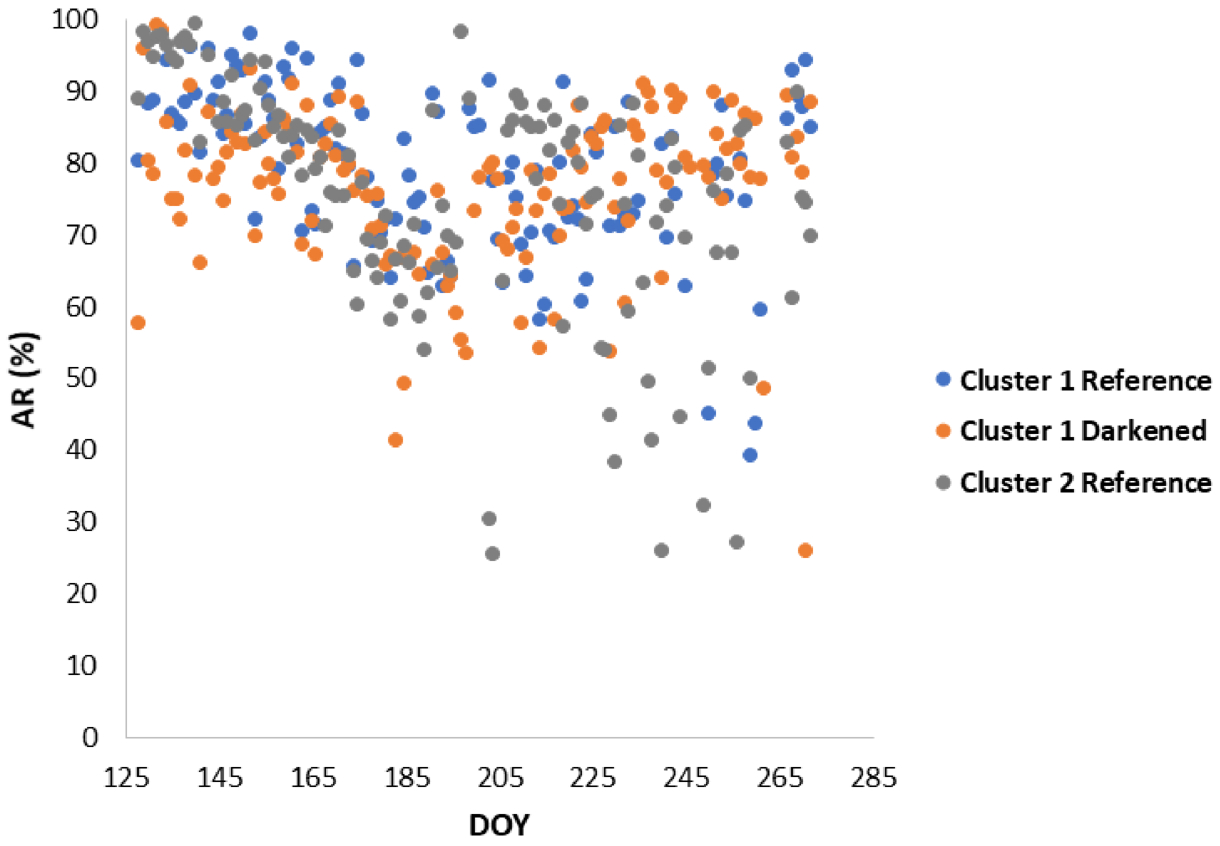


Figure 5.5 AR contributions (%) derived for the darkened plot and reference plot in cluster 1, and reference plot in cluster 2.

5.4.5 Statistical analyses

Repeated measures ANOVA show that the fluxes from the different manipulation treatments (ER vs. HR) were significantly different between the reference and clipped plots in Cluster 1 (F = 245.4, P < 0.00001) and cluster 2 (F = 451.3, P < 0.00001). ER measured from the clipped plots during the day was significantly different than ER estimated using night-time relationships with temperature in Cluster 1 (T = -3.7, P = 0.0001). But the difference in ER fluxes between the two clusters was much more significant (T = -18.0, P < 0.00001). HR fluxes between the two clusters were also significantly different (T = -6.7, P < 0.00001).

Linear regression analyses support these findings. In the reference plot of Cluster 1, when environmental variables were considered individually, ER and AR correlated more with air temperature and somewhat with WT depth above 35 cm and soil temperature, whereas HR correlated more with WT depth and somewhat with air temperature. More variance was explained by the interaction of environmental variables for AR only when multiple regression was used. It was a similar case in Cluster 2, where ER and AR were associated more with air temperature and somewhat with WT depth above 35 cm and soil temperature, whereas HR was correlated more with WT depth and somewhat with air temperature. However, the interaction of multiple variables increased the variance explained for all three fluxes (Table 5.2).

In contrast, for the darkened plot in Cluster 1, ER, AR and HR were all mostly correlated with WT depth above 35 cm, where more than 50% of the variance was explained, and air temperature explained less than 15% of the variance for all three fluxes when linear regression was used. There were no significant relationships with soil temperature for the darkened plot, and the interaction of multiple variables did not increase the variance explained for any of the fluxes when multiple regression was used (Table 5.2). There were no significant relationships found with WT depth when the WT dropped below 35 cm depth for any of the automatic chambers.

Table 5.2 Coefficient of determination (R^2) for linear and multiple regressions between the respiration fluxes (ER, AR, and HR) in the automatic chamber plots and the environmental variables in 2019. WT is water table depth above 35 cm depth, Soil T is soil temperature at 10 cm depth, and Air T is air temperature measured at the flux tower. All relationships are significant at $P < 0.001$; All blank entries are not significant.

Automatic chamber	**Respiration Flux**	**WT**	**Air T**	**Soil T**	**WT + Air T**	**WT + Air T + Soil T**
Cluster 1, darkened plot	**ER**	0.64	0.09		0.68	
	AR	0.52			0.55	
	HR	0.50	0.15		0.51	
Cluster 1, reference plot	**ER**	0.52	0.93	0.26	0.93	0.91
	AR	0.32	0.79	0.17	0.87	0.84
	HR	0.53	0.23		0.53	
Cluster 2	**ER**	0.53	0.93	0.21	0.93	0.89
	AR	0.28	0.50	0.14	0.85	0.82
	HR	0.63	0.36		0.76	

5.5 Discussion

5.5.1 AR and HR contributions to ER

The magnitude of ER was much lower in the automatic chambers with less biomass, regardless of the method used to measure or estimate ER. Periodic re-clipping of the shrubs throughout the growing season was necessary, suggesting that a lower ER was a result of a lower HR between the plots. One would assume the HR in the clipped plots to be the same between the two clusters. However, with a greater abundance of vascular plants, a greater contribution of residual decomposing roots is expected (Zeh et al., 2020). The difference in HR could also be due to the species composition of the plots prior to clipping, where the automatic chambers that had a slightly greater contribution of *Ledum* would have led to a difference in decomposition rates (Murphy et al., 2009; Murphy and Moore, 2010).

An alternative, or perhaps an additional explanation is that the vascular plants were inhibiting the respiration of the microbes below, with the mosses providing a priming effect to heterotrophic respiration. Gavazov et al. (2018) found enhanced heterotrophic decomposition of peat carbon due to rhizosphere priming. Metcalfe et al. (2011) suggest that the amount of carbon allocated belowground is governed by the total amount of C acquired by photosynthesis (GPP), which is likely to be higher for plants that have both a greater leaf area and higher photosynthetic rates. At Mer Bleue, the mosses assimilate C from the roots of the shrubs and release that back to the atmosphere as an additional source of respiration. Turetsky and Wieder (1999) saw this similar phenomenon in their study. Considering that mosses are sensitive to changes in CO_2 concentration (Serk and Schleucher, 2021), it is possible that where there were less shrubs present, there was a lower contribution of plant-associated HR, and more peat decomposition. For example, Shao

(2022) showed in his modelling study that when the ericoid mycorrhiza fungi around the shrub roots were removed from the model, the autotrophic respiration of the mosses increased from ~ 75 $gCm^{-2}yr^{-1}$ to ~ 125 $gCm^{-2}yr^{-1}$, highlighting the importance of shrub-moss-mycorrhizae associations to carbon cycling in peatlands.

Since AR is derived from the difference between ER and HR, AR fluxes were low when ER fluxes were low (Figure C1). Although overall AR contributions (%) were slightly lower in the automatic chambers with less biomass, the AR contributions to ER at Mer Bleue was around 75%, which is slightly higher than the contribution of AR reported in other studies of bogs. Moore et al. (2002) for example, estimated that AR contributed about 54% to total ER at Mer Bleue by using a peatland decomposition model, and Hardie et al. (2009) report AR contributions from a blanket bog in the UK uplands to range between 41% and 54% of the total ecosystem CO_2 flux using direct static chamber measurements. It is possible that the AR contributions we found at Mer Bleue are due to the specific environmental conditions the plants were subjected to in 2019, and it would have been interesting to see the comparison with results from 2018 to confirm this. It is more likely though, that the more consistent, higher than expected, AR contributions to ER was from the change in HR.

5.5.2 Variability in ER, AR, and HR fluxes

Although vegetation dynamics may explain the magnitude of the respiration fluxes and the contributions of HR and AR, it seems to be that environmental variables determine the trends in respiration and its components. Temporal and spatial variability in ER arose because AR and HR differ in their response and sensitivity to changes in temperature and/or water table position. Wang et al. (2014) found that both HR and AR are affected by changes in air temperature, but that HR does not acclimate as fast as AR. Similarly, Grogan and Jonasson (2005) found that newly photosynthesized C by plants was more sensitive to changes in temperature than the C derived from older stores of SOM deeper in the peat, so we often see a shift towards lower AR contributions in warming experiments. Cai et al. (2010) discovered, though, that both photosynthesis and respiration rates were higher in drier *and* warmer conditions in a treed fen. Similarly, Waddington et al. (2015) point out that understanding the role of hydrological feedback in regulating changes in both precipitation (wetness) *and* temperature is essential to understanding the resistance and vulnerability of peatlands to a changing climate.

Indeed, AR contributions to ER were highest in cooler and wetter conditions and lowest in hotter and drier conditions (Figure 5.5). As 2019 was characterised by less variable weather conditions than normal, and was much wetter in May and June, we saw higher AR towards the start of the growing season that slowly decreased into the hotter and drier parts of the summer. DOY 191 – 217 in 2019 was one of the hotter and drier parts of the growing season with less sporadic rain events, and is consequently where we see the lowest AR.

However, while AR was related mostly to air temperature, HR was related mostly to WT depth (Table 5.2). Bubier et al. (1998) also found that lower water tables corresponded with higher CO_2 emissions. This could be due to local WT changes between the automatic chambers influencing the HR dynamics. For example, in Cluster 1, when the WT started to drop and air temperatures were still rising, we saw a decrease in HR until a certain threshold was met (~ 40 cm), and when the WT continually dropped below 55 cm, we saw HR start to jump up. However, in Cluster 2, where the WT never dropped below 55 cm depth (Figure 5.2), we did not see this same rise in HR. Belyea and Malmer (2004) also found an increase in C sequestration with a shift in vegetation to the more productive plant species, *Sphagnum*, which they associated with an increase in wetness.

It is also likely that an interactive effect of species composition and WT depth influenced the HR dynamics at Mer Bleue. The *Chamaedaphne* shrubs in this study allocate most of their biomass to belowground roots that spread out laterally and remain relatively close to the surface. Thus, if the WT drops below a certain threshold, the hydrological dynamics may become disconnected from surface processes, and the shrubs rely more on the water retained in the mosses (Murphy et al., 2009a; Murphy et al., 2009b). Consequently, it is more likely that we found a change in AR because of a change in HR, where drier conditions allowed for more aeration of the peat with a drop in WT depth, and hence a greater HR contribution with more decomposition led to a decrease in AR. It is also possible that we found a change in HR because of a change in AR. When the WT dropped below 35 cm, this may have led to a decrease in AR, especially in the respiration from the roots in the drier conditions, and subsequently we saw an increase in HR contributions.

5.5.3 Effects of measurement method on the interpretation of ER fluxes

ER was lower in magnitude for most of the growing season when measured with a darkened chamber during the day versus when ER was interpolated from night-time relationships with temperature. The noticeable differences in the magnitudes and trends of ER may be due to the process of photorespiration, whereby plants take up oxygen in the light and release carbon dioxide, contrary to the general pattern of photosynthesis (Wingler et al., 2000). Consequently, photorespiration is reduced in dark measurements during the day (Pirk et al., 2016). Similarly, Cai et al. (2010) found that ER measured during the day with darkened chambers was lower than ER determined by night-time relationships with temperature in a treed fen in Alberta, which they also associated with photorespiratory effects.

Alternatively, this difference in ER fluxes may be because the relationship with temperature is not an accurate assumption of determining ER fluxes. Reichstein et al. (2005) suggest that night-time extrapolations to daytime ER use a temperature dependency from annual data, which may not be a valid assumption in all ecosystems as seasonal temperature sensitivity does not necessarily reflect hour-to-hour sensitivity to temperature. We found that WT depth (when the WT was above 35 cm depth) seemed to explain most of the variability in ER and its components rather than temperature when ER was measured directly during the day. In contrast, where ER fluxes were estimated by night-time relationships with temperature, air and soil temperature explained most of the variability in ER. This may be due to an assumed temperature response where it was not the most important factor related to ER fluxes. It is likely a combination of the method used and environmental conditions, especially the interaction of air temperature and WT depth, that explains the variability in ER fluxes throughout the growing season. It has been shown that photorespiration is stimulated in high temperature and water stress conditions (Dusenge et al., 2019; Lloyd, 2006), which would explain why the difference in ER fluxes between the measurement methods was not as pronounced when conditions became drier and warmer later in the growing season. Similarly, a discrepancy between the same two measurement methods was found at the Degero Stormyr fen in Umea, Sweden, where the darkened chambers revealed a bimodal diel pattern in ER fluxes. They attribute this to divergent temperature dependencies of day-time and night-time ER by varying contributions from HR and AR (Jarveoja et al., 2020).

5.5.4 Respiration comparison between bogs and other ecosystems

The diel pattern found by (Jarveoja et al., 2020) was most pronounced during the middle of the growing season as compared to the green up and senescence periods. We don’t see the same double peak in ER fluxes at Mer Bleue though, which may have to do with differences in environmental conditions and in geographical location. Degero Stormyr is located more north than Mer Bleue and consequently, the environmental conditions for most of the growing season are wetter and cooler. Annual average air temperatures are around 1.2 °C, with July and January average temperatures of 14.7 °C, and -12.4 °C, respectively, and WT depths are much closer to the surface (never dropping below 25 cm) despite a lower average annual rainfall than Mer Bleue of 523 mm (Nilsson et al., 2008). Due to its higher latitude, the amount of solar radiation also allows for longer days and evening periods at Degero Stormyr.

Subsequently, there could also be a vegetation effect with a greater abundance of sedges at Degero Stromyr. The average AR/HR ratio at Mer Bleue was ~ 3.0, but varied considerably, decreasing in drier and warmer conditions. In comparison, the average AR/HR ratio at the Degero fen was ~ 1.5 (Järveoja et al., 2018). Manual chamber methods measuring CO_2 fluxes were conducted at Mer Bleue on both the dominant shrub species, but also on the less abundant sedge species, *Eriophorum* (Rankin et al., 2022). Average AR/HR ratios for the shrubs was also ~ 3.0 as was found with the automatic chambers, but the average AR/HR ratio for the sedges was ~ 1.2, closer to that found in the sedge-dominated fen.

The difference in AR/HR ratio may also be due to the different environmental conditions between the two peatlands. The Degero fen in Sweden has a much lower average temperature than Mer Bleue and the WT is much closer to the surface for most of the growing season despite having a lower overall rainfall (Peichl et al., 2014). Based on our results though, the lower temperatures and wetter conditions at the Degero fen should have led to a greater AR. It is more likely then, that the lower contribution of AR to HR at Degero is due to the interactive effect of different environmental conditions and Mer Bleue having a greater biomass of shrubs than Degero has of sedges.

One of the keys to understanding how the vegetation adapts to their surrounding environment is to determine how they deal with water excess or stress (Belyea and Malmer, 2004). Sedges have root structures that extend vertically downwards, sometimes up to 50 cm depth, and can consequently tap into the water table at deeper depths even during the drier parts of the season as well as support a greater aboveground biomass than shrubs, especially when WT depths fluctuate a lot (Buttler et al., 2015; Pouliot et al., 2012). In contrast, the shrubs allocate more of their biomass to belowground roots, which tend to spread out laterally rather than vertically with root lengths limited to within the first 20-30 cm of the surface (Iversen et al., 2018; Murphy et al., 2009a), hence supporting a greater belowground/aboveground biomass than sedges. Shrubs also allocate energy to needle-like stems (small in diameter but great in height) so they can make use of whatever water is available to the plants in the soil, while minimizing the loss of water through transpiration (Bonan, 2008). These shrub stems are also buried annually by the mosses, contributing significantly to the greater belowground biomass (Murphy et al., 2009b). Considering that shrubs are more disconnected from the water table for large parts of the growing season, they tend to rely on the water retained by the mosses closer to the surface, and hence show a greater magnitude in AR as compared to other peatland types like fens, which are comprised of more sedge-like plants (Mccarter and Price, 2014). This may also explain why the daily pattern in contributions from AR and HR at the Degero fen may be more varied than at Mer Bleue.

We hypothesised that shrubs would show a higher contribution of HR to total ER than forested ecosystems. But AR contributions to ER in forested ecosystems seem to range more between 50 and 70% (Hahn et al., 2006; Maier and Kress, 2000; Schuur and Trumbore, 2006). This may be due to the higher contribution of plant-associated HR in forested ecosystems, where the more expansive root structures of trees can access carbon at deeper depths. The higher contributions of AR at Mer Bleue are more similar to those found in cooler regions. For example, Hicks Pries et al. (2015) found AR/HR ratios to average about 1.0 at a subarctic bog in Sweden that is underlain with permafrost, but this ratio substantially increased to almost 2.0 after subjected to warming experiments, which translates to an AR contribution of about 60%. And, in a tundra site in Alaska, Hicks Pries et al. (2013) found AR contributions to be closer to 70% at the peak of the growing season. Perhaps the wetter conditions at Mer Bleue mimic the moisture conditions in a site with thawing permafrost, which is generally associated with greater production and respiration by plant parts.

5.6 Conclusion

ER fluxes were lower when measured directly with a darkened chamber than when interpolated from night-time relationships with temperature, which we attributed to photorespiratory effects. The relative magnitude of ER, AR and HR fluxes changed drastically depending on the plant biomass present in the plots, whereas the differing trends in respiration fluxes were related more to environmental conditions than vegetation dynamics. AR contributions to ER were generally high at Mer Bleue, with an average of 75%, but decreased substantially in extended periods of drought, mainly due to a shift in plant functioning with warmer and drier conditions. The resulting average AR/HR ratio of 3.0 at Mer Bleue is consequently high as compared to the average AR/HR ratio found at the Degero fen (~ 1.5), where temperatures are lower, water tables are much less variable, and plant biomass is not as great.

It would have been beneficial to have results from the 2018 growing season for Mer Bleue, which was globally a warmer growing season than normal and where environmental conditions were much more variable (Jarveoja et al., 2020; Rankin et al., 2022). The inter-annual comparison at the automatic chamber scale for AR and HR dynamics would have allowed us to see any difference in sensitivity to changes in climate between the two peatlands and would have further improved our understanding of the controls on AR and HR contributions. Future studies should obtain an inter-annual comparison of respiration and its components across the various plant types found in peatlands.

5.7 References

Abdi, H.: Coefficient of Variation, Encycl. Res. Des., 1, 169–171, 2010.

Baldwin, A. H. and Batzer, D. P.: Northern Peatlands, in Wetland Habitats of North America: Ecology and Conservation Concerns, pp. 119–134, University of California Press., 2012.

Basiliko, N., Stewart, H., Roulet, N. T. and Moore, T. R.: Do Root Exudates Enhance Peat Decomposition?, Geomicrobiol. J., 29(4), 374–378, doi:10.1080/01490451.2011.568272, 2012.

Belyea, L. R. and Malmer, N.: Carbon sequestration in peatland: patterns and mechanisms of response to climate change, Glob. Chang. Biol., 10, 1043–1052, doi:10.1111/j.1365-2486.2004.00783.x, 2004.

Blodau, C.: Carbon cycling in peatlands - A review of processes and controls, Environ. Rev., 10(2), 111–134, doi:10.1139/a02-004, 2002.

Bonan, G.: Ecological Climatology, Cambridge University Press., 2008.

Bond-Lamberty, B., Wang, C. and Gower, S. T.: A global relationship between the heterotrophic and autotrophic components of soil respiration?, Glob. Chang. Biol., 10(10), 1756–1766, doi:10.1111/j.1365-2486.2004.00816.x, 2004.

Bonham, C. D.: Measurements for Terrestrial Vegetation, John Wiley & Sons., 2013.

Bubier, J. L., Crill, P. M., Moore, T. R. and Savage, K.: Seasonal patterns and controls on net ecosystem exchange in a boreal peatland complex, Global Biogeochem. Cycles, 12(4), 703–714, 1998.

Bubier, J. L., Moore, T. R. and Bledzki, L. A.: Effects of nutrient addition on vegetation and carbon cycling in an ombrotrophic bog, Glob. Chang. Biol., 13(6), 1168–1186, doi:10.1111/j.1365-2486.2007.01346.x, 2007.

Buttler, A., Robroek, B. J. M., Laggoun-Défarge, F., Jassey, V. E. J., Pochelon, C., Bernard, G., Delarue, F., Gogo, S., Mariotte, P., Mitchell, E. A. D. and Bragazza, L.: Experimental warming interacts with soil moisture to discriminate plant responses in an ombrotrophic peatland, J. Veg. Sci., 26(5), 964–974, doi:10.1111/jvs.12296, 2015.

Cai, T., Flanagan, L. B. and Syed, K. H.: Warmer and drier conditions stimulate respiration more than photosynthesis in a boreal peatland ecosystem: Analysis of automatic chambers and eddy covariance measurements, Plant, Cell Environ., 33(3), 394–407, doi:10.1111/j.1365-3040.2009.02089.x, 2010.

Chapin, F. S., Woodwell, G. M., Randerson, J. T., Rastetter, E. B., Lovett, G. M., Baldocchi, D. D., Clark, D. A., Harmon, M. E., Schimel, D. S., Valentini, R., Wirth, C., Aber, J. D., Cole, J. J., Goulden, M. L., Harden, J. W., Heimann, M., Howarth, R. W., Matson, P. A., McGuire, A. D., Melillo, J. M., Mooney, H. A., Neff, J. C., Houghton, R. A., Pace, M. L., Ryan, M. G., Running, S. W., Sala, O. E., Schlesinger, W. H. and Schulze, E. D.: Reconciling carbon-cycle concepts, terminology, and methods, Ecosystems, 9(7), 1041–1050, doi:10.1007/s10021-005-0105-7, 2006.

Charman, D. J., Beilman, D. W., Blaauw, M., Booth, R. K., Brewer, S., Chambers, F. M., Christen, J. A., Gallego-Sala, A., Harrison, S. P., Hughes, P. D. M., Jackson, S. T., Korhola, A., Mauquoy, D., Mitchell, F. J. G., Prentice, I. C., van der Linden, M., De Vleeschouwer, F., Yu, Z. C., Alm, J., Bauer, I. E., Corish, Y. M. C., Garneau, M., Hohl, V., Huang, Y., Karofeld, E., Le Roux, G., Loisel, J., Moschen, R., Nichols, J. E., Nieminen, T. M., MacDonald, G. M., Phadtare, N. R., Rausch, N., Sillasoo, Ü., Swindles, G. T., Tuittila, E.-S., Ukonmaanaho, L., Väliranta, M., van Bellen, S., van Geel, B., Vitt, D. H. and Zhao, Y.: Climate-related changes in peatland carbon accumulation during the last millennium, Biogeosciences, 10(2), 929–944, doi:10.5194/bg-10-929-2013, 2013.

Crow, S. E. and Wieder, R. K.: Sources of CO_2 emission from a northern peatland: Root respiration, exudation, and decomposition, Ecology, 86(7), 1825–1834, doi:10.1890/04-1575, 2005.

Dorrepaal, E., Toet, S., van Logtestijn, R. S. P., Swart, E., van de Weg, M. J., Callaghan, T. V., Aerts, R., Logtestijn, V., Richard, S. P., Swart, E., Weg, V. De, Martine, J., Callaghan, T. V., Aerts, R., van Logtestijn, R. S. P., Swart, E., van de Weg, M. J., Callaghan, T. V. and Aerts, R.: Carbon respiration from subsurface peat accelerated by climate warming in the subarctic, Nature, 460, 616–619, doi:10.1038/nature08216, 2009.

Dusenge, M. E., Duarte, A. G. and Way, D. A.: Plant carbon metabolism and climate change: elevated CO_2 and temperature impacts on photosynthesis, photorespiration and respiration, New Phytol., 221, 32–49, doi:10.1111/nph.15283, 2019.

Fan, Z., David Mcguire, A., Turetsky, M. R., Harden, J. W., Michael Waddington, J. and Kane, E. S.: The response of soil organic carbon of a rich fen peatland in interior Alaska to projected climate change, Glob. Chang. Biol., 19(2), 604–620, doi:10.1111/gcb.12041, 2013.

Flanagan, L. B. and Syed, K. H.: Stimulation of both photosynthesis and respiration in response to warmer and drier conditions in a boreal peatland ecosystem, Glob. Chang. Biol., 17(7), 2271–2287, doi:10.1111/j.1365-2486.2010.02378.x, 2011.

Gavazov, K., Albrecht, R., Buttler, A., Dorrepaal, E., Garnett, M. H., Gogo, S., Hagedorn, F., Mills, R. T. E., Robroek, B. J. M. and Bragazza, L.: Vascular plant-mediated controls on atmospheric carbon assimilation and peat carbon decomposition under climate change, Glob. Chang. Biol., 24(9), 3911–3921, doi:10.1111/gcb.14140, 2018.

Griffis, T. J., Rouse, W. R. and Waddington, J. M.: Interannual variability of net ecosystem CO_2 exchange at a subarctic fen, Geography, 14(4), 1109–1121, 2000.

Grogan, P. and Jonasson, S.: Temperature and substrate controls on intra-annual variation in ecosystem respiration in two subarctic vegetation types, Glob. Chang. Biol., 11(3), 465–475, doi:10.1111/j.1365-2486.2005.00912.x, 2005.

Hahn, V., Högberg, P. and Buchmann, N.: ^{14}C - A tool for separation of autotrophic and heterotrophic soil respiration, Glob. Chang. Biol., 12(6), 972–982, doi:10.1111/j.1365-2486.2006.001143.x, 2006.

Hardie, S. M. L., Garnett, M. H., Fallick, A. E., Ostle, N. J. and Rowland, A. P.: Bomb-^{14}C analysis of ecosystem respiration reveals that peatland vegetation facilitates release of old carbon, Geoderma, 153(3–4), 393–401, 2009.

Van Hees, P. A. W., Jones, D. L., Finlay, R., Godbold, D. L. and Lundström, U. S.: The carbon we do not see - The impact of low molecular weight compounds on carbon dynamics and respiration in forest soils: A review, Soil Biol. Biochem., 37(1), 1–13, doi:10.1016/j.soilbio.2004.06.010, 2005.

Heimann, M. and Reichstein, M.: Terrestrial ecosystem carbon dynamics and climate feedbacks, Nature, 451(7176), 289–292, doi:10.1038/nature06591, 2008.

Hicks Pries, C. E., Schuur, E. A. G. and Crummer, K. G.: Thawing permafrost increases old soil and autotrophic respiration in tundra: Partitioning ecosystem respiration using $\delta^{13}C$ and ^{14}C, Glob. Chang. Biol., 19(2), 649–661, doi:10.1111/gcb.12058, 2013.

Hicks Pries, C. E., Van Logtestijn, R. S. P., Schuur, E. A. G., Natali, S. M., Cornelissen, J. H. C., Aerts, R. and Dorrepaal, E.: Decadal warming causes a consistent and persistent shift from heterotrophic to autotrophic respiration in contrasting permafrost ecosystems, Glob. Chang. Biol., 21(12), 4508–4519, doi:10.1111/gcb.13032, 2015.

Humphreys, E. R., Charron, C., Brown, M. and Jones, R.: Two Bogs in the Canadian Hudson Bay Lowlands and a Temperate Bog Reveal Similar Annual Net Ecosystem Exchange of CO_2, Arctic, Antarct. Alp. Res., 46(1), 103–113, doi:10.1657/1938-4246.46.1.103, 2014.

Hungate, B. A., Holland, E. A., Jackson, R. B., FS, C., HA, M. and Cb, F.: The fate of carbon in grasslands under carbon dioxide enrichment, Nature, 388(6642), 576–579, doi:10.1038/41550, 1997.

Iversen, C. M., Childs, J., Norby, R. J., Ontl, T. A., Kolka, R. K., Brice, D. J., McFarlane, K. J. and Hanson, P. J.: Fine-root growth in a forested bog is seasonally dynamic, but shallowly distributed in nutrient-poor peat, Plant Soil, 424(1–2), 123–143, doi:10.1007/s11104-017-3231-z, 2018.

Janska, V., Jimenez-Alfaro, B., Chytrý, M., Divísek, J., Anenkhonov, O., Korolyuk, A., Lashchinskyi, N. and Culek, M.: Palaeodistribution modelling of European vegetation types at the Last Glacial Maximum using modern analogues from Siberia: Prospects and limitations, Quarternary Sci. Rev., 159, 103–115, doi:10.1016/j.quascirev.2017.01.011, 2017.

Jarveoja, J., Nilsson, M. B., Crill, P. M. and Peichl, M.: Bimodal diel pattern in peatland ecosystem respiration rebuts uniform temperature response, Nat. Commun., 11(4255), 1–9, doi:10.1038/s41467-020-18027-1, 2020.

Järveoja, J., Nilsson, M. B., Gažovič, M., Crill, P. M. and Peichl, M.: Partitioning of the net CO_2 exchange using an automated chamber system reveals plant phenology as key control of production and respiration fluxes in a boreal peatland, Glob. Chang. Biol., 24(8), 3436–3451, doi:10.1111/gcb.14292, 2018.

Jimenez-Alfaro, B.: Vegetation diversity and conservation of European mires., Provincial Council of Bizkaia., 2018.

Kuiper, J. J., Mooij, W. M., Bragazza, L. and Robroek, B. J. M.: Plant functional types define magnitude of drought response in peatland CO_2 exchange, Ecology, 95(1), 123–131, doi:10.1890/13-0270.1, 2014.

Kurbatova, J., Tatarinov, F., Molchanov, A., Varlagin, A., Avilov, V., Kozlov, D., Ivanov, D. and Valentini, R.: Partitioning of ecosystem respiration in a paludified shallow-peat spruce forest in the southern taiga of European Russia, Environ. Res. Lett., 8(4), doi:10.1088/1748-9326/8/4/045028, 2013.

Lafleur, P. M., Moore, T. R., Roulet, N. T. and Frolking, S.: Ecosystem Respiration in a Cool Temperate Bog Depends on Peat Temperature But Not Water Table, Ecosystems, 8(6), 619–629, doi:10.1007/s10021-003-0131-2, 2005.

Lai, D. Y. F., Roulet, N. T. and Moore, T. R.: The spatial and temporal relationships between CO_2 and CH_4 exchange in a temperate ombrotrophic bog, Atmos. Environ., 89, 249–259, doi:10.1016/j.atmosenv.2014.02.034, 2014.

Lai, Y. F.: Spatial and Temporal Variations of Carbon Dioxide and Methane Fluxes Measured by Autochambers at the Mer Bleue Bog, McGill University., PhD Thesis., 2012.

Lloyd, C. R.: Annual carbon balance of a managed wetland meadow in the Somerset Levels, UK, Agricultural and Forest Meteorology., 138, 168–179, doi:10.1016/j.agrformet.2006.04.005, 2006.

Loisel, J., Yu, Z., Beilman, D. W., Camill, P., Alm, J., Amesbury, M. J., Anderson, D., Andersson, S., Bochicchio, C., Barber, K., Belyea, L. R., Bunbury, J., Chambers, F. M., Charman, D. J., Vleeschouwer, F. De, Fiałkiewicz-kozieł, B., Finkelstein, S. A., Gałka, M., Garneau, M., Hammarlund, D., Hinchcliffe, W., Holmquist, J., Hughes, P., Jones, M. C., Klein, E. S., Kokfelt, U., Korhola, A., Kuhry, P., Lamarre, A., Lamentowicz, M., Large, D., Lavoie, M., Macdonald, G., Mäkilä, M., Mallon, G., Mathijssen, P., Mauquoy, D., Moore, T. R., Nichols, J., Reilly, B. O., Oksanen, P., Packalen, M., Peteet, D., Richard, P. J. H., Robinson, S., Ronkainen, T., Rundgren, M., Sannel, A. B. K., Tarnocai, C., Thom, T., Tuittila, E. S., Turetsky, M. R., Valiranta, M., van der Linden, M., van Geel, B., van Bellen, S., Vitt, D. H., Zhao, Y. and Zhou, W.: A database and synthesis of northern peatland soil properties and Holocene carbon and nitrogen accumulation, Holocene Spec. Issue, 24(9), 1028–1042, doi:10.1177/0959683614538073, 2014.

Maier, C. A. and Kress, L. W.: Soil CO_2 evolution and root respiration in 11 year-old loblolly pine (Pinus taeda) plantations as affected by moisture and nutrient availability, Can. J. For. Res., 30(3), 347–359, doi:10.1139/cjfr-30-3-347, 2000.

Malhotra, A., Brice, D. J., Childs, J., Graham, J. D., Hobbie, E. A., Vander Stel, H., Feron, S. C., Hanson, P. J. and Iversen, C. M.: Peatland warming strongly increases fine-root growth, Proc. Natl. Acad. Sci. U. S. A., 117(30), 17627–17634, doi:10.1073/pnas.2003361117, 2020.

Manzoni, S. and Porporato, A.: Soil carbon and nitrogen mineralization: Theory and models across scales, Soil Biol. Biochem., 41(7), 1355–1379, doi:10.1016/j.soilbio.2009.02.031, 2009.

Marinier, M., Glatzel, S. and Moore, T.: The role of cotton-grass (Eriophorum vaginatum) in the exchange of CO_2 and CH_4 at two restored peatlands, eastern Canada, Ecoscience., 11(2), 141–149, 2004.

Mccarter, C. P. R. and Price, J. S.: Ecohydrology of Sphagnum moss hummocks: Mechanisms of capitula water supply and simulated effects of evaporation, Ecohydrology, 7(1), 33–44, doi:10.1002/eco.1313, 2014.

Metcalfe, D. B., Fisher, R. A. and Wardle, D. A.: Plant communities as drivers of soil respiration: Pathways, mechanisms, and significance for global change, Biogeosciences, 8(8), 2047–2061, doi:10.5194/bg-8-2047-2011, 2011.

Minkkinen, K., Laine, J., Shurpali, N. J., Makiranta, P., Alm, J. and Penttilä, T.: Heterotrophic soil respiration in forestry-drained peatlands, Boreal Environ. Res., 12(May), 115–126, 2007.

Mitsch, W. J. and Gosselink, J. G.: Wetlands, 4th ed., John Wiley & Sons., 2007.

Moore, P. D.: Wetlands, revised., Facts on File Inc., 2008.

Moore, T. R., Bubier, J. L., Frolking, S. E., Lafleur, P. M. and Roulet, N. T.: Plant biomass and production and CO_2 exchange in an ombrotrophic bog, J. Ecol., 90(1), 25–36, doi:10.1046/j.0022-0477.2001.00633.x, 2002.

Murphy, M., Laiho, R. and Moore, T. R.: Effects of water table drawdown on root production and aboveground biomass in a boreal Bog, Ecosystems, 12(8), 1268–1282, doi:10.1007/s10021-009-9283-z, 2009a.

Murphy, M. T. and Moore, T. R.: Linking root production to aboveground plant characteristics and water table in a temperate bog, Plant Soil, 336(1), 219–231, doi:10.1007/s11104-010-0468-1, 2010.

Murphy, M. T., McKinley, A. and Moore, T. R.: Variations in above-and below-ground vascular plant biomass and water table on a temperate ombrotrophic peatland, Botany, 87(9), 845–853, doi:10.1139/B09-052, 2009b.

Nilsson, M., Sagerfors, J., Buffam, I., Laudon, H., Eriksson, T., Grelle, A., Klemedtsson, L., Weslien, P. and Lindroth, A.: Contemporary carbon accumulation in a boreal oligotrophic minerogenic mire - A significant sink after accounting for all C-fluxes, Glob. Chang. Biol., 14(10), 2317–2332, doi:10.1111/j.1365-2486.2008.01654.x, 2008.

Ojanen, P., Minkkinen, K., Lohila, A., Badorek, T. and Penttilä, T.: Chamber measured soil respiration: A useful tool for estimating the carbon balance of peatland forest soils?, For. Ecol. Manage., 277, 132–140, doi:10.1016/j.foreco.2012.04.027, 2012.

Oke, T. A. and Hager, H. A.: Plant community dynamics and carbon sequestration in Sphagnum-dominated peatlands in the era of global change, Glob. Ecol. Biogeogr., 29(10), 1610–1620, doi:10.1111/geb.13152, 2020.

Peichl, M., Öquist, M., Ottosson Löfvenius, M., Ilstedt, U., Sagerfors, J., Grelle, A., Lindroth, A. and Nilsson, M. B.: A 12-year record reveals pre-growing season temperature and water table level threshold effects on the net carbon dioxide exchange in a boreal fen, Environ. Res. Lett., 9(5), doi:10.1088/1748-9326/9/5/055006, 2014.

Phillips, C. L., Bond-Lamberty, B., Desai, A. R., Lavoie, M., Risk, D., Tang, J., Todd-Brown, K. and Vargas, R.: The value of soil respiration measurements for interpreting and modeling terrestrial carbon cycling, Plant Soil, 413, 1–25, doi:10.1007/s11104-016-3084-x, 2017.

Pirk, N., Mastepanov, M., Parmentier, F. W., Lund, M. and Crill, P.: Calculations of automatic chamber flux measurements of methane and carbon dioxide using short time series of concentrations, Biogeosciences., 903–912, doi:10.5194/bg-13-903-2016, 2016.

Pouliot, R., Rochefort, L. and Karofeld, E.: Initiation of microtopography in re-vegetated cutover peatlands: Evolution of plant species composition, Appl. Veg. Sci., 15(3), 369–382, doi:10.1111/j.1654-109X.2011.01164.x, 2012.

Rankin, T. E., Roulet, N. T. and Moore, T. R.: Controls on autotrophic and heterotrophic respiration in an ombrotrophic bog, Biogeosciences, 19, 3285-3303, https://doi.org/10.5194/bg-19-3285-2022, 2022.

Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., Berbigier, P., Bernhofer, C., Buchmann, N., Gilmanov, T., Granier, A., Grunwald, T., Havrankova, K., Ilvesniemi, H., Janous, D., Knohl, A., Laurila, T., Lohila, A., Loustau, D., Matteucci, G., Meyers, T., Miglietta, F., Ourcival, J.-M., Pumpanen, J., Rambal, S., Rotenberg, E., Sanz, M., Tenhunen, J., Seufert, G., Vaccari, F., Vesala, T., Yakir, D. and Valentini, R.: On the separation of net ecosystem exchange into assimilation and ecosystem respiration : review and improved algorithm, Glob. Chang. Biol., 11, 1424–1439, doi:10.1111/j.1365-2486.2005.001002.x, 2005.

Roulet, N. T., Lafleur, P. M., Richard, P. J. H., Moore, T. R., Humphreys, E. R. and Bubier, J.: Contemporary carbon balance and late Holocene carbon accumulation in a northern peatland, Glob. Chang. Biol., 13(2), 397–411, doi:10.1111/j.1365-2486.2006.01292.x, 2007.

Ryan, M. G. and Law, B. E.: Interpreting, measuring, and modeling soil respiration, Biogeochemistry, 73(1), 3–27, doi:10.1007/s10533-004-5167-7, 2005.

Schuur, E. A. G. and Trumbore, S. E.: Partitioning sources of soil respiration in boreal black spruce forest using radiocarbon, Glob. Chang. Biol., 12, 165–176, doi:10.1111/j.1365-2486.2005.01066.x, 2006.

Serk, H. and Schleucher, J.: CO_2 fertilization of Sphagnum peat mosses is modulated by water table level and other environmental factors, (August 2020), 1756–1768, doi:10.1111/pce.14043, 2021.

Shao, S.: Modeling microbial dynamics and nutrient cycles in ombrotrophic peatlands, McGill University., PhD thesis, 2022.

Shao, S., Wu, J., He, H. and Roulet, N.: Integrating McGill Wetland Model (MWM) with peat cohort tracking and microbial controls, Sci. Total Environ., 806, 151223, doi:10.1016/j.scitotenv.2021.151223, 2022.

St-Hilaire, F., Wu, J., Roulet, N. T., Frolking, S., Lafleur, P. M., Humphreys, E. R. and Arora, V.: McGill wetland model: Evaluation of a peatland carbon simulator developed for global assessments, Biogeosciences Discuss., 5(2), 1689–1725 [online] Available from: https://hal.archives-ouvertes.fr/hal-00297998, 2008.

Sulman, B. N., Desai, A. R., Saliendra, N. Z., Lafleur, P. M., Flanagan, L. B., Sonnentag, O., MacKay, D. S., Barr, A. G. and Van Der Kamp, G.: CO_2 fluxes at northern fens and bogs have opposite responses to inter-annual fluctuations in water table, Geophys. Res. Lett., 37(19), 3–7, doi:10.1029/2010GL044018, 2010.

Tarnocai, C.: The effect of climate change on carbon in Canadian peatlands, Glob. Planet. Change, 53(4), 222–232, doi:10.1016/j.gloplacha.2006.03.012, 2006.

Tarnocai, C., Kettles, I. and Ballard, M.: Peatlands of Canada, Geol. Surv. Canada open file 6561, doi:https://doi.org/10.4095/288786, 2011.

Teklemariam, T. A., Lafleur, P. M., Moore, T. R., Roulet, N. T. and Humphreys, E. R.: The direct and indirect effects of inter-annual meteorological variability on ecosystem carbon dioxide exchange at a temperate ombrotrophic bog, Agric. For. Meteorol., 150(11), 1402–1411, doi:10.1016/j.agrformet.2010.07.002, 2010.

Turetsky, M. R. and Wieder, R. K.: Boreal bog Sphagnum refixes soil-produced and respired $^{14}CO_2$, Ecoscience, 6(4), 587–591, doi:10.1080/11956860.1999.11682559, 1999.

Waddington, J. M., Morris, P. J., Kettridge, N., Granath, G., Thompson, D. K. and Moore, P. a.: Hydrological feedbacks in northern peatlands, Ecohydrology, 8(1), 113–127, doi:10.1002/eco.1493, 2015.

Wang, X., Liu, L., Piao, S., Janssens, I. A., Tang, J., Liu, W., Chi, Y., Wang, J. and Xu, S.: Soil respiration under climate warming: Differential response of heterotrophic and autotrophic respiration, Glob. Chang. Biol., 20(10), 3229–3237, doi:10.1111/gcb.12620, 2014.

Wingler, A., Lea, P. J., Quick, W. P. and Leegood, R. C.: Photorespiration: metabolic pathways and their role in stress protection, Phil.Trans. R. Soc. Lond. B., doi:10.1098/rstb.2000.0712, 2000.

Zeh, L., Theresa Igel, M., Schellekens, J., Limpens, J., Bragazza, L. and Kalbitz, K.: Vascular plants affect properties and decomposition of moss-dominated peat, particularly at elevated temperatures, Biogeosciences, 17(19), 4797–4813, doi:10.5194/bg-17-4797-2020, 2020.

Chapter 6: Summary and Conclusions

6.1 Summarizing statements

This thesis explored the processes that relate to autotrophic respiration (AR) and heterotrophic respiration (HR) at Mer Bleue, an ombrotrophic bog, which will improve our understanding of peatland carbon cycling. Results showed that a plant's response to climate change depends on which respiration source controls the response. In Chapter 3, using manual chamber methods, results show that AR contributions were ~ 60% at Mer Bleue, which is greater than what was hypothesized in Chapter 2; it was assumed that with a greater depth of aerobic processes and oxygen availability in a raised bog, that HR contributions would be greater. However, AR contributions did vary, sometimes substantially depending on the environmental conditions. Results show that both AR and HR correlated primarily with air and soil temperature, but WT depth played an important role in some cases. Indeed, the AR fluxes decreased substantially during extended periods of drought, which was especially prevalent in the anomalously warm year of 2018. There was also a difference in AR contributions between the plant types at Mer Bleue, where a higher variability in respiration existed for the shrubs than the sedges, especially in 2018 when water table levels were more variable, primarily due to a difference in the plants' root structure. The shrubs are not disconnected from the dynamics closer to the surface as the sedges are (Murphy et al., 2009b; Buttler et al., 2015).

This thesis also revealed the importance of belowground processes in respiration dynamics in peatlands. By conducting nutrient and root exudate analyses, Chapter 4 supports the claim from Chapter 3 that the shrubs obtain water and nutrient sources retained closer to the surface by the mosses, whereas the sedges obtain water and nutrients at depth with the more vertical extension of their roots. The difference in environmental conditions between the growing seasons of 2018 and 2019 influenced the nutrient availability and hence the plant functioning and consequently the respiration from the bog. Results also showed higher amounts of phosphate (PO_4) at depth being used by the sedges and not the shrubs, and the higher $\delta^{13}C$ values in the "shrub only" plots depict a removal of the process whereby mosses refix CO_2 from the roots of the vascular plants around them (Kuiper et al., 2014; Turetsky and Wieder., 1999). The fact that the difference in $\delta^{13}C$ values between the reference plots and the plots where mosses were removed was greater in the shrub section than the difference in these plots in the sedge section, seems to also highlight a tighter relationship between the shrubs and mosses than between the sedges and the mosses, as was also suggested in Chapter 3.

Similarly, in Chapter 5, an automatic chamber set up was used to partition AR and HR from shrub-dominated plots and results show AR contributions to be ~ 75%, which is generally higher than AR contributions from fens that consist more of sedges and whose AR contributions are closer to 50% (Jarveoja et al. 2018; Nilsson et al. 2008). Findings also show that our interpretation of ecosystem respiration (ER) fluxes using the traditional method of estimating ER fluxes from relationships between night-time respiration measurements and temperature (Cai et al. 2010) can be altered and that direct measurements of dark respiration during the day may be a better approach. However, the relative magnitude of ER, AR and HR fluxes in the automatic chamber plots changed drastically depending on the plant biomass of the vascular plants present, highlighting the possibility that HR depends on vegetation dynamics as well as environmental conditions such as temperature and moisture.

The growth and maintenance of AR is well understood as well as how to describe classical HR (decomposer using C fixed by others). However, the highly available and labile C compounds associated with exudates are technically respired as HR. Also, the provision of the substrate is not related to biomass production of the plants, but rather to root-soil interactions and to the biochemistry of plant C fixation and respiration. Heterotrophic respiration has recently been shown to be more related to vegetation dynamics (He et al., 2018; Shao et al., 2022), but most peatland carbon models still simulate HR relating it to parameters like litter quality, microbial activity and moisture, and most field measurements of peatland respiration still only crudely partition AR and HR. So, this thesis also aimed to improve our conceptualization of HR. It is also still not well documented whether a more dynamic nature of HR exists in shrub-dominated ecosystems, like bogs, where the water table is further away from the surface, as seems to be the case in sedge-dominated ecosystems (Kurbatova et al., 2013; Wang et al., 2014).

All three Manuscripts show that HR is not straight forward at the Mer Bleue bog and is more linked to vegetation dynamics than previously thought, where plant-soil-root relationships played an important role. Chapter 3 showed greater fluxes from the clipped plots than the "Shrub only" and "sedge only" plots, suggesting that the mosses may be inhibiting the respiration of the microbes belowground, and that there is a strong relationship between the mycorrhizae around the roots of the woody shrubs and the mosses (Shao, 2022; Baldwin & Batzer, 2012), which may be considered a plant-associated component of HR. Chapter 4 showed that AR is releasing carbon that is fixed within the past few years, while HR is being fuelled by carbon that is a few decades old but is essentially the same as the plants in terms of $\delta^{13}C$, revealing that there must be a distinct carbon pool at depth that we don't see contributing to HR. And finally, the findings from Chapter 5 suggest there's a possibility that a lower abundance of shrubs, and hence less mycorrhizae fungi present to produce an alternate C source to be refixed by the mosses, may result in a lower contribution of plant-associated HR. Consequently, it is essential to separate the plant-associated HR from what traditionally would be defined as HR (i.e., respiration released from the decomposition of plant tissues by the microbial bacteria communities), as was suggested in Chapter 1 (Figure 1.1).

6.2 Conclusions and future work

Northern peatlands are significant carbon stores (Tarnocai et al., 2011; Tarnocai, 2006). The main goal of this thesis was to provide empirically derived estimates of the AR and HR contributions to ER at a temperate, ombrotrophic bog in south-eastern Ontario (Mer Bleue) and gain a better understanding of the processes and mechanisms that affect respiration. Using a variety of methodological approaches, results showed that AR contributions ranged between 60 and 75% depending on the measurement method as well as environmental and biogeochemical conditions but decreased is periods of drought. Additionally, a plant's respiration response to changes in climate is related to different mechanisms of obtaining water and nutrient resources. Another objective was to improve our conceptualization of HR, especially with regards to the link between soil organisms and plant functioning. We showed that the vascular plants at Mer Bleue use associations with other plants around them, with the shrubs likely being more closely associated with mosses than are the sedges, highlighting the importance of plant-microbial-root interactions to peatland respiration.

Although my findings have improved our understanding of peatland CO_2 processes and cycling, I have a few recommendations of what future studies should explore to better tease apart the influence of vegetation to HR. First, an inter-annual comparison with more than just a couple of growing seasons and using both automatic and manual chamber set ups to measure fluxes from all plant functional types in a bog would be beneficial to see the full effect of changing environmental conditions from year to year as well as better tease out the dependence of HR on plant type. Second, the role of belowground processes can be explored further, especially since results showed root exudates and nutrient availability seemed to influence respiration, but with less time and financial limitations, future studies can delve into nutrient depth profiles and isotope labelling to get a better grasp on the carbon and nutrient cycling in peatlands. The clipping method that was used assumed full decomposition of the roots of the plants, which may not have been a realistic assumption, at least for the first year where periodic re-clipping was still necessary throughout the growing season. If a live root system is distinguishable from any decomposed parts of the roots, then it would also be beneficial to measure respiration from the roots separately as it will help determine any residual effects in plots that are manipulated and where vegetation is removed. It would also help distinguish between HR by decomposition of roots and any contribution from a plant-associated component to HR. Finally, further exploring the stable isotopes across time and along depth profiles would be beneficial to detect the differences between the various plant types and will also help gain a better understanding of carbon allocation in peatland plants. Particularly considering the possible refixation of CO_2 by the mosses, which this thesis has shown provides a detectable difference in $\delta^{13}C$ values between the mosses and the vascular plants, where values were non-distinguishable between the shrub-dominated and the sedge-dominated plots.

Chapter 7: Master Reference List

Abdalla, M., Hastings, A., Bell, M. J., Smith, J. U., Richards, M., Nilsson, M. B., Peichl, M., Löfvenius, M. O., Lund, M., Helfter, C., Nemitz, E., Sutton, M. A., Aurela, M., Lohila, A., Laurila, T., Dolman, A. J., Belelli-Marchesini, L., Pogson, M., Jones, E., Drewer, J., Drosler, M. and Smith, P.: Simulation of CO_2 and attribution analysis at six european peatland sites using the ECOSSE model, Water. Air. Soil Pollut., 225(11), doi:10.1007/s11270-014-2182-8, 2014.

Abdi, H.: Coefficient of Variation, Encycl. Res. Des., 1, 169–171, 2010.

Arain, M. A., Xu, B., Brodeur, J. J., Khomik, M., Peichl, M., Beamesderfer, E., Couple, N. R. and Thorne, R.: Heat and drought impact on carbon exchange in an age - sequence of temperate pine forests, Ecol. Process., doi:10.1186/s13717-021-00349-7, 2022.

Aravena, R., Warner, B. G., Charman, D. J., Belyea, L. R., Mathur, S. P. and Dinel, H.: Carbon isotopic composition of deep carbon gases in an ombrogenous peatland, northwestern Ontario, Canada, Radiocarbon, 35(2), 271–276, 1993.

Baldwin, A. H. and Batzer, D. P.: Northern Peatlands, in Wetland Habitats of North America: Ecology and Conservation Concerns, pp. 119–134, University of California Press., 2012.

Basiliko, N., Stewart, H., Roulet, N. T. and Moore, T. R.: Do Root Exudates Enhance Peat Decomposition?, Geomicrobiol. J., 29(4), 374–378, doi:10.1080/01490451.2011.568272, 2012.

Belyea, L. R. and Malmer, N.: Carbon sequestration in peatland: patterns and mechanisms of response to climate change, Glob. Chang. Biol., 10, 1043–1052, doi:10.1111/j.1365-2486.2004.00783.x, 2004.

Blodau, C.: Carbon cycling in peatlands - A review of processes and controls, Environ. Rev., 10(2), 111–134, doi:10.1139/a02-004, 2002.

Bonan, G.: Ecological Climatology, Cambridge University Press., 2008.

Bond-Lamberty, B., Wang, C. and Gower, S. T.: A global relationship between the heterotrophic and autotrophic components of soil respiration?, Glob. Chang. Biol., 10(10), 1756–1766, doi:10.1111/j.1365-2486.2004.00816.x, 2004.

Bonham, C. D.: Measurements for Terrestrial Vegetation, John Wiley & Sons., 2013.

Bridgham, S. D., Updegraff, K. and Pastor, J.: Carbon, nitrogen, and phosphorus mineralization in northern wetlands, Ecology, 79(5), 1545–1561, doi:10.1890/0012-9658(1998)079[1545:CNAPMI]2.0.CO;2, 1998.

Brieman, L., FriedmanJ., Olshen, R. and C., S.: Classification and Regression Trees, Routledge, Wadworth, Belmont., 1984.

Bubier, J. L., Crill, P. M., Moore, T. R. and Savage, K.: Seasonal patterns and controls on net ecosystem exchange in a boreal peatland complex, Global Biogeochem. Cycles, 12(4), 703–714, 1998.

Bubier, J. L., Moore, T. R. and Bledzki, L. A.: Effects of nutrient addition on vegetation and carbon cycling in an ombrotrophic bog, Glob. Chang. Biol., 13(6), 1168–1186, doi:10.1111/j.1365-2486.2007.01346.x, 2007.

Bunsen, M. S. and Loisel, J.: Carbon storage dynamics in peatlands: Comparing recent- and long-term accumulation histories in southern Patagonia, Glob. Chang. Biol., 26(10), 5778–5795, doi:10.1111/gcb.15262, 2020.

Von Buttlar, J., Zscheischler, J., Rammig, A., Sippel, S., Reichstein, M., Knohl, A., Jung, M., Menzer, O., Altaf Arain, M., Buchmann, N., Cescatti, A., Gianelle, D., Kiely, G., Law, B. E., Magliulo, V., Margolis, H., McCaughey, H., Merbold, L., Migliavacca, M., Montagnani, L., Oechel, W., Pavelka, M., Peichl, M., Rambal, S., Raschi, A., Scott, R. L., Vaccari, F. P., Van Gorsel, E., Varlagin, A., Wohlfahrt, G. and Mahecha, M. D.: Impacts of droughts and extreme-temperature events on gross primary production and ecosystem respiration: A systematic assessment across ecosystems and climate zones, Biogeosciences, 15(5), 1293–1318, doi:10.5194/bg-15-1293-2018, 2018.

Buttler, A., Robroek, B. J. M., Laggoun-Défarge, F., Jassey, V. E. J., Pochelon, C., Bernard, G., Delarue, F., Gogo, S., Mariotte, P., Mitchell, E. A. D. and Bragazza, L.: Experimental warming interacts with soil moisture to discriminate plant responses in an ombrotrophic peatland, J. Veg. Sci., 26(5), 964–974, doi:10.1111/jvs.12296, 2015.

Cai, T., Flanagan, L. B. and Syed, K. H.: Warmer and drier conditions stimulate respiration more than photosynthesis in a boreal peatland ecosystem: Analysis of automatic chambers and eddy covariance measurements, Plant, Cell Environ., 33(3), 394–407, doi:10.1111/j.1365-3040.2009.02089.x, 2010.

Chapin, C. T., Bridgham, S. D. and Pastor, J.: pH and nutrient effects on above-ground net primary production in a Minnesota, USA bog and fen, Wetlands, 24(1), 186–201, doi:10.1672/0277-5212(2004)024[0186:PANEOA]2.0.CO;2, 2004.

Chapin, F. S., Matson, P. and Mooney, H. a: Terrestrial Production Processes, in Principles of Terrestrial Ecosystem Ecology, pp. 123–150., 2002.

Chapin, F. S., Woodwell, G. M., Randerson, J. T., Rastetter, E. B., Lovett, G. M., Baldocchi, D. D., Clark, D. A., Harmon, M. E., Schimel, D. S., Valentini, R., Wirth, C., Aber, J. D., Cole, J. J., Goulden, M. L., Harden, J. W., Heimann, M., Howarth, R. W., Matson, P. A., McGuire, A. D., Melillo, J. M., Mooney, H. A., Neff, J. C., Houghton, R. A., Pace, M. L., Ryan, M. G., Running, S. W., Sala, O. E., Schlesinger, W. H. and Schulze, E. D.: Reconciling carbon-cycle concepts, terminology, and methods, Ecosystems, 9(7), 1041–1050, doi:10.1007/s10021-005-0105-7, 2006.

Charman, D. J., Beilman, D. W., Blaauw, M., Booth, R. K., Brewer, S., Chambers, F. M., Christen, J. A., Gallego-Sala, A., Harrison, S. P., Hughes, P. D. M., Jackson, S. T., Korhola, A., Mauquoy, D., Mitchell, F. J. G., Prentice, I. C., van der Linden, M., De Vleeschouwer, F., Yu, Z. C., Alm, J., Bauer, I. E., Corish, Y. M. C., Garneau, M., Hohl, V., Huang, Y., Karofeld, E., Le Roux, G., Loisel, J., Moschen, R., Nichols, J. E., Nieminen, T. M., MacDonald, G. M., Phadtare, N. R., Rausch, N., Sillasoo, Ü., Swindles, G. T., Tuittila, E.-S., Ukonmaanaho, L., Väliranta, M., van Bellen, S., van Geel, B., Vitt, D. H. and Zhao, Y.: Climate-related changes in peatland carbon accumulation during the last millennium, Biogeosciences, 10(2), 929–944, doi:10.5194/bg-10-929-2013, 2013.

Chen, Y. and Murrell, C. J.: methanotrophs in moss Ice-sheet uncertainty, Geomicrobiol. J., 3(September 2010), doi:10.1099/ijs.0.020149-0, 2010.

Chiapusio, G., Jassey, V. E. J., Bellvert, F., Comte, G., Weston, L. A., Delarue, F., Buttler, A., Toussaint, M. L. and Binet, P.: Sphagnum Species Modulate their Phenolic Profiles and Mycorrhizal Colonization of Surrounding Andromeda polifolia along Peatland Microhabitats, J. Chem. Ecol., 44(12), 1146–1157, doi:10.1007/s10886-018-1023-4, 2018.

Christiansen, J. R., Outhwaite, J. and Smukler, S.: Comparison of CO_2, CH_4 and N^2O soil-atmosphere exchange measured in static chambers with cavity ring-down spectroscopy and gas chromotography, Agric. For. Meteorol., 211–212, 48–57, doi:10.1016/j.agrformet.2015.06.004, 2015.

Clymo, R. S. and Bryant, C. L.: Diffusion and mass flow of dissolved carbon dioxide, methane, and dissolved organic carbon in a 7-m deep raised peat bog, Geochimica et Cosmochimica Acta, 72, 2048–2066, doi:10.1016/j.gca.2008.01.032, 2008.

Corbett, J. E., Tfaily, M. M., Burdige, D. J., Cooper, W. T., Glaser, H. and Chanton, J. P.: Partitioning pathways of CO_2 production in peatlands with stable carbon isotopes Partitioning pathways of CO2 production in peatlands with stable carbon isotopes, Biogeochemistry, 114, 327–340, doi:10.1007/s, 2013.

Cornwell, W. K., Bedford, B. L. and Chapin, C. T.: Occurrence of arbuscular mycorrhizal fungi in a phosphorus -poor wetland and mycorrhizal response to phosphorus fertilization, Am. J. Bot., 88(10), 1824–1829, doi:10.2307/3558359, 2001.

Crann, C. A., Murseli, S., St-Jean, G., Zhao, X., Clark, I. D. and Kieser, W. E.: First Status Report on Radiocarbon Sample Preparation Techniques at the A.E. Lalonde AMS Laboratory (Ottawa, Canada), Radiocarbon, 59(3), 695–704, doi:10.1017/RDC.2016.55, 2017.

Crow, S. E. and Wieder, R. K.: Sources of CO_2 emission from a northern peatland: Root respiration, exudation, and decomposition, Ecology, 86(7), 1825–1834, doi:10.1890/04-1575, 2005.

Dieleman, C. M., Lindo, Z., Mclaughlin, J. W., Craig, A. E. and Branfireun, B. A.: Climate change effects on peatland decomposition and porewater dissolved organic carbon biogeochemistry, Biogeochemistry, 128, 385–396, doi:10.1007/s10533-016-0214-8, 2016.

Dorrepaal, E., Toet, S., van Logtestijn, R. S. P., Swart, E., van de Weg, M. J., Callaghan, T. V., Aerts, R., Logtestijn, V., Richard, S. P., Swart, E., Weg, V. De, Martine, J., Callaghan, T. V., Aerts, R., van Logtestijn, R. S. P., Swart, E., van de Weg, M. J., Callaghan, T. V. and Aerts, R.: Carbon respiration from subsurface peat accelerated by climate warming in the subarctic, Nature, 460, 616–619, doi:10.1038/nature08216, 2009.

Drollinger, S., Kuzyakov, Y. and Glatzel, S.: Catena Effects of peat decomposition on δ^{13}C and δ^{15}N depth profiles of Alpine bogs, Catena, 178(March), 1–10, doi:10.1016/j.catena.2019.02.027, 2019.

Dusenge, M. E., Duarte, A. G. and Way, D. A.: Plant carbon metabolism and climate change: elevated CO_2 and temperature impacts on photosynthesis, photorespiration and respiration, New Phytol., 221, 32–49, doi:10.1111/nph.15283, 2019.

Edwards, K. R., Kaštovská, E., Borovec, J., Šantrůčková, H. and Picek, T.: Species effects and seasonal trends on plant efflux quantity and quality in a spruce swamp forest, Plant Soil, 426(1–2), 179–196, doi:10.1007/s11104-018-3610-0, 2018.

Ehleringer, J. R., Buchmann, N. and Flabagan, L. B.: Carbon Isotope Ratios in Belowground Carbon Cycle Processes, Ecol. Appl., 10(2), 412–422, 2000.

Environment Canada: Historical Weather Data, Gov. Canada [online] Available from: https://climate.weather.gc.ca/historical_data/search_historic_data_e.html, 2021.

Fan, Z., David Mcguire, A., Turetsky, M. R., Harden, J. W., Michael Waddington, J. and Kane, E. S.: The response of soil organic carbon of a rich fen peatland in interior Alaska to projected climate change, Glob. Chang. Biol., 19(2), 604–620, doi:10.1111/gcb.12041, 2013.

Fenner, N. and Freeman, C.: Drought-induced carbon loss in peatlands, Nat. Geosci., 4(December), 0–5, doi:10.1038/ngeo1323, 2011.

Flanagan, L. B. and Syed, K. H.: Stimulation of both photosynthesis and respiration in response to warmer and drier conditions in a boreal peatland ecosystem, Glob. Chang. Biol., 17(7), 2271–2287, doi:10.1111/j.1365-2486.2010.02378.x, 2011.

Flanagan, L. B., Kubien, D. S. and Ehleringer, J. R.: Spatial and temporal variation in the carbon and oxygen stable isotope ratio of respired CO2 in a boreal forest ecosystem, Tellus, Ser. B Chem. Phys. Meteorol., 51(2), 367–384, doi:10.3402/tellusb.v51i2.16306, 1999.

Fraser, C.: The hydrology and dissolved organic carbon (DOC) biogeochemistry in a boreal peatland, McGill University., PhD thesis., 1999.

Frolking, S., Roulet, N. T., Moore, T. R., Lafleur, P. M., Bubier, J. L. and Crill, P. M.: Modeling seasonal to annual carbon balance of Mer Bleue Bog, Ontario, Canada, Global Biogeochem. Cycles, 16(3), doi:10.1029/2001GB001457, 2002.

Frolking, S., Roulet, N. T., Tuittila, E., Bubier, J. L., Quillet, A., Talbot, J. and Richard, P. J. H.: A new model of Holocene peatland net primary production, decomposition, water balance, and peat accumulation, Earth Syst. Dyn. Discuss., 1(1), 115–167, doi:10.5194/esdd-1-115-2010, 2010.

Frolking, S. E., Bubier, J., Moore, T. R., Ball, T., Bellisario, L. M., Bhardwaj, A., Carroll, P., Crill, P. M., Lafleur, P. M., McCaughey, J. H., Roulet, N. T., Suyker, A. E., Verma, S. B., Waddington, J. M. and Whiting, G. J.: Relationship between ecosystem productivity and photosynthetically active radiation for northern peatlands, Global Biogeochem. Cycles, 12(1), 115–126, 1998.

Garnett, M. H., Hardie, S. M. L. and Murray, C.: Radiocarbon analysis reveals that vegetation facilitates the release of old methane in a temperate raised bog, Biogeochemistry, 148(1), 1–17, doi:10.1007/s10533-020-00638-x, 2020.

Gaudinski, J. B., Trumbore, S. E., Eric, A. and Zheng, S.: Soil Carbon Cycling in a Temperate Forest: Radiocarbon-Based Estimates of Residence Times, Sequestration Rates and Partitioning of Fluxes Author (s): Julia B. Gaudinski, Susan E. Trumbore, Eric A. Davidson and Shuhui Zheng Published by: Springer, Biogeochemistry, 51(1), 33–69, 2000.

Gavazov, K., Albrecht, R., Buttler, A., Dorrepaal, E., Garnett, M. H., Gogo, S., Hagedorn, F., Mills, R. T. E., Robroek, B. J. M. and Bragazza, L.: Vascular plant-mediated controls on atmospheric carbon assimilation and peat carbon decomposition under climate change, Glob. Chang. Biol., 24(9), 3911–3921, doi:10.1111/gcb.14140, 2018.

Glatzel, S., Basiliko, N. and Moore, T.: Carbon dioxide and methane production potentials of peats from natural, harvested and restored sites, eastern Quebec, Canada, Wetlands, 24(2), 261–267, 2004.

Griffis, T. J., Rouse, W. R. and Waddington, J. M.: Interannual variability of net ecosystem CO_2 exchange at a subarctic fen, Geography, 14(4), 1109–1121, 2000.

Grogan, P. and Jonasson, S.: Temperature and substrate controls on intra-annual variation in ecosystem respiration in two subarctic vegetation types, Glob. Chang. Biol., 11(3), 465–475, doi:10.1111/j.1365-2486.2005.00912.x, 2005.

Hahn, V., Högberg, P. and Buchmann, N.: ^{14}C - A tool for separation of autotrophic and heterotrophic soil respiration, Glob. Chang. Biol., 12(6), 972–982, doi:10.1111/j.1365-2486.2006.001143.x, 2006.

Hanson, P. J., Edwards, N. T., Garrten, C. T. and Andrews, J. A.: Separating Root and Soil Microbial Contributions to Soil Respiration: A Review of Methods and Observations, Biogeochemistry, 48, 115–146, doi:10.1023/A:1006244819642, 2000.

Hardie, S. M. L., Garnett, M. H., Fallick, A. E., Ostle, N. J. and Rowland, A. P.: Bomb-^{14}C analysis of ecosystem respiration reveals that peatland vegetation facilitates release of old carbon, Geoderma, 153(3–4), 393–401, 2009.

He, H., Meyer, A., Svensson, M., Rütting, T. and Klemedtsson, L.: Simulating ectomycorrhiza in boreal forests: Implementing ectomycorrhizal fungi model MYCOFON in CoupModel (v5), Geosci. Model Dev., 11(2), 725–751, doi:10.5194/gmd-11-725-2018, 2018.

He, H., Jansson, P. E. and Gärdenäs, A. I.: CoupModel (v6.0): An ecosystem model for coupled phosphorus, nitrogen, and carbon dynamics - Evaluated against empirical data from a climatic and fertility gradient in Sweden, Geosci. Model Dev., 14(2), 735–761, doi:10.5194/gmd-14-735-2021, 2021.

Van Hees, P. A. W., Jones, D. L., Finlay, R., Godbold, D. L. and Lundström, U. S.: The carbon we do not see - The impact of low molecular weight compounds on carbon dynamics and respiration in forest soils: A review, Soil Biol. Biochem., 37(1), 1–13, doi:10.1016/j.soilbio.2004.06.010, 2005.

Heimann, M. and Reichstein, M.: Terrestrial ecosystem carbon dynamics and climate feedbacks, Nature, 451(7176), 289–292, doi:10.1038/nature06591, 2008.

Heinemeyer, A., Croft, S., Garnett, M. H., Gloor, E., Holden, J., Lomas, M. R. and Ineson, P.: The MILLENNIA peat cohort model: Predicting past, present and future soil carbon budgets and fluxes under changing climates in peatlands, Clim. Res., 45(1), 207–226, doi:10.3354/cr00928, 2010.

Helbig, M., Humphreys, E. R. and Todd, A.: Contrasting Temperature Sensitivity of CO_2 Exchange in Peatlands of the Hudson Bay Lowlands, Canada, J. Geophys. Res. Biogeosciences, 124(7), 2126–2143, doi:10.1029/2019JG005090, 2019.

Herndon, E. M., Costello, L. K., Duroe, K. A., Mills, J., Kane, E. S., Sebestyen, S. D., Thompson, A. A. and Wullschleger, S. D.: Iron (Oxyhydr) Oxides Serve as Phosphate Traps in Tundra and Boreal Peat Soils, , 227–246, doi:10.1029/2018JG004776, 2019.

Hicks Pries, C. E., Schuur, E. A. G. and Crummer, K. G.: Thawing permafrost increases old soil and autotrophic respiration in tundra: Partitioning ecosystem respiration using δ^{13}C and ^{14}C, Glob. Chang. Biol., 19(2), 649–661, doi:10.1111/gcb.12058, 2013.

Hicks Pries, C. E., Van Logtestijn, R. S. P., Schuur, E. A. G., Natali, S. M., Cornelissen, J. H. C., Aerts, R. and Dorrepaal, E.: Decadal warming causes a consistent and persistent shift from heterotrophic to autotrophic respiration in contrasting permafrost ecosystems, Glob. Chang. Biol., 21(12), 4508–4519, doi:10.1111/gcb.13032, 2015.

Hobbie, E. A., Chen, J., Hanson, P. J., Iversen, C. M., Mcfarlane, K. J., Thorp, N. R. and Hofmockel, K. S.: Long-term carbon and nitrogen dynamics at SPRUCE revealed through stable isotopes in peat profiles, Biogeosciences, 2481–2494, doi:10.5194/bg-14-2481-2017, 2017.

Hogberg, P. and Read, D. J.: Towards a more plant physiological perspective on soil ecology, Trends Ecol. Evol., 21(10), doi:10.1016/j.tree.2006.06.004, 2006.

Humphreys, E. R., Charron, C., Brown, M. and Jones, R.: Two Bogs in the Canadian Hudson Bay Lowlands and a Temperate Bog Reveal Similar Annual Net Ecosystem Exchange of CO_2, Arctic, Antarct. Alp. Res., 46(1), 103–113, doi:10.1657/1938-4246.46.1.103, 2014.

Hungate, B. A., Holland, E. A., Jackson, R. B., FS, C., HA, M. and Cb, F.: The fate of carbon in grasslands under carbon dioxide enrichment, Nature, 388(6642), 576–579, doi:10.1038/41550, 1997.

Inisheva, L. I., Szajdak, L. and Sergeeva, M. A.: Dynamics of biochemical processes and redox conditions in geochemically linked landscapes of oligotrophic bogs, Eurasian Soil Sci., 49(4), 466–474, doi:10.1134/S1064229316040050, 2016.

Iversen, C. M., Childs, J., Norby, R. J., Ontl, T. A., Kolka, R. K., Brice, D. J., McFarlane, K. J. and Hanson, P. J.: Fine-root growth in a forested bog is seasonally dynamic, but shallowly distributed in nutrient-poor peat, Plant Soil, 424(1–2), 123–143, doi:10.1007/s11104-017-3231-z, 2018.

Iversen, C. M., Latimer, J., Brice, D. J., Childs, J., Vander Stel, H. M., Defrenne, C. E., Graham, J., Griffiths, N. A., Malhotra, A., Norby, R. J., Oleheiser, K. C., Phillips, J. R., Salmon, V. G., Sebestyen, S. D., Yang, X. and Hanson, P. J.: Whole-Ecosystem Warming Increases Plant-Available Nitrogen and Phosphorus in an Ombrotrophic Bog, Ecosystems, doi:10.1007/s10021-022-00744-x, 2022.

Jacoby, R., Peukert, M., Succurro, A., Koprivova, A. and Kopriva, S.: The role of soil microorganisms in plant mineral nutrition—current knowledge and future directions, Front. Plant Sci., 8(September), 1–19, doi:10.3389/fpls.2017.01617, 2017.

Janska, V., Jimenez-Alfaro, B., Chytrý, M., Divísek, J., Anenkhonov, O., Korolyuk, A., Lashchinskyi, N. and Culek, M.: Palaeodistribution modelling of European vegetation types at the Last Glacial Maximum using modern analogues from Siberia: Prospects and limitations, Quarternary Sci. Rev., 159, 103–115, doi:10.1016/j.quascirev.2017.01.011, 2017.

Jarveoja, J., Nilsson, M. B., Crill, P. M. and Peichl, M.: Bimodal diel pattern in peatland ecosystem respiration rebuts uniform temperature response, Nat. Commun., 11(4255), 1–9, doi:10.1038/s41467-020-18027-1, 2020.

Järveoja, J., Nilsson, M. B., Gažovič, M., Crill, P. M. and Peichl, M.: Partitioning of the net CO_2 exchange using an automated chamber system reveals plant phenology as key control of production and respiration fluxes in a boreal peatland, Glob. Chang. Biol., 24(8), 3436–3451, doi:10.1111/gcb.14292, 2018.

Jassey, V. E. J. and Signarbieux, C.: Effects of climate warming on Sphagnum photosynthesis in peatlands depend on peat moisture and species-specific anatomical traits, Glob. Chang. Biol., 25(11), 3859–3870, doi:10.1111/gcb.14788, 2019.

Jimenez-Alfaro, B.: Vegetation diversity and conservation of European mires., Provincial Council of Bizkaia., 2018.

Jonasson, S. and Stuart Chapin, F.: Significance of sequential leaf development for nutrient balance of the cotton sedge, Eriophorum vaginatum L., Oecologia, 67(4), 511–518, doi:10.1007/BF00790022, 1985.

Jones, M. C., Peteet, D. M. and Sambrotto, R.: Late-glacial and Holocene $\delta^{15}N$ and $\delta^{13}C$ variation from a Kenai Peninsula, Alaska peatland, Palaeogeogr. Palaeoclimatol. Palaeoecol., 293(1–2), 132–143, doi:10.1016/j.palaeo.2010.05.007, 2010.

Juszczak, R., Humphreys, E., Acosta, M., Michalak-Galczewska, M., Kayzer, D. and Olejnik, J.: Ecosystem respiration in a heterogeneous temperate peatland and its sensitivity to peat temperature and water table depth, Plant Soil, 366, 505–520, doi:10.1007/s11104-012-1441-y, 2013.

Kalacska, M., Arroyo-Mora, J. P., de Gea, J., Snirer, E., Herzog, C. and Moore, T. R.: Videographic analysis of Eriophorum vaginatum spatial coverage in an Ombotrophic bog, Remote Sens., 5(12), 6501–6512, doi:10.3390/rs5126501, 2013.

Keiser, A. D., Smith, M., Bell, S. and Hofmockel, K. S.: Peatland microbial community response to altered climate tempered by nutrient availability, Soil Biol. Biochem., 137(December 2018), 107561, doi:10.1016/j.soilbio.2019.107561, 2019.

Keller, J. K. and Bridgham, S. D.: Pathways of anaerobic carbon cycling across an ombrotrophic – minerotrophic peatland gradient, Limnol. Oceanogr., 52(1), 96–107, 2007.

Knorr K.-H., Glaser, B. and Blodau, C.: Fluxes and ^{13}C isotopic composition of dissolved carbon and pathways of methanogenesis in a fen soil exposed to experimental drought, Biogeosciences, 5, 1457–1473, 2008.

Kohn, M. J.: Carbon isotope compositions of terrestrial C3 plants as indicators of (paleo) ecology and (paleo) climate, PNAS, 107(46), 19691–19695, doi:10.1073/pnas.1004933107, 2010.

Kox, M. A. R., Elzen, E. Van Den, Lamers, L. P. M., Jetten, M. S. M. and Kessel, M. A. H. J. Van: Microbial nitrogen fixation and methane oxidation are strongly enhanced by light in Sphagnum mosses, AMB Express, doi:10.1186/s13568-020-00994-9, 2020.

Krohn, J., Lozanovska, I., Kuzyakov, Y., Parvin, S. and Dorodnikov, M.: Science of the Total Environment CH_4 and CO_2 production below two contrasting peatland micro-relief forms: An inhibitor and $\delta^{13}C$ study, Sci. Total Environ., 586, 142–151, doi:10.1016/j.scitotenv.2017.01.192, 2017.

Krüger, J. P., Leifeld, J. and Alewell, C.: Degradation changes stable carbon isotope depth profiles in palsa peatlands, Biogeosciences, 3369–3380, doi:10.5194/bg-11-3369-2014, 2014.

Kuiper, J. J., Mooij, W. M., Bragazza, L. and Robroek, B. J. M.: Plant functional types define magnitude of drought response in peatland CO_2 exchange, Ecology, 95(1), 123–131, doi:10.1890/13-0270.1, 2014.

Kurbatova, J., Tatarinov, F., Molchanov, A., Varlagin, A., Avilov, V., Kozlov, D., Ivanov, D. and Valentini, R.: Partitioning of ecosystem respiration in a paludified shallow-peat spruce forest in the southern taiga of European Russia, Environ. Res. Lett., 8(4), doi:10.1088/1748-9326/8/4/045028, 2013.

Lafleur, P. M.: Connecting Atmosphere and Wetland: Energy and Water Vapour Exchange, Geogr. Compass, 2(4), 1027–1057, doi:10.1111/j.1749-8198.2007.00132.x, 2008.

Lafleur, P. M., Moore, T. R., Roulet, N. T. and Frolking, S.: Ecosystem Respiration in a Cool Temperate Bog Depends on Peat Temperature But Not Water Table, Ecosystems, 8(6), 619–629, doi:10.1007/s10021-003-0131-2, 2005.

Lai, D. Y. F., Moore, T. R. and Roulet, N. T.: Spatial and temporal variations of methane flux measured by autochambers in a temperate ombrotrophic peatland, J. Geophys. Res., 119, 864–880, doi:10.1002/2013JG002410.Received, 2014a.

Lai, D. Y. F., Roulet, N. T. and Moore, T. R.: The spatial and temporal relationships between CO_2 and CH_4 exchange in a temperate ombrotrophic bog, Atmos. Environ., 89, 249–259, doi:10.1016/j.atmosenv.2014.02.034, 2014b.

Lai, Y. F.: Spatial and Temporal Variations of Carbon Dioxide and Methane Fluxes Measured by Autochambers at the Mer Bleue Bog, McGill University., PhD Thesis., 2012.

Larmola, T., Tuittila, E.-S., Tiirola, M., Nykanen, H., Martikainen, P. J., Yrjala, K., Tuomivirta, T. and Fritze, H.: The role of Sphagnum mosses in the methane cycling of a boreal mire, Ecology, 91(8), 2356–2365, 2010.

Larmola, T., Bubier, J. L., Kobyljanec, C., Basiliko, N., Juutinen, S., Humphreys, E., Preston, M. and Moore, T. R.: Vegetation feedbacks of nutrient addition lead to a weaker carbon sink in an ombrotrophic bog, Glob. Chang. Biol., 19(12), 3729–3739, doi:10.1111/gcb.12328, 2013.

Larmola, T., Kiheri, H., Bubier, J. L., Dijk, N. Van, Dise, N. and Fritze, H.: Impact of simulated atmospheric nitrogen deposition on nutrient cycling and carbon sink via mycorrhizal fungi in two nutrient-poor peatlands, Geophysical Research Abstracts, 19, 3179, 2017.

Lavoie, C., Grosvernier, P., Girard, M. and Marcoux, K.: Spontaneous revegetation of mined peatlands: An useful restoration tool?, Wetl. Ecol. Manag., 11, 97–107, 2003.

Lees, K. J., Artz, R. R. E., Chandler, D., Aspinall, T., Boulton, C. A., Buxton, J., Cowie, N. R. and Lenton, T. M.: Science of the Total Environment Using remote sensing to assess peatland resilience by estimating soil surface moisture and drought recovery, Sci. Total Environ., 761, 143312, doi:10.1016/j.scitotenv.2020.143312, 2021.

Leith, F. I., Garnett, M. H., Dinsmore, K. J., Billett, M. F. and Heal, K. V: Source and age of dissolved and gaseous carbon in a peatland – riparian – stream continuum: a dual isotope (^{14}C and δ^{13}C) analysis, Biogeochemistry, 415–433, doi:10.1007/s10533-014-9977-y, 2014.

Liebner, S., Zeyer, J., Wagner, D., Schubert, C., Pfeiffer, E. and Knoblauch, C.: Methane oxidation associated with submerged brown mosses reduces methane emissions from Siberian polygonal tundra, Journal of Ecology, 914–922, doi:10.1111/j.1365-2745.2011.01823.x, 2011.

Lin, X., Tfaily, M. M., Steinweg, J. M., Chanton, P., Esson, K., Yang, Z. K., Chanton, J. P., Cooper, W., Schadt, C. W. and Kostka, J. E.: Microbial community stratification linked to utilization of carbohydrates and phosphorus limitation in a Boreal Peatland at Marcell Experimental Forest, Minnesota, USA, Appl. Environ. Microbiol., 80(11), 3518–3530, doi:10.1128/AEM.00205-14, 2014.

Lloyd, C. R.: Annual carbon balance of a managed wetland meadow in the Somerset Levels, UK, Agricultural and Forest Meteorology, 138, 168–179, doi:10.1016/j.agrformet.2006.04.005, 2006.

Loader, N. J., Mccarroll, D., Knaap, W. O. Van Der, Robertson, I. and Gagen, M.: Characterizing carbon isotopic variability in Sphagnum, The Holocene, 3, 403–410, 2007.

Loader, N. J., Mauquoy, D., Roland, T. P., Bellen, S. V. A. N., Daley, T. J., Davies, D., Hughes, P. D. M., Pancotto, V. O., Young, G. H. F., Amesbury, M. J., Charman, D. J. and Mallon, G.: Measurements of hydrogen , oxygen and carbon isotope variability in Sphagnum moss along a micro-topographical gradient in a southern Patagonian peatland, Journal of Quaternary Science, 31, 426–435, doi:10.1002/jqs.2871, 2016.

Loisel, J., Yu, Z., Beilman, D. W., Camill, P., Alm, J., Amesbury, M. J., Anderson, D., Andersson, S., Bochicchio, C., Barber, K., Belyea, L. R., Bunbury, J., Chambers, F. M., Charman, D. J., Vleeschouwer, F. De, Fiałkiewicz-kozieł, B., Finkelstein, S. A., Gałka, M., Garneau, M., Hammarlund, D., Hinchcliffe, W., Holmquist, J., Hughes, P., Jones, M. C., Klein, E. S., Kokfelt, U., Korhola, A., Kuhry, P., Lamarre, A., Lamentowicz, M., Large, D., Lavoie, M., Macdonald, G., Mäkilä, M., Mallon, G., Mathijssen, P., Mauquoy, D., Moore, T. R., Nichols, J., Reilly, B. O., Oksanen, P., Packalen, M., Peteet, D., Richard, P. J. H., Robinson, S., Ronkainen, T., Rundgren, M., Sannel, A. B. K., Tarnocai, C., Thom, T., Tuittila, E. S., Turetsky, M. R., Valiranta, M., van der Linden, M., van Geel, B., van Bellen, S., Vitt, D. H., Zhao, Y. and Zhou, W.: A database and synthesis of northern peatland soil properties and Holocene carbon and nitrogen accumulation, Holocene Spec. Issue, 24(9), 1028–1042, doi:10.1177/0959683614538073, 2014.

Lu, F., Wu, J., Yi, B., Xu, Z., Wang, M., Sundberg, S. and Bu, Z. J.: Long-Term Phosphorus Addition Strongly Weakens the Carbon Sink Function of a Temperate Peatland, Ecosystems, doi:10.1007/s10021-022-00754-9, 2022.

Lu, L.: The cascade of Dissolved Organic Matter Through an Ombrotrophic Bog, McGill University., Master's thesis., 2019.

Maier, C. A. and Kress, L. W.: Soil CO_2 evolution and root respiration in 11 year-old loblolly pine (Pinus taeda) plantations as affected by moisture and nutrient availability, Can. J. For. Res., 30(3), 347–359, doi:10.1139/cjfr-30-3-347, 2000.

Mäkiranta, P., Riutta, T., Penttilä, T. and Minkkinen, K.: Dynamics of net ecosystem CO_2 exchange and heterotrophic soil respiration following clearfelling in a drained peatland forest, Agric. For. Meteorol., 150(12), 1585–1596, doi:10.1016/j.agrformet.2010.08.010, 2010.

Malhotra, A., Brice, D. J., Childs, J., Graham, J. D., Hobbie, E. A., Vander Stel, H., Feron, S. C., Hanson, P. J. and Iversen, C. M.: Peatland warming strongly increases fine-root growth, Proc. Natl. Acad. Sci. U. S. A., 117(30), 17627–17634, doi:10.1073/pnas.2003361117, 2020.

Manzoni, S. and Porporato, A.: Soil carbon and nitrogen mineralization: Theory and models across scales, Soil Biol. Biochem., 41(7), 1355–1379, doi:10.1016/j.soilbio.2009.02.031, 2009.

Marinier, M., Glatzel, S. and Moore, T.: The role of cotton-grass (Eriophorum vaginatum) in the exchange of CO_2 and CH_4 at two restored peatlands, eastern Canada, Ecoscience, 11(2), 141–149, 2004.

Mccarter, C. P. R. and Price, J. S.: Ecohydrology of Sphagnum moss hummocks: Mechanisms of capitula water supply and simulated effects of evaporation, Ecohydrology, 7(1), 33–44, doi:10.1002/eco.1313, 2014.

McGill, W. B. and Cole, C. V.: Comparative aspects of cycling of organic C, N, S an P through soil organic matter, Geoderma, 26, 267–286 [online] Available from: papers2://publication/uuid/C9FDF338-7106-4C1A-AE5B-64CC25970798, 1981.

Melling, L., Hatano, R. and Goh, K. J.: Soil CO_2 flux from three ecosystems in tropical peatland of Sarawak, Tellus B Chem. Phys. Meteorol., 57(1), doi:10.3402/tellusb.v57i1.16772, 2017.

Metcalfe, D. B., Fisher, R. A. and Wardle, D. A.: Plant communities as drivers of soil respiration: Pathways, mechanisms, and significance for global change, Biogeosciences, 8(8), 2047–2061, doi:10.5194/bg-8-2047-2011, 2011.

Migliavacca, M., Musavi, T., Mahecha, M. D., Nelson, J. A., Knauer, J., Baldocchi, D. D., Perez-priego, O., Christiansen, R., Peters, J., Anderson, K., Bahn, M., Black, T. A., Blanken, P. D., Bonal, D., Buchmann, N., Caldararu, S., Carrara, A., Carvalhais, N., Cescatti, A., Chen, J., Cleverly, J., Cremonese, E., Desai, A. R., El-madany, T. S., Farella, M. M., Fernández-martínez, M., Filippa, G., Forkel, M., Galvagno, M., Gomarasca, U., Gough, C. M., Göckede, M., Ibrom, A., Ikawa, H., Janssens, I. A., Jung, M., Kattge, J., Keenan, T. F., Knohl, A., Kobayashi, H., Kraemer, G., Law, B. E., Liddell, M. J., Ma, X., Mammarella, I., Martini, D., Macfarlane, C., Matteucci, G., Montagnani, L., Pabon-moreno, D. E., Panigada, C., Papale, D., Pendall, E., Penuelas, J., Phillips, R. P., Reich, P. B., Rossini, M., Rotenberg, E., Scott, R. L., Stahl, C., Weber, U., Wohlfahrt, G., Wolf, S., Wright, I. J., Yakir, D., Zaehle, S. and Reichstein, M.: The three major axes of terrestrial ecosystem function, Nature, 598(October), doi:10.1038/s41586-021-03939-9, 2021.

Minkkinen, K., Laine, J., Shurpali, N. J., Makiranta, P., Alm, J. and Penttilä, T.: Heterotrophic soil respiration in forestry-drained peatlands, Boreal Environ. Res., 12(May), 115–126, 2007.

Mitsch, W. J. and Gosselink, J. G.: Wetlands, 4th ed., John Wiley & Sons., 2007.

Moinet, G. Y. K., Hunt, J. E., Kirschbaum, M. U. F., Morcom, C. P., Midwood, A. J. and Millard, P.: The temperature sensitivity of soil organic matter decomposition is constrained by microbial access to substrates, Soil Biol. Biochem., 116(November 2017), 333–339, doi:10.1016/j.soilbio.2017.10.031, 2018.

Moore, P. D.: Wetlands, revised., Facts on File Inc., 2008.

Moore, T. R., Bubier, J. L., Frolking, S. E., Lafleur, P. M. and Roulet, N. T.: Plant biomass and production and CO_2 exchange in an ombrotrophic bog, J. Ecol., 90(1), 25–36, doi:10.1046/j.0022-0477.2001.00633.x, 2002.

Morris, P. J., Belyea, L. R. and Baird, A. J.: Ecohydrological feedbacks in peatland development: a theoretical modelling study, Journal of Ecology., 1190–1201, doi:10.1111/j.1365-2745.2011.01842.x, 2011.

Murphy, M., Laiho, R. and Moore, T. R.: Effects of water table drawdown on root production and aboveground biomass in a boreal Bog, Ecosystems, 12(8), 1268–1282, doi:10.1007/s10021-009-9283-z, 2009a.

Murphy, M. T. and Moore, T. R.: Linking root production to aboveground plant characteristics and water table in a temperate bog, Plant Soil, 336(1), 219–231, doi:10.1007/s11104-010-0468-1, 2010.

Murphy, M. T., McKinley, A. and Moore, T. R.: Variations in above-and below-ground vascular plant biomass and water table on a temperate ombrotrophic peatland, Botany, 87(9), 845–853, doi:10.1139/B09-052, 2009b.

Nijp, J. J., Metselaar, K., Limpens, J., Teutschbein, C., Peichl, M., Nilsson, M. B., Berendse, F. and van der Zee, S. E. A. T. M.: Including hydrological self-regulating processes in peatland models: Effects on peatmoss drought projections, Sci. Total Environ., 580, 1389–1400, doi:10.1016/j.scitotenv.2016.12.104, 2017.

Nilsson, M., Sagerfors, J., Buffam, I., Laudon, H., Eriksson, T., Grelle, A., Klemedtsson, L., Weslien, P. and Lindroth, A.: Contemporary carbon accumulation in a boreal oligotrophic minerogenic mire - A significant sink after accounting for all C-fluxes, Glob. Chang. Biol., 14(10), 2317–2332, doi:10.1111/j.1365-2486.2008.01654.x, 2008.

Norby, R. J., Childs, J., Hanson, P. J. and Warren, J. M.: Rapid loss of an ecosystem engineer: Sphagnum decline in an experimentally warmed bog, Ecology and Evolution, (September), 12571–12585, doi:10.1002/ece3.5722, 2019.

Normand, A. E., Turner, B. L., Lamit, L. J., Smith, A. N., Baiser, B., Clark, M. W., Hazlett, C., Kane, E. S., Lilleskov, E., Long, J. R., Grover, S. P. and Reddy, K. R.: Organic Matter Chemistry Drives Carbon Dioxide Production of Peatlands, Geophys. Res. Lett., 48, 1–9, doi:10.1029/2021GL093392, 2021.

O’Connell, K. E. B., Gower, S. T. and Norman, J. M.: Net ecosystem production of two contrasting boreal black spruce forest communities, Ecosystems, 6(3), 248–260, doi:10.1007/s10021-002-0202-9, 2003.

Ohno, T. and Zibilske, L. M.: Determination of Low Concentrations of Phosphorus in Soil Extracts Using Malachite Green, Soil Sci. Soc. Am. J., 55(3), 892–895, doi:10.2136/sssaj1991.03615995005500030046x, 1991.

Ojanen, P., Minkkinen, K., Lohila, A., Badorek, T. and Penttilä, T.: Chamber measured soil respiration: A useful tool for estimating the carbon balance of peatland forest soils?, For. Ecol. Manage., 277, 132–140, doi:10.1016/j.foreco.2012.04.027, 2012.

Oke, T. A. and Hager, H. A.: Plant community dynamics and carbon sequestration in Sphagnum-dominated peatlands in the era of global change, Glob. Ecol. Biogeogr., 29(10), 1610–1620, doi:10.1111/geb.13152, 2020.

Pataki, D. E., Ehleringer, J. R., Flanagan, L. B., Yakir, D., Bowling, D. R., Still, C. J., Buchmann, N., Kaplan, J. O. and Berry, J. A.: The application and interpretation of Keeling plots in terrestrial carbon cycle research, Global Biogeochem. Cycles, 17(1), doi:10.1029/2001GB001850, 2003.

Peichl, M., Öquist, M., Ottosson Löfvenius, M., Ilstedt, U., Sagerfors, J., Grelle, A., Lindroth, A. and Nilsson, M. B.: A 12-year record reveals pre-growing season temperature and water table level threshold effects on the net carbon dioxide exchange in a boreal fen, Environ. Res. Lett., 9(5), doi:10.1088/1748-9326/9/5/055006, 2014.

Pelletier, L., Moore, T. R., Roulet, N. T., Garneau, M. and Beaulieu-Audy, V.: Carbon dioxide and methane fluxes of three peatlands in the La Grande Rivière watershed, James Bay lowland, Canada, J. Geophys. Res. Biogeosciences, 112(1), 2007.

Phillips, C. L., Bond-Lamberty, B., Desai, A. R., Lavoie, M., Risk, D., Tang, J., Todd-Brown, K. and Vargas, R.: The value of soil respiration measurements for interpreting and modeling terrestrial carbon cycling, Plant Soil, 413, 1–25, doi:10.1007/s11104-016-3084-x, 2017.

Pirk, N., Mastepanov, M., Parmentier, F. W., Lund, M. and Crill, P.: Calculations of automatic chamber flux measurements of methane and carbon dioxide using short time series of concentrations, Biogeosciences, 903–912, doi:10.5194/bg-13-903-2016, 2016.

Porporato, A., Daly, E. and Rodriguez-Iturbe, I.: Soil water balance and ecosystem response to climate change, Am. Nat., 164(5), 625–632, doi:10.1086/424970, 2004.

Pouliot, R., Rochefort, L. and Karofeld, E.: Initiation of microtopography in re-vegetated cutover peatlands: Evolution of plant species composition, Appl. Veg. Sci., 15(3), 369–382, doi:10.1111/j.1654-109X.2011.01164.x, 2012.

Price, G. D., Hoper, T., Mckenzie, J. E. and Pilcher, J. R.: Carbon-isotope variation in Sphagnum from hummock-hollow complexes: implications for Holocene climate reconstruction, The Holocene., 7(2)., 229–233, 1996.

Rankin, T. E., Roulet, N. T. and Moore, T. R.: Controls on autotrophic and heterotrophic respiration in an ombrotrophic bog, Biogeosciences, 19, 3285-3303, https://doi.org/10.5194/bg-19-3285-2022, 2022.

Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., Berbigier, P., Bernhofer, C., Buchmann, N., Gilmanov, T., Granier, A., Grunwald, T., Havrankova, K., Ilvesniemi, H., Janous, D., Knohl, A., Laurila, T., Lohila, A., Loustau, D., Matteucci, G., Meyers, T., Miglietta, F., Ourcival, J.-M., Pumpanen, J., Rambal, S., Rotenberg, E., Sanz, M., Tenhunen, J., Seufert, G., Vaccari, F., Vesala, T., Yakir, D. and Valentini, R.: On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm, Glob. Chang. Biol., 11, 1424–1439, doi:10.1111/j.1365-2486.2005.001002.x, 2005.

Reimer, P., Bard, E., Bayliss, A., Beck, J. W., Blackwell, P., Ramsey, C. B., Buck, C., Cheng, H., Edwards, R. L., Friedrich, M., Reimer, P., Bard, E., Bayliss, A., Beck, J. W. and Blackwell, P.: IntCal13 and Marine13 Radiocarbon Age Calibration Curves 0 – 50 , 000 Years cal BP To cite this version : HAL Id : hal-02470111, Radiocarbon, 55(4), 1869–1887, 2013.

Rewcastle, K. E., Moore, J. A. M., Henning, J. A., Mayes, M. A., Patterson, C. M., Wang, G., Metcalfe, D. B. and Classen, A. T.: Investigating drivers of microbial activity and respiration in a forested bog, Pedosphere, 30(1), 135–145, 2020.

Robroek, B. J. M., Albrecht, R. J. H., Hamard, S., Pulgarin, A., Bragazza, L., Buttler, A. and Jassey, V. E. J.: Peatland vascular plant functional types affect dissolved organic matter chemistry, Plant Soil, 407, 135–143, doi:10.1007/s11104-015-2710-3, 2016.

Roulet, N. T., Lafleur, P. M., Richard, P. J. H., Moore, T. R., Humphreys, E. R. and Bubier, J.: Contemporary carbon balance and late Holocene carbon accumulation in a northern peatland, Glob. Chang. Biol., 13(2), 397–411, doi:10.1111/j.1365-2486.2006.01292.x, 2007.

Ryan, M. G. and Law, B. E.: Interpreting, measuring, and modeling soil respiration, Biogeochemistry, 73(1), 3–27, doi:10.1007/s10533-004-5167-7, 2005.

Schuur, E. A. G. and Trumbore, S. E.: Partitioning sources of soil respiration in boreal black spruce forest using radiocarbon, Glob. Chang. Biol., 12, 165–176, doi:10.1111/j.1365-2486.2005.01066.x, 2006.

Serk, H. and Schleucher, J.: CO_2 fertilization of Sphagnum peat mosses is modulated by water table level and other environmental factors, (August 2020), 1756–1768, doi:10.1111/pce.14043, 2021.

Shao, S.: Modeling microbial dynamics and nutrient cycles in ombrotrophic peatlands, McGill University., PhD Thesis., 2022.

Shao, S., Wu, J., He, H. and Roulet, N.: Integrating McGill Wetland Model (MWM) with peat cohort tracking and microbial controls, Sci. Total Environ., 806, 151223, doi:10.1016/j.scitotenv.2021.151223, 2022.

Smolders, A. J. P., Tomassen, H. B. M., Pijnappel, H. W., Lamers, L. P. M. and Roelofs, J. G. M.: Substrate-derived CO_2 is important in the development of Sphagnum spp., New Phytol., 152(2), 325–332, doi:10.1046/j.0028-646X.2001.00261.x, 2001.

St-Hilaire, F., Wu, J., Roulet, N. T., Frolking, S., Lafleur, P. M., Humphreys, E. R. and Arora, V.: McGill wetland model: Evaluation of a peatland carbon simulator developed for global assessments, Biogeosciences Discuss., 5(2), 1689–1725 [online] Available from: https://hal.archives-ouvertes.fr/hal-00297998, 2008.

St-Jean, G., Kieser, W. E., Crann, C. A. and Murseli, S.: Semi-Automated Equipment for CO_2 Purification and Graphitization at the A.E. Lalonde AMS Laboratory (Ottawa, Canada), Radiocarbon, 59(3), 941–956, doi:10.1017/RDC.2016.57, 2017.

Stewart, H.: Partitioning belowground respiration in a northern peatland, McGill University., PhD Thesis., 2006.

Strack, M.: Peatlands and Climate Change, edited by Dr. Maria Strack, International Peat Society., 2008.

Straková, P., Penttilä, T., Laine, J. and Laiho, R.: Disentangling direct and indirect effects of water table drawdown on above- and belowground plant litter decomposition: Consequences for accumulation of organic matter in boreal peatlands, Glob. Chang. Biol., 18(1), 322–335, doi:10.1111/j.1365-2486.2011.02503.x, 2012.

Sulman, B. N., Desai, A. R., Saliendra, N. Z., Lafleur, P. M., Flanagan, L. B., Sonnentag, O., MacKay, D. S., Barr, A. G. and Van Der Kamp, G.: CO_2 fluxes at northern fens and bogs have opposite responses to inter-annual fluctuations in water table, Geophys. Res. Lett., 37(19), 3–7, doi:10.1029/2010GL044018, 2010.

Tarnocai, C.: The effect of climate change on carbon in Canadian peatlands, Glob. Planet. Change, 53(4), 222–232, doi:10.1016/j.gloplacha.2006.03.012, 2006.

Tarnocai, C., Kettles, I. and Ballard, M.: Peatlands of Canada, Geol. Surv. Canada open file 6561, doi:https://doi.org/10.4095/288786, 2011.

Teklemariam, T. A., Lafleur, P. M., Moore, T. R., Roulet, N. T. and Humphreys, E. R.: The direct and indirect effects of inter-annual meteorological variability on ecosystem carbon dioxide exchange at a temperate ombrotrophic bog, Agric. For. Meteorol., 150(11), 1402–1411, doi:10.1016/j.agrformet.2010.07.002, 2010.

Turetsky, M. R. and Wieder, R. K.: Boreal bog Sphagnum refixes soil-produced and respired $^{14}CO_2$, Ecoscience, 6(4), 587–591, doi:10.1080/11956860.1999.11682559, 1999.

Waddington, J. M., Strack, M. and Greenwood, M. J.: Toward restoring the net carbon sink function of degraded peatlands: Short-term response in CO_2 exchange to ecosystem-scale restoration, J. Geophys. Res., 115(G1), G01008, doi:10.1029/2009JG001090, 2010.

Waddington, J. M., Morris, P. J., Kettridge, N., Granath, G., Thompson, D. K. and Moore, P. a.: Hydrological feedbacks in northern peatlands, Ecohydrology, 8(1), 113–127, doi:10.1002/eco.1493, 2015.

Wang, J., Song, C., Zhang, J., Wang, L., Zhu, X. and Shi, F.: Catena Temperature sensitivity of soil carbon mineralization and nitrous oxide emission in different ecosystems along a mountain wetland-forest ecotone in the continuous permafrost of Northeast China, Catena, 121, 110–118, doi:10.1016/j.catena.2014.05.007, 2014a.

Wang, M., Larmola, T., Murphy, M. T., Moore, T. R. and Bubier, J. L.: Stoichiometric response of shrubs and mosses to long-term nutrient (N, P and K) addition in an ombrotrophic peatland, Plant Soil., 403–416, doi:10.1007/s11104-015-2744-6, 2016.

Wang, X., Liu, L., Piao, S., Janssens, I. A., Tang, J., Liu, W., Chi, Y., Wang, J. and Xu, S.: Soil respiration under climate warming: Differential response of heterotrophic and autotrophic respiration, Glob. Chang. Biol., 20(10), 3229–3237, doi:10.1111/gcb.12620, 2014b.

Wang, Z.: The change of ecosystem carbon fluxes with permafrost thaw: dominant factors and biogeochemical mechanisms in a subarctic peatland, McGill University., PhD Thesis., [online] Available from: http://digitool.library.mcgill.ca/webclient/DeliveryManager?pid=146941&custom_att_2=direct, 2016.

Wang, Z. and Roulet, N.: Comparison of plant litter and peat decomposition changes with permafrost thaw in a subarctic peatland, Plant Soil, 417, 197–216, doi:10.1007/s11104-017-3252-7, 2017.

Warren, J. M., Jensen, A. M., Ward, E. J., Guha, A., Childs, J., Wullschleger, S. D. and Hanson, P. J.: Divergent species-specific impacts of whole ecosystem warming and elevated CO_2 on vegetation water relations in an ombrotrophic peatland, Glob. Chang. Biol., 27(9), 1820–1835, doi:10.1111/gcb.15543, 2021.

Werner, C., Schnyder, H., Cuntz, M., Keitel, C., Zeeman, M. J., Dawson, T. E., Badeck, F. and Brugnoli, E.: Progress and challenges in using stable isotopes to trace plant carbon and water relations across scales, Biogeosciences., 3083–3111, doi:10.5194/bg-9-3083-2012, 2012.

Wingler, A., Lea, P. J., Quick, W. P. and Leegood, R. C.: Photorespiration: metabolic pathways and their role in stress protection, Phil.Trans. R. Soc. Lond. B., doi:10.1098/rstb.2000.0712, 2000.

Wu, J., Roulet, N. T., Sagerfors, J. and Nilsson, M. B.: Simulation of six years of carbon fluxes for a sedge-dominated oligotrophic minerogenic peatland in Northern Sweden using the McGill Wetland Model (MWM), J. Geophys. Res. Biogeosciences, 118(2), 795–807, doi:10.1002/jgrg.20045, 2013.

Xu, J., Morris, P. J., Liu, J. and Holden, J.: Catena PEATMAP: Refining estimates of global peatland distribution based on a meta-analysis, Catena., 160(April 2017), 134–140, doi:10.1016/j.catena.2017.09.010, 2018.

Yang, Y., Siegwolf, R. T. W. and Körner, C.: Species specific and environment induced variation of $\delta^{13}C$ and $\delta^{15}N$ in alpine plants, Frontiers in Plant Science., 6(June), 1–14, doi:10.3389/fpls.2015.00423, 2015.

Zeh, L., Theresa Igel, M., Schellekens, J., Limpens, J., Bragazza, L. and Kalbitz, K.: Vascular plants affect properties and decomposition of moss-dominated peat, particularly at elevated temperatures, Biogeosciences, 17(19), 4797–4813, doi:10.5194/bg-17-4797-2020, 2020.

Appendix A – Figures for Chapter 1

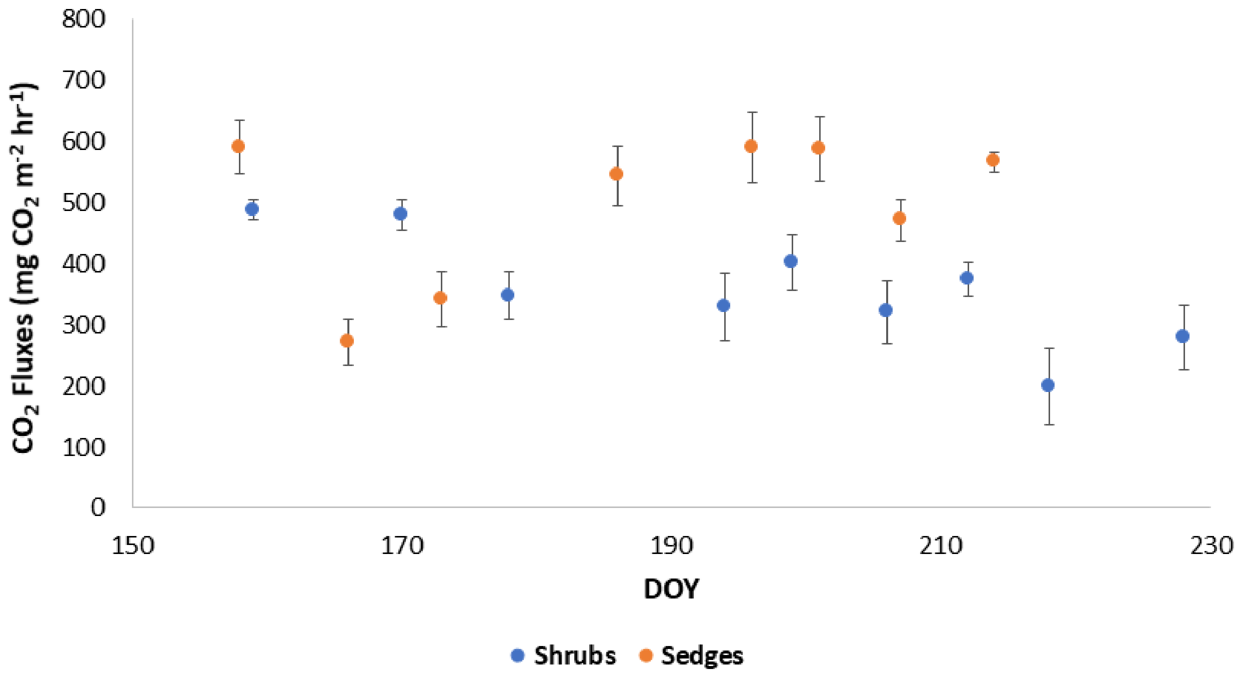


Figure A1 CO_2 fluxes for the shrubs and sedges from the manual chambers in 2017 (+/- standard error)

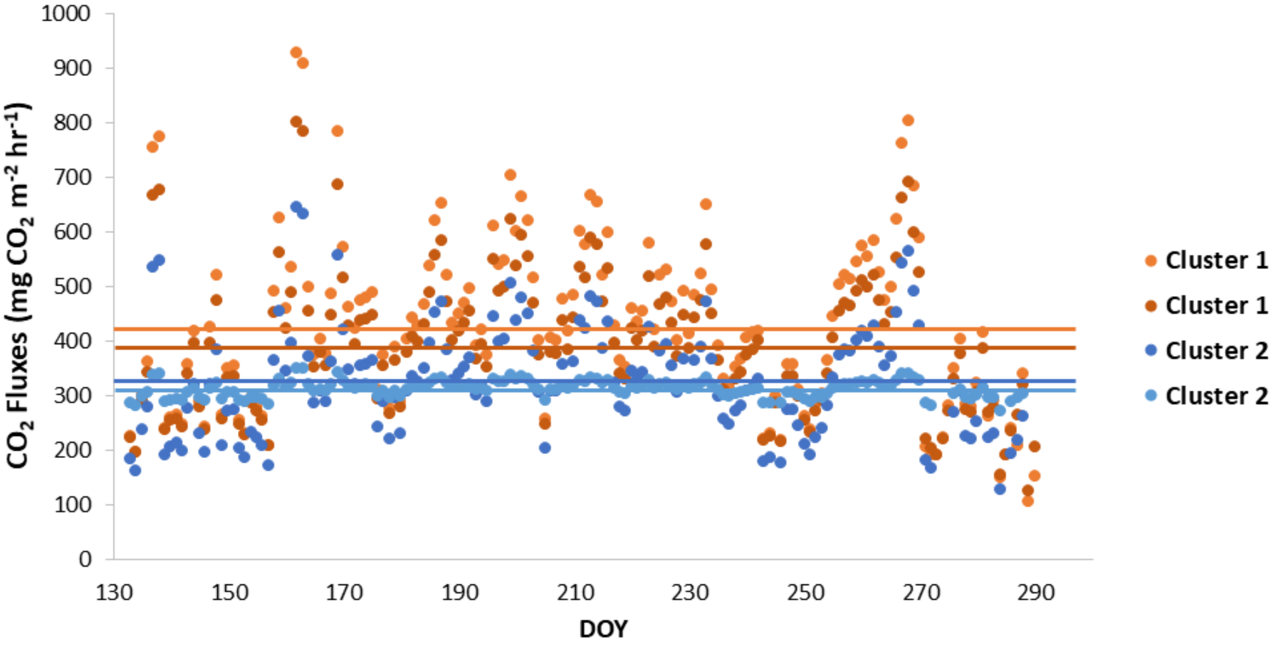


Figure A2 CO$_2$ fluxes from the automatic chamber plots in 2017. Note: One of the CO$_2$ flux time series from Cluster 1 is missing due to instrument error. The solid lines depict the growing season average ecosystem respiration.

Appendix B – Figures and Table for Chapter 3

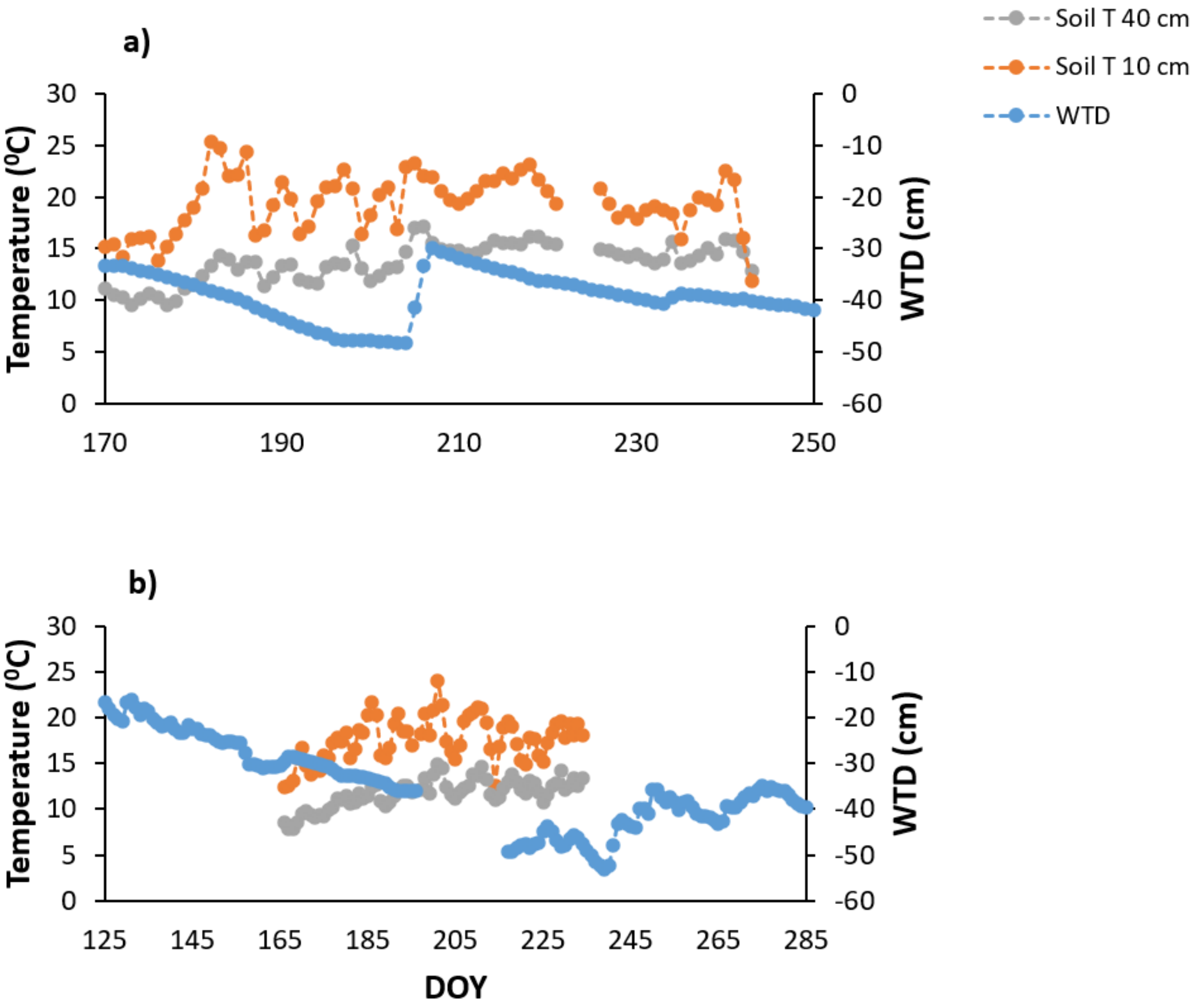


Figure B1 Continuous measures of soil temperatures (Soil T) at 10 cm and 40 cm and water table depth (WTD) for the growing seasons of a) 2018 and b) 2019 derived from the eddy covariance tower near the manual chamber set up.

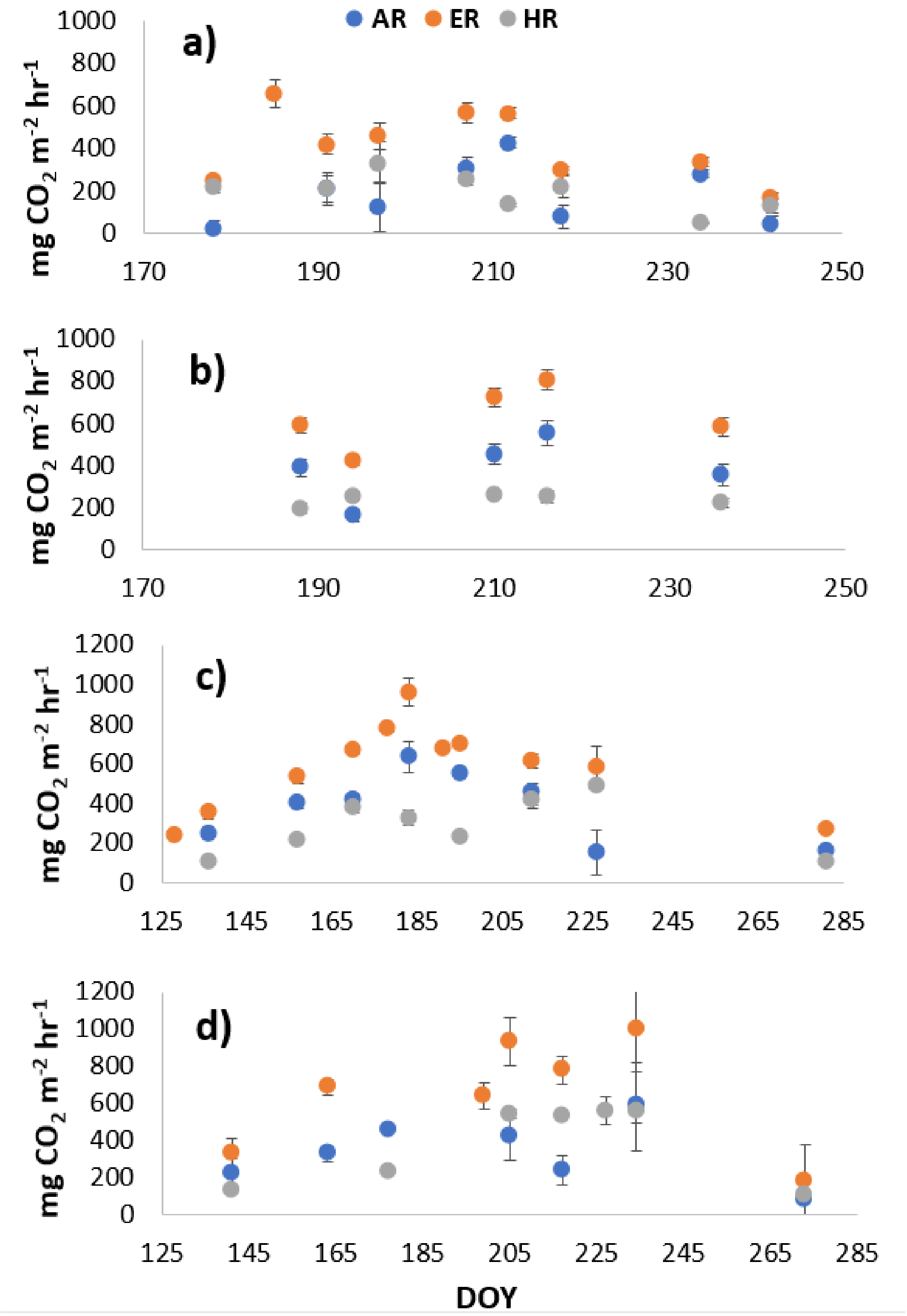


Figure B2 Average CO$_2$ fluxes in the a) shrub plots and b) sedge plots across the growing season of 2018, and CO$_2$ fluxes in the c) shrub plots and d) sedge plots across the growing season of 2019.

Table B1 Correlation coefficients for relationships between respiration (ER, AR and HR) and environmental variables in 2018 and 2019. WT is water table depth, Air T is air temperature measured at the flux tower, Soil T is soil temperature at 10 cm depth.

Environmental Variable		**Shrubs**			**Sedges**		
		ER	**HR**	**AR**	**ER**	**HR**	**AR**
Air T	**2018**	**0.76**	**0.86**	0.33	**0.77**	**0.86**	0.65
	2019	**0.85**	**0.86**	**0.79**	**0.80**	**0.67**	**0.81**
Soil T	**2018**	**0.79**	**0.76**	0.46	0.65	**0.80**	0.74
	2019	0.60	0.52	0.71	**0.75**	0.52	**0.88**
WT	**2018**	-0.17	-0.49	0.12	0.14	-0.06	0.39
	2019	-0.09	-0.70	-0.08	-0.56	**-0.80**	-0.45

Appendix C: Figure for Chapter 5

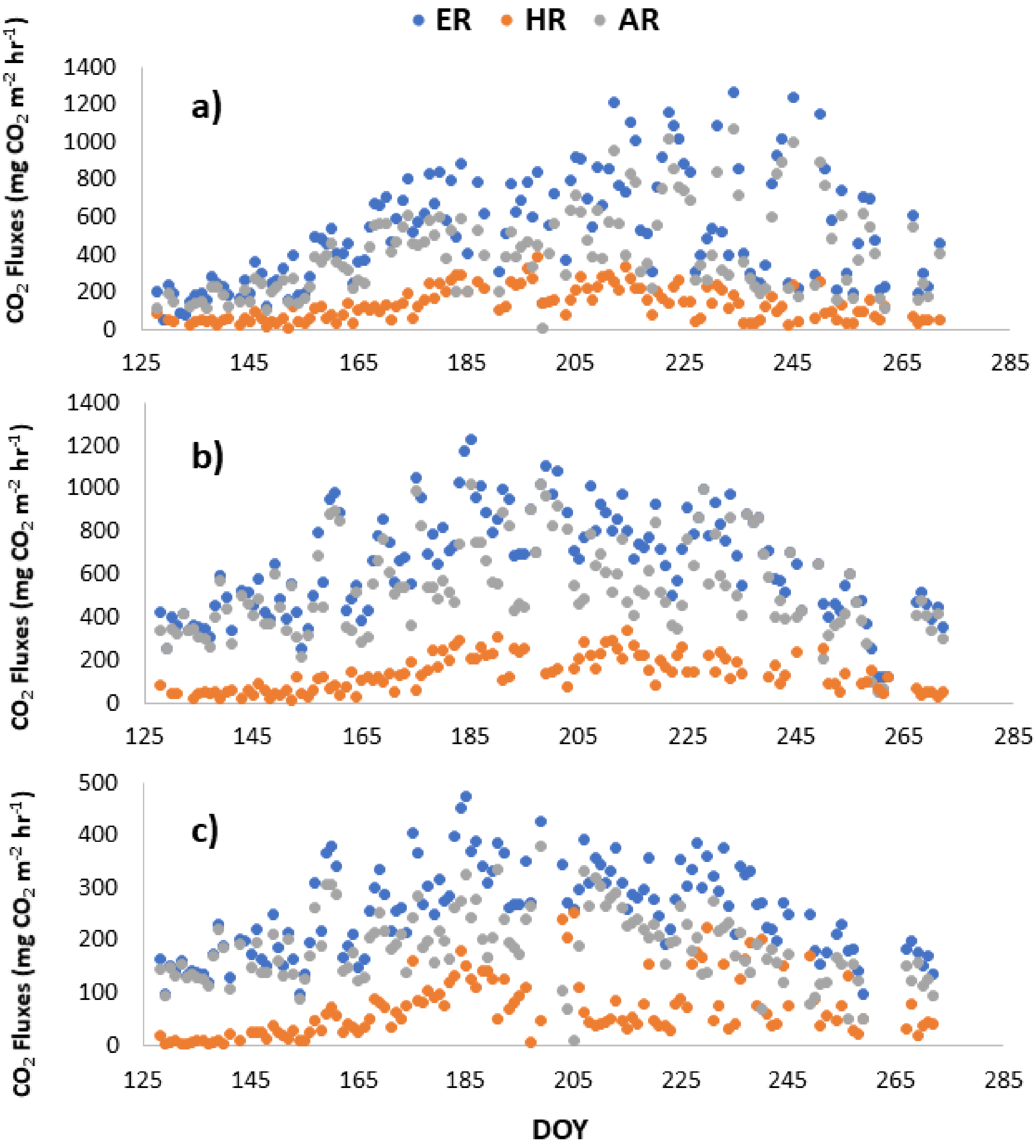


Figure C1 ER, HR, and AR fluxes in 2019 for the a) darkened plot and b) reference plot in cluster 1, and c) reference plot in cluster 2.