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Magnitude and controls on the net carbon balance of a New Zealand raised bog

A thesis
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of the requirements for the degree
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Abstract

Peatlands play an important role in the Earth system as both persistent carbon dioxide (CO_2) sinks and methane (CH_4) sources. However, large uncertainties remain in our understanding of peatland carbon cycle – climate feedbacks. The majority of research has been conducted in the Northern Hemisphere as most of the global peatland area is located there. Few data have been collected in Southern Hemisphere peatlands and there is a limited basis for predicting how these systems will respond to changing climatic drivers and other anthropogenic forcings such as drainage for agriculture. Furthermore, it is unclear whether our knowledge of peatland functioning and carbon (C) cycling from the Northern Hemisphere translates to systems that have developed under different climatic and hydrologic settings with unique vegetation.

To gain a better understanding of peatland carbon and greenhouse gas exchange in a globally distinct and unique peatland type, I used eddy covariance to measure net ecosystem CO_2 exchange (NEE) and CH_4 flux (F_{CH_4}) in an undisturbed New Zealand raised bog over ~2.5 years. The overarching goals of this research were to determine magnitudes of the main components of the ecosystem C budget, gross primary production (GPP), ecosystem respiration (ER), and F_{CH_4} , and their sensitivity to environmental and physical drivers.

With respect to CO_2 exchange, high VPD periods restricted the light-saturated photosynthetic capacity during clear sky days. Elevated VPD was also the only condition that led to reductions in daily total GPP, a response likely triggered to reduce transpiration water losses. These results have important implications for

the future C sink strength of New Zealand peatlands given a trend toward drier summers with clearer skies and higher VPD.

With respect to F_{CH_4} , a severe drought during summer 2013 allowed me to explore the interacting controls of temperature and water table depth. During 2012, a relatively average meteorological year, annual total F_{CH_4} was $21.5 \text{ g CH}_4\text{-C m}^{-2} \text{ yr}^{-1}$, whereas total F_{CH_4} during the drought year (2013) was $14.5 \text{ g CH}_4\text{-C m}^{-2} \text{ yr}^{-1}$. I found that water table depth was the most important overarching control on F_{CH_4} over various timescales from weekly to inter-annual. Water table depth regulated the temperature sensitivity of F_{CH_4} , which was highest when the water table was within 50 – 80 mm of the surface. This depth range corresponds to the relatively shallow rooting zone of the dominant vegetation, which may provide much of the substrate for methane production.

Kopuatai bog was a very strong C sink compared to Northern Hemisphere bogs and fens. Despite the elevated ER during the drought year, Kopuatai was a sink of 74.5 gC m^{-2} , which is at the high end of published Northern Hemisphere estimates. The more average meteorological year (2012) resulted in a much larger sink of 152 gC m^{-2} . This work has revealed the importance of atmospheric controls on plant CO_2 uptake and hydrologic (i.e. water table) effects on ecosystem respiration and F_{CH_4} , when considering the overall C balance. These effects imply that the future C sink capacity of Kopuatai bog may be reduced due to the long-term trend toward drier, sunnier summers and more frequent droughts in the region.

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Chapter 1. Introduction

1.1. Threats to the global peatland carbon sink

Peatlands classified as bog or fen cover approximately 0.5 – 3% of global land area (Lehner and Döll, 2004; Yu et al., 2010). Relative to their areal extent, these peatlands store large amounts of carbon (C) with estimates ranging from 30 – 50% of the global soil carbon pool (Blodau, 2002; Yu et al., 2010). This C has accumulated throughout the Holocene due to the small but persistent imbalance of plant CO₂ uptake over ecosystem C losses (Gorham, 1991), largely due to the saturated conditions and low nutrient litter that restrict decomposition rates (Aerts, 1997; Belyea, 1996).

Peatland carbon fluxes are sensitive to environmental drivers and, because of the size of global peatland C stocks, there is growing concern about potential climate feedbacks associated with losing this C back to the atmosphere (Frolking et al., 2011; Gorham, 1991; Limpens et al., 2008; Roulet, 2000). Although most peatlands are net annual CO₂ sinks, extreme climate events such as droughts can result in annual C losses or reduced gains (Alm et al., 1999; Aurela et al., 2007; Bubier et al., 2003; Griffis et al., 2000; Lund et al., 2012; Roulet et al., 2007). In addition, the saturated conditions that restrict aerobic decomposition lead to substantial production and emission of CH₄ (Dise, 1993; Freeman et al., 2002; Lai, 2009; Moore and Roulet, 1993; Whalen, 2005). As a result, peatlands are significant global sources of atmospheric CH₄ (Kirschke et al., 2013), and despite contributing a relatively small percentage of the overall carbon balance, CH₄ is estimated to be 28.5 times more potent as a greenhouse gas than CO₂, considering a 100-year time horizon (IPCC, 2013). This leads to contrasting

climate impacts of peatland CO₂ uptake (net cooling effect on the atmosphere) and CH₄ emission (net warming effect on the atmosphere). Therefore, understanding both aspects of peatland carbon cycling is critical towards reducing the uncertainty associated with establishing the current and future role of peatlands in the Earth system (Frolking et al., 2011). For example, Frolking et al. (2006) demonstrated that over the 'lifetime' of a typical peatland, from initiation to present-day, the ecosystem will have had an overall net cooling effect on the atmosphere, since the atmospheric lifetime of CH₄ is relatively short (~12 years) and the CO₂ sink effect is cumulative. Nonetheless, many researchers attempt to equate annual CH₄ emissions with CO₂ sink strength and compute a greenhouse gas balance, which often suggests that natural peatlands have a net warming effect on climate in a given year depending on climatic conditions (Whiting and Chanton, 2001; Friberg et al., 2003).

Additionally, pressures from human land use and conversion alter peatland carbon balances (Couwenberg, 2011). In particular, drainage for agriculture can result in large initial carbon losses through aerobic decomposition (Baldocchi, 2008) as well as peat subsidence (Pronger et al., 2014; Schipper and McLeod, 2002). Once drained and converted to pasture, peatlands are often annual sources of CO₂ to the atmosphere (Campbell et al., 2015) and although CH₄ emissions from peat soils are reduced, CH₄ fluxes from drainage ditches can remain high (Schrier-Uijl et al., 2010; Teh et al., 2011). Such abrupt changes are also likely to dramatically alter the relationship between peatland ecosystems and climate, whereby short-term reductions in the greenhouse gas balance

resulting from lower CH₄ fluxes are offset by longer-term reductions in overall carbon sink strength (Frolking et al., 2014).

In New Zealand, the majority of peatlands have been drained and converted to pasture production or cropping (Pronger et al., 2014). There is growing interest in constraining estimates of carbon and greenhouse gas budgets from managed peatlands nationally (Campbell et al., 2015; Nieveen et al., 2005), however little work has been conducted to quantify C and greenhouse gas fluxes from these systems in their unaltered state. New Zealand peatlands are also dominated by globally distinctive vegetation of the family Restionaceae ('restiads') and occupy climatic zones atypical of Northern Hemisphere peatland systems (McGlone, 2009). Furthermore, data from Southern Hemisphere peatlands are generally lacking despite providing unique settings in which to evaluate current understanding of peatland carbon cycling and biogeochemistry gained from Northern Hemisphere research.

1.2. Kopuatai bog

The work presented in this thesis was conducted within Kopuatai bog (Appendix 1), which is the largest remaining unaltered peatland in New Zealand and represents a globally unique case in terms of the combination of vegetation, climatic setting, and hydrology. Newnham et al. (1995) outlined the developmental history of Kopuatai. Briefly; twenty kilometres from the Firth of Thames on the North Island/Te Ika-a-Māui, New Zealand, Kopuatai is situated within the Hauraki Lowlands (Fig. 1), a fault-bounded depression roughly 25 km wide and 200 km long (Hochstein et al., 1986; Newnham et al., 1995). The ancestral Waikato River previously discharged to the Firth of Thames via braided

channel networks in the Hauraki Basin, but changed course roughly 15,000 BP, to its current position in the Hamilton Basin, discharging to the Tasman Sea. Following this switch, peat began accumulating in the northern Hauraki Basin (Newnham et al., 1995). Swamp forest, in addition to sedge and shrub-dominated fens, likely initiated peatland development, while domed ombrotrophic conditions developed roughly 9K-7.3K BP (Newnham et al., 1995). As ombrotrophic conditions set in, vegetation succession followed a sequence of dominance by sedges, then *Empodisma robustum*¹ (Wagstaff and Clarkson, 2012), and finally *Sporadanthus ferrugineus* (Clarkson et al., 2004). However, *E. robustum* is the main peat forming species through accumulation of its root clusters and was essentially present during each stage of bog development (Agnew et al., 1993; Clarkson et al., 2004). Drainage for agricultural production beginning in the early 20th century has reduced the extent of Kopuatai bog somewhat (Figure 1.1; Pronger et al., 2014), however ~9,000 ha remain unaltered and relatively unaffected with respect to hydrology and nutrient drift (Schipper et al., 1998). Peat depths at the dome crests reach 14 m with an average peat accumulation rate throughout the Holocene of 0.9 mm yr⁻¹ (Newnham et al., 1995). However, this rate was likely not constant throughout bog development but rather dependent on successional stage, frequency of disturbance such as fire (Clarkson, 1997; Newnham et al., 1995), or volcanic tephra deposition.

¹ Earlier publications may refer to *Empodisma minus*, but a distinct northern (<38°S) New Zealand species has now been recognized (Wagstaff and Clarkson, 2012).

The bog is situated between the Piako River to the west, and the Waihou River to the east, exemplifying the idealized case considered by classic bog formation models where peat accumulates on a lowland area between two parallel rivers atop impermeable mineral sediments (Belyea and Baird, 2006). Therefore, Kopuatai represents a familiar morphological case, vegetated by globally distinctive vascular species, with water tables maintained relatively close to the surface compared to typical Northern Hemisphere bogs (Hodges and Rapson, 2010, Turetsky et al., 2014). This provides a unique combination of ecosystem characteristics ideal for evaluating carbon cycling and biogeochemical ideas derived from Northern Hemisphere systems.

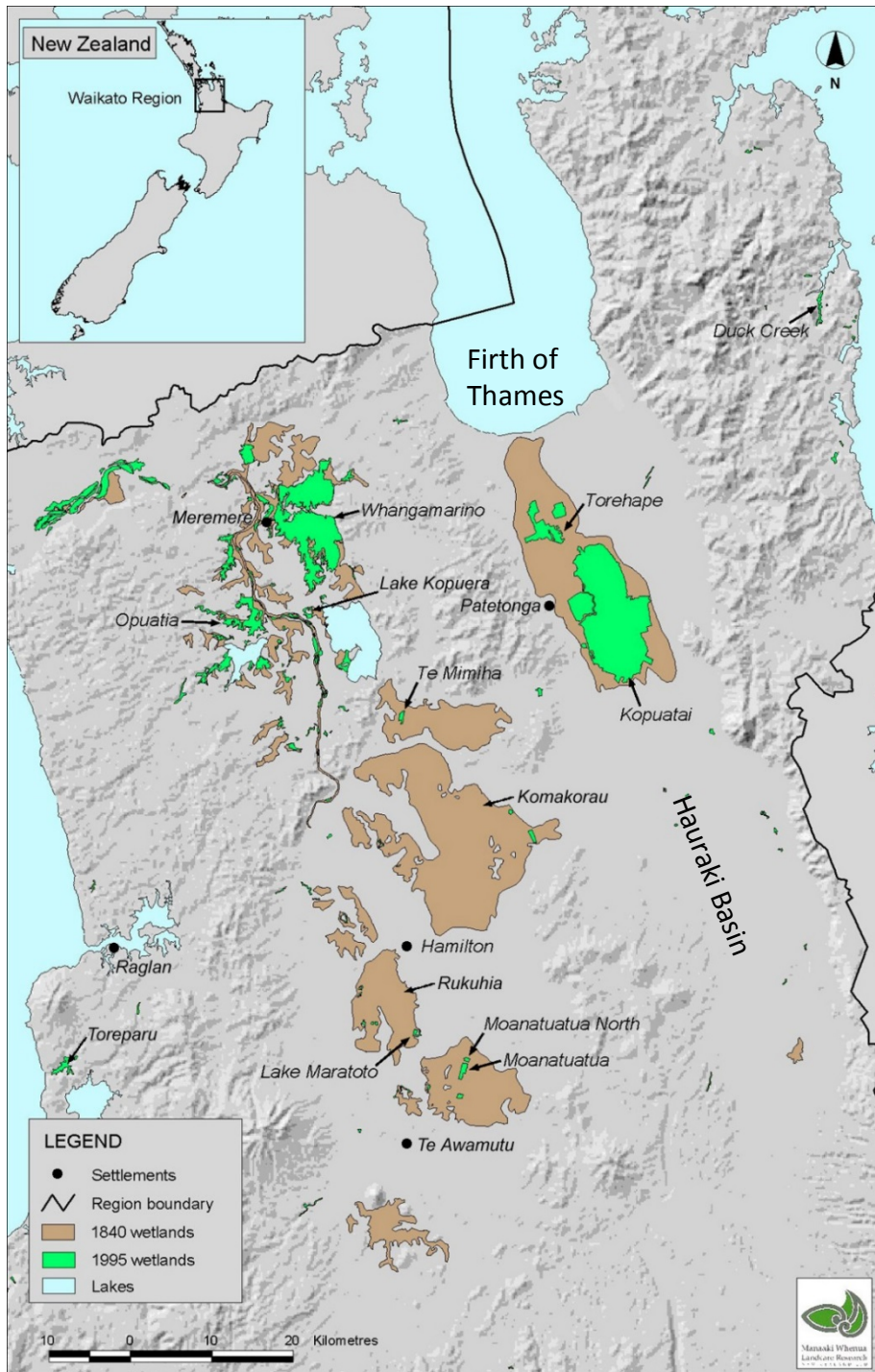


Figure 1.1. Map showing the location and current extent of Kopuatai bog within the Hauraki Lowlands in relation to other peatland areas on the North Island and historic wetland extent. (Source: Landcare Research, Manaaki Whenua, Lincoln, NZ.)

1.3. Thesis aims and objectives

I began this research with the aim to quantify the net ecosystem C balance (NECB) and to understand the sensitivity of the gaseous component fluxes to environmental change at Kopuatai bog. To achieve this aim, my main objectives were to:

1) determine magnitudes and drivers of gross primary production (GPP), which is usually the largest peatland C input, from half-hourly to weekly timescales;

2) quantify annual methane fluxes and determine the relative importance of temperature and water table depth in driving daily to annual temporal variability;

3) couple CO₂ and CH₄ fluxes to develop a full carbon balance for Kopuatai and explore the effects of drought on each carbon balance component at monthly to annual timescales, with a particular focus on CO₂-C components (ER and GPP).

1.4. Thesis outline

The thesis is organized as follows:

Chapter 2 is a focused literature review, intended to provide background on the main research themes. My goal in this chapter was to identify shortcomings in current understanding with respect to the thesis objectives listed above and to provide the motivation for conducting the research detailed in subsequent chapters.

Chapters 3-5 describe the main results of the research and specifically address each of the three thesis objectives, listed above, in turn. Each of these chapters is treated as an independent manuscript with its own methods description and relevant discussion of the results as they relate to previously published literature. At the time of thesis completion, Chapter 3 had been published by the journal *Agricultural and Forest Meteorology* (Goodrich et al., 2015a) and Chapter 4 had been published by the *Journal of Geophysical Research – Biogeosciences* (Goodrich et al., 2015b). Both have been included as chapters in Word format as accepted by each journal. Chapter 5 still remains to be submitted to a peer-reviewed journal. As independent manuscripts, there is some repetition among Chapters 3-5 with respect to introduction material, site and methodology description, and references.

Chapter 6 summarises the overall results and conclusions obtained from this research, and describes the overarching themes that unify the main results chapters. In addition, it provides some insight into broader implications of the work.

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Chapter 2. Literature Review

Peatlands are defined as ecosystems that have accumulated at least 40 cm of surface organic material. There are various peatland classification schemes based on hydrology, nutrient status, and vegetation composition but there are broadly two main peatland types. Fens receive water and nutrients to varying degrees from groundwater and rain, whereas bogs receive water and nutrients only from rain (Rydin and Jeglum, 2013). Hydrology influences both peatland morphology as well as chemical and nutrient status, which in turn determines vegetation composition (Zoltai and Vitt, 1995). Fens are generally higher in nutrients (minerotrophic), wetter, and dominated by mosses, sedges, and grasses, whereas bogs are low nutrient (oligotrophic), tend to have deeper water tables, and support *Sphagnum spp.* mosses, low shrubs, and stunted trees (Rydin and Jeglum, 2013; Vitt, 1994).

2.1. Peatland C balance components and terms

The peatland net ecosystem carbon balance (NECB) is primarily composed of the net exchange of CO₂, and losses of CH₄ and dissolved organic carbon (DOC) (Koehler et al., 2011; Nilsson et al., 2008; Roulet et al., 2007). Additional losses of carbon in the form of non-methane volatile organic compounds (Olefeldt et al., 2012) and other sub-surface dissolved fractions (Dinsmore et al., 2010) may contribute smaller percentages but are usually ignored in NECB considerations. DOC in rain represents a small carbon input, which is also often ignored (see Sturgeon, 2013). The net ecosystem exchange of CO₂ (NEE) is composed of two larger terms, gross primary production (GPP) and ecosystem respiration (ER), which are generally the largest terms in the overall budget (Flanagan and Syed,

2011; McVeigh et al., 2014; Peichl et al., 2014; Sottocornola and Kiely, 2010). ER can be further disaggregated into several respiration components including above- and below-ground autotrophic, and soil heterotrophic CO₂ respiration (Figure 2.1). Moore et al. (2002) and Frolking et al. (2002) estimated the breakdown of autotrophic to heterotrophic respiration to be about 50% each, while others have suggested slightly lower contributions (35-45%) of autotrophic respiration (Silvola et al., 1996). However, there can be a large range in the estimated contributions of below ground autotrophic respiration (35 – 75%) to ER, with heterotrophic respiration contributing 37 – 57%, depending on vegetation and peat type (Crow and Wieder, 2005). The value of NEE follows an atmospheric sign convention whereby negative values indicate a net flux into the ecosystem, whereas the same quantity from the ecosystem perspective is denoted net ecosystem production or NEP and has the opposite sign (Figure 2.1).

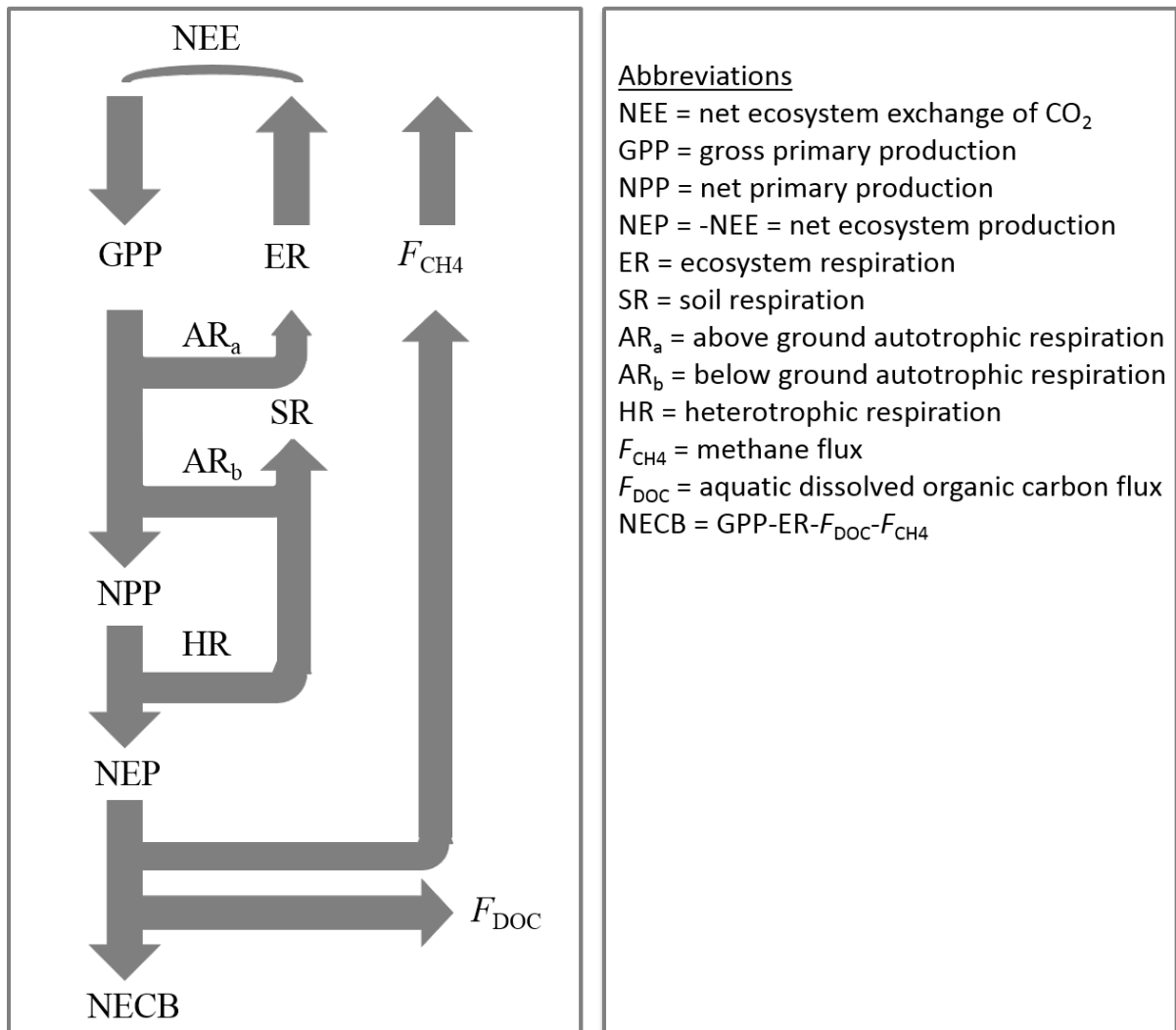


Figure 2.1. Illustration of the major net ecosystem carbon balance components for a peatland. Adapted from Luyssaert et al. (2007) and Rutledge (2010).

2.2. Carbon dioxide exchange

2.2.1. Gross primary production

Gross primary production (GPP) is the main carbon input to peatlands, especially in ombrotrophic (rain fed) systems, and can be particularly variable among peatland types (Lund et al., 2010). As the largest input, small proportional changes in GPP can have a large impact on the C budget, further magnifying the importance of understanding controls on this flux component.

Peatlands are generally characterized by relatively low species diversity owing to the low nutrients and saturated conditions that select for specialized plant assemblages (Glaser, 1992). Northern Hemisphere bogs are often dominated by *Sphagnum* mosses, ericaceous shrubs (e.g., *Camaedaphne calyculata*, *Ledum groenlandicum*) and small trees (e.g. *Picea mariana*, *Larix laricina*), whereas wetter, higher nutrient fens typically support sedges (e.g., *Carex spp.* and *Eriophorum spp.*) and grasses with fewer shrubs and trees but often continuous *Sphagnum* moss cover, albeit different *Sphagnum* species to bogs (Gignac et al., 1991). Frohking et al. (1998) showed that northern bogs and fens possess distinct photosynthetic light response characteristics but can also be combined to form a separate vegetation class from forests, crops, and grasslands with lower maximum light-saturated photosynthetic potential and apparent quantum yield (Ruimy et al., 1995). However, very little is known about the light response of *E. robustum* and its role in the carbon balance of New Zealand peatlands.

Reduced stomatal aperture in response to elevated VPD limits plant water loss but also restricts CO₂ uptake (Körner, 1995). This has been demonstrated at the ecosystem scale in several peatlands and can substantially reduce the annual CO₂ sink strength (Aurela et al., 2007; Kwon et al., 2006; Olefeldt et al., 2012). Bowen ratio measurements at an *E. robustum*-dominated peatland revealed conservative evaporation rates due to high stomatal resistance during dry periods with high vapor pressure deficit (VPD), and a physical mulching effect from standing dead plant litter (Campbell and Williamson, 1997).

In addition to the atmospheric stress of elevated VPD, lowered water tables during dry conditions can restrict photosynthetic productivity of peatland plants

(Sonnentag et al., 2010). In northern fens and bogs where mosses contribute the majority of GPP, lowered water tables have resulted in reduced GPP (Alm et al., 1999; Griffis et al., 2000), whereas those where photosynthesis is dominated by shrubs and trees are somewhat more resistant to the effects of dry conditions (Arneeth et al., 2002; Bubier et al., 2003). This may be the result of vascular vegetation's ability to better regulate the uptake of water and their more conservative stomatal behaviour (Riutta et al., 2007). The only data relating CO₂ fluxes to water table depth in New Zealand peatlands were obtained from Moanatuatua bog. This small remnant is dominated by both *E. robustum* and *S. ferrugineus* and is potentially impacted by surrounding land drainage with particularly low water table depths; routinely >40 cm and up to 80 cm below surface (Campbell et al., 2014). Monthly and annual GPP at Moanatuatua were high relative to Northern Hemisphere bogs despite the dry conditions, however the measurement record did not include comparisons of wet vs. dry years or summers (Campbell et al., 2014). Furthermore, the dry conditions in Moanatuatua are atypical of other New Zealand peatlands, with Kopuatai water tables reported within the range 0 – 12 cm from the surface (Campbell and Williamson, 1997; Kuder et al., 1998). Although few data are available on the CO₂ exchange in New Zealand peatlands during abnormally dry conditions, the persistent peat accumulation in a region with frequent summer water deficits suggests some degree of adaptation to moisture stress (McGlone, 2009).

Another critical factor determining the importance of GPP in annual peatland carbon budgets is growing season length. In Northern Hemisphere peatlands, the growing season, either defined as the season of sustained net CO₂ uptake or

actively photosynthesizing vegetation, is bounded by freezing temperatures during shoulder seasons (spring and autumn) (Lund et al., 2010) or by light limitation in milder maritime regions (Sottocornola and Kiely, 2005). Therefore, the effective duration of a growing season depends on factors such as snowmelt date and variable spring temperatures (Aurela et al., 2004; Lafleur and Humphreys, 2008; Moore et al., 2006), as well as vegetation specific phenology (Kross et al., 2014; Zona et al., 2011). At Moanatuatua bog in New Zealand, mild temperatures led to essentially year-round growing conditions with actively photosynthesizing vegetation throughout winter months and net CO₂ uptake during 10 months of study years (Campbell et al., 2014). The implications of such a long growing season are important to carbon budget considerations given the potential to dampen the impact of summer dynamics. For example, Aurela et al. (2007) found that increased respiration losses of CO₂ in a boreal sedge fen during summer drought was partially offset by warm autumn temperatures that allowed an extended period of photosynthetic activity and CO₂ uptake. Lack of sufficient data presently precludes us from determining the annual impact of short-term perturbations to C exchanges caused by drought events in New Zealand peatlands.

2.2.2. Ecosystem respiration

Ecosystem respiration (ER) is generally the largest C export pathway in peatlands (Gažovič et al., 2013; Heikkinen et al., 2004) and is primarily comprised of above and below ground autotrophic respiration as well as heterotrophic respiration from microbial decomposition of organic matter (Kuzyakov, 2006). This, in addition to correlations among driver variables, contributes to difficulty in

disentangling the controls on peatland ER. Water table depth has a strong influence on peat decomposition through its control over anaerobiosis, whereby dropping water tables lead to increased peat aeration and CO₂ losses (Moore and Knowles, 1989; Nykänen et al., 1998). However, field studies have shown variable ER response to water table variations (Juszczak et al., 2013; Sulman et al., 2010). Most often, drier years result in larger annual ER than wetter years in peatlands (Alm et al., 1999; Bubier et al., 2003; Lund et al., 2012). However, if surface peat becomes too dry as water tables drop, microbial communities may become stressed or limited by access to substrate (Mäkiranta et al., 2009; Updegraff et al., 1995). Dimitrov et al. (2010) also showed that respiration may be reduced in surface peat where microbes are moisture limited, but ER may be offset by increased respiration in deeper zones where oxygen supply increases as water tables drops. Lafleur et al. (2005) found that ER was strongly temperature dependent in a Canadian bog and did not respond to changes in water table depth even over a large range of 30 – 70 cm from the surface. The authors also pointed out that below-ground autotrophic respiration was most likely less responsive to changes in water table depth than to changes in temperature, which may have contributed to the stronger temperature dependence of total ER. Whatever the ratio of heterotrophic to autotrophic contributions to ER however, the apparent temperature response of peatland ER may ultimately depend on water table depth (Juszczak et al., 2013; Updegraff et al., 2001) because of its regulation of peat thermal properties (e.g., Weiss et al., 2006), oxygen availability (Skopp et al., 1990), and access to substrate (Updegraff et al., 1995).

Surface plant litter decomposition rates (and thus ER) are also dependent on dominant vegetation and litter quality, which leads to differences among dominant vegetation types (Moore et al., 2007). In Northern Hemisphere peatlands, *Sphagnum spp.* mosses generally exhibit low decomposition rates (Hogg, 1993; Johnson and Damman, 1993), which also contributes to persistent C accumulation over millennia (Frolking et al., 2001). In New Zealand peatlands, *E. robustum* root material has similar decay rates to *Sphagnum spp.* in Northern Hemisphere peatlands, suggesting restiads may play a similar role in restricting decomposition and promoting long-term peat accumulation (Clarkson et al., 2014).

2.3. Methane flux

Methane production is the last step in a chain of anaerobic decomposition reactions that successively deplete the most energetically favourable substrates and electron acceptors before organic matter fermentation and CO₂ reduction commences and methane is produced (Whalen, 2005). The amount of methane produced in peatlands is thus controlled by degree of saturation and water table depth (Roulet et al., 1993), substrate availability (Coles and Yavitt, 2002; Yavitt and Seidman-Zager, 2006), presence of alternate electron acceptors (Knorr and Blodau, 2009), and temperature (Dunfield et al., 1993; Valentine et al., 1994).

Methane produced at depth can be transported to the surface by diffusion along the developed concentration gradient, by release of bubbles (ebullition), or by way of plant-mediated aerenchymous transport (Le Mer and Roger, 2001).

However, some of the methane produced in the saturated peat can be oxidized by a subset of eubacteria termed methanotrophs, which are generally confined

to the surface, unsaturated peat (Whalen, 2005), although elevated rhizospheric oxygen can facilitate methanotrophy in otherwise saturated conditions (Bouchard et al., 2007; Bridgham et al., 2013; Fritz et al., 2011; Laanbroek, 2010).

Peatlands dominated by aerenchymous vegetation are generally greater sources of methane because flow through these plant tissues allows CH₄ to bypass the main oxidation zone in the surface peat (Joabsson et al., 1999; Noyce et al., 2014). In addition, many aerenchymous plants have been found to exude fresh organic compounds from their roots, which can facilitate methanogenesis despite the elevated oxygen in the rhizosphere (Bellisario et al., 1999; Whiting and Chanton, 1992). Ebullition of high concentration methane bubbles can also contribute large proportions of methane to the overall ecosystem flux (Glaser et al., 2004) but this transport pathway is highly heterogeneous and notoriously difficult to quantify (Goodrich et al., 2015). Nonetheless, the contribution of ebullition is thought to depend on peat structure (Coulthard et al., 2009), hydrology (Rosenberry et al., 2003; Strack et al., 2005), and atmospheric and hydrostatic pressure (Fechner-Levy and Hemond, 1996; Kellner et al., 2006).

In general, wetter areas of a peatland contribute larger proportions to the total CH₄ flux than drier areas (Bubier et al., 1993) and wetter years result in greater fluxes than drier years (Moore et al., 2011). However, short-term (days to weeks) temporal variability in CH₄ fluxes is often better explained by temperature than water table, which may be due, in part, to limited variations in water table depth on those timescales at some (Jackowicz-Korczynski et al., 2010; Olson et al., 2013). Lai et al. (Lai et al., 2014a) found that the temperature response of

peatland CH₄ emissions can be over-ridden by changes in water table depth, suggesting strongly interacting controls.

2.4. Dissolved organic carbon export

A more comprehensive review covering aquatic peatland carbon losses was conducted in a parallel study by Sturgeon (2013). For completeness, I discuss some key aspects of this peatland carbon budget term below. Dissolved organic carbon (DOC) is defined as organic compounds in water that pass through a 0.45 µm filter (Roulet and Moore, 2006). Comprised of a diverse array of organic acids (Blodau, 2002), the primary sources of DOC is organic matter, through decomposition and mineralization as well as release from plant roots (Usselman et al., 2007). As such, production and concentration of DOC increase with temperature (Moore and Dalva, 2001), and depend on plant production rates and vegetation type (Camino-Serrano et al., 2014), as well as moisture status (Kane et al., 2010). The relationship between water table depth and DOC concentration and export is complicated by competing factors. Lowered water tables can increase DOC concentration (Blodau and Siems, 2012), however if DOC export is related to runoff rates (Blodau, 2002), then periods with low precipitation may reduce the potential for DOC export. Despite its importance to peatland carbon cycling and biogeochemistry, the effects of variable water table on DOC concentration and export are still relatively poorly understood (Hribljan et al., 2014).

Peatland losses of DOC occur in runoff or stream outflow, which results in downstream export from the system (Dinsmore et al., 2010). Estimates of DOC export in peatlands are usually made by measuring DOC concentrations in

discharging streams in conjunction with flow rates (Dinsmore et al., 2010; Koehler et al., 2011; Roulet et al., 2007). Annual estimates from these methods range from $2.76 - 38.6 \text{ gC m}^{-2} \text{ yr}^{-1}$ (Billett et al., 2004; Olefeldt et al., 2012). However, measuring export from discharging streams may lead to bias resulting from edge effects (Fraser et al., 2001). Furthermore, peatlands do not always have a clear outflow or discharging stream, and others have used runoff estimates based on precipitation and evaporation measurements to estimate dissolved carbon losses (Olson et al., 2013).

Very little work has been done to estimate concentrations and losses of DOC from New Zealand peatlands. Moore and Clarkson (2007) found relatively high DOC concentrations in ombrotrophic peatlands in northern New Zealand, suggesting DOC export could range $10 - 50 \text{ gC m}^{-2} \text{ yr}^{-1}$. However, a thorough spatial and temporal investigations of DOC concentrations at Kopuatai bog along with a water balance approach to estimating DOC export suggests relative low annual values for this carbon loss pathway in restiad bogs (Sturgeon, 2013; Campbell et al., in preparation).

2.5. Ecosystem-scale carbon budget estimates

2.5.1. Methodological considerations for measuring CO_2 and CH_4 fluxes

Much of our knowledge of the magnitudes and controls on CO_2 and CH_4 fluxes from peatlands in the field comes from chamber-based measurements (e.g., Carroll and Crill, 1997; Christensen et al., 2003; Crill et al., 1988; Lai et al., 2014a; Lai et al., 2014b; Turetsky et al., 2014). Manual static chamber measurements allow for good spatial coverage over discrete elements of heterogeneous

ecosystems (e.g., Burrows et al., 2005; Treat et al., 2007). For this approach, permanent collars are installed in the peat surface where an open-bottom chamber can be placed for measurements of headspace gas concentration increase over time. This is a relatively labor intensive flux sampling method since headspace samples must either be collected with syringes for laboratory analysis (Carroll and Crill, 1997) or deployed with a portable gas analyzer (Treat et al., 2007). As a result, manual chamber measurements are usually limited to weekly (or longer) time resolution. Automated chambers employ a similar conceptual approach but offer increased temporal resolution by incorporating mechanical or pneumatic valves to control the opening and closing of chamber lids, overseen by data loggers (Goulden and Crill, 1997). Although automated chambers provide increased temporal coverage and the ability to isolate dominant vegetation zones within an ecosystem, both manual and automated chambers are limited by the area over which the flux measurement is representative (Burrows et al., 2005). Typically, chambers cover areas of 0.25 – 1 m² of the ecosystem surface and these measurements can be extrapolated to estimate ecosystem-scale flux estimates in conjunction with process models (e.g., Zhang et al., 2012) or by weighting the fluxes based on some classification of ecosystem units (e.g., vegetation type, open water etc.) (Schrier-Uijl et al., 2010). However, this approach introduces uncertainty because of the spatial heterogeneity characteristic of peatlands, which can lead to orders of magnitude differences in estimated carbon fluxes across metre-scale distances (Mastepanov et al., 2008). For integrated ecosystem-scale flux measurements with continuous temporal coverage, the micrometeorological eddy covariance

technique has become widely adopted, with continual technological advances that make application of this technique increasingly practical and attractive to ecosystem scientists (Baldocchi, 2014).

The eddy covariance technique involves high frequency measurements of variations in turbulence and gas concentrations to enable calculation of the covariances between deviations in vertical wind speed and concentrations of the gas species of interest (e.g., CO₂, CH₄, H₂O) (Baldocchi, 2003; Goulden et al., 1996; Moncrieff et al., 1997; Moore, 1986; Webb et al., 1980). This is achieved by mounting sensors on a tower within the ecosystem, causing minimal disturbance to the surface being measured since fluxes are integrated over hectare to square kilometre scales (Horst and Weil, 1994; Schuepp et al., 1990). For a detailed description of the eddy covariance technique see Aubinet et al. (2012) and references therein. Briefly, observations at a point (i.e. on a tower) need to measure variations of vertical wind speed and scalar quantities at high enough frequencies to capture fast moving 'small eddies' and over sufficiently long averaging intervals to capture slower moving 'large eddies' (Aubinet et al., 2012; Stull, 1988). Generally, observations at 10-20 Hz are required to capture high frequency deviations and an averaging interval of at least 30 minutes is required to sufficiently capture the low frequency flux contributions (Loescher et al., 2006). The technological requirements of eddy covariance limited widespread application early on (1980-90s), however continual advancements have increased its application across disciplines globally (Baldocchi, 2014; Baldocchi et al., 2001) and increasingly standardized data processing protocols

allow opportunities for invaluable synthetic analyses (Lund et al., 2010; Schwalm et al., 2010).

There are some important limitations of the eddy covariance technique to consider when analysing and interpreting flux data. The technique requires well-developed turbulence to ensure a well-mixed atmosphere and that scalar transport is dominated by turbulent mixing rather than advection, for which the technique cannot account without substantial additional measurement infrastructure (Aubinet, 2008; Leuning et al., 2008; Massman and Lee, 2002).

This issue is most often addressed by applying a threshold for a quantity (usually friction velocity) representing the boundary of well-mixed and stable conditions (Gu et al., 2005; Loescher et al., 2006), which can lead to under-representation of night time respiration fluxes (Barr et al., 2002; Goulden et al., 1996).

Additional considerations of sensor configuration can have important implications for data coverage and quality. Closed-path gas analyzers utilize pumps to draw air samples through tubes to the sensor, which requires a large power supply and leads to signal tube attenuation (Leuning and Moncrieff, 1990). Open-path analyzers require less power to operate but fluxes need to be corrected for air density fluctuations (Webb et al., 1980) and data are lost during rain events or when dust accumulates on sensor windows/mirrors (Sturtevant et al., 2012). The choice of analyser therefore requires careful consideration of the specific site characteristics and limitations, but many issues can be dealt with by careful site set-up and with data post-processing (Aubinet et al., 2012).

When interpreting eddy covariance fluxes it is important to consider that only the net flux integrated over a large area is being measured. For example,

daytime measurements of NEE do not distinguish GPP from ER, and one must employ modeling techniques to partition NEE into its components. The most common flux partitioning approach for CO₂ is to assume that night time NEE represents only ER, since photosynthesis does not occur at night, then to fit relationships between ER and temperature and apply those night time relationships to daytime (Reichstein et al., 2005). This approach also assumes that night time temperature dependence of ER can be extrapolated to daytime, although this may not to be entirely accurate due to light-induced respiratory suppression (Atkin et al., 2000; Brooks and Farquhar, 1985). Nevertheless, standard flux partitioning methods are becoming widely adopted (Lasslop et al., 2010; Moffat et al., 2007; Reichstein et al., 2005), while chamber measurements can also be useful in further partitioning ER by measuring dark fluxes during daytime for representative areas (e.g., Phillips et al., 2010). Additionally, recent developments in isotopic sensors are beginning to enable high frequency measurements of both CO₂ and CH₄ isotopologues, offering the opportunity for source attribution of bulk fluxes (e.g., Griffis, 2013; Santoni et al., 2012).

2.5.2. Published peatland eddy covariance CO₂ fluxes

As more eddy covariance CO₂ flux data from peatland systems becomes available, flux comparisons among sites, and among years at the same site, provide new insights into the controls and magnitudes of fluxes (Lund et al., 2010), and inform models used for coupled climate simulations (Sulman et al., 2012). A growing body of literature reporting eddy covariance CO₂ fluxes from peatlands has revealed that average annual NEE from bogs and fens are remarkably similar despite the generalized differences in hydrology, nutrient

status, vegetation and climatic setting (Lafleur, 2009). Results from studies published since Lafleur's review in 2009 lead to a similar conclusion, with bog and fen mean ($\pm$ standard deviation) annual NEE of $-70.5 (\pm 63.2)$ and $-74.5 (\pm 60.5)$ $\text{gC m}^{-2} \text{yr}^{-1}$, respectively (Table 2.1). However, while the average magnitude of annual NEE may be similar between bogs and fens, the component magnitudes of GPP and ER can vary substantially among peatland types. The range of published annual GPP for bog sites is $298 - 1148 \text{ gC m}^{-2} \text{yr}^{-1}$ and for ER is $232 - 906 \text{ gC m}^{-2} \text{yr}^{-1}$ (Table 2.1). Relatively few peatland studies report annual estimates of GPP and ER along with NEE. Of those that do not, some provide growing season averages or totals. From Western Canada, Adkinson et al. (2011) reported integrated growing season GPP consistently around $350 \text{ gC m}^{-2} \text{season}^{-1}$ at a *Sphagnum*-dominated poor fen site and ranging $350 - 550 \text{ gC m}^{-2} \text{season}^{-1}$ at a sedge-dominated extreme rich fen while ER was around $220 \text{ gC m}^{-2} \text{season}^{-1}$ at the poor fen and ranged $310 - 400 \text{ gC m}^{-2} \text{season}^{-1}$ at the extreme rich fen. These data suggest that, despite the greater potential for plant C uptake, the extreme rich fen had higher ER and greater sensitivity to environmental drivers among years. At Mer Bleue bog in Ontario, Canada, Strilesky and Humphreys (2012) found that average growing season GPP and ER were $147 \text{ gC m}^{-2} \text{mo}^{-1}$ and $111 \text{ gC m}^{-2} \text{mo}^{-1}$, respectively, at an open bog site, and $129 \text{ gC m}^{-2} \text{mo}^{-1}$ and $105 \text{ gC m}^{-2} \text{mo}^{-1}$ at the treed bog site. This was a somewhat surprising result given the higher leaf area at the treed bog; a trait that is generally correlated with higher GPP (Lund et al. 2010).

A unifying theme across sites and peatland types has been in the NEE response to dry conditions and droughts. At all sites included in Table 2.1, the lowest

annual CO₂ uptake occurred during years with lower than average water tables. However, the relative contribution of increased ER vs. decreased GPP was variable and Lafleur (2009) pointed out the lack of consensus regarding their relative contributions to peatland drought response. The recent observation of very large component fluxes from a relatively 'dry' (low water table) New Zealand bog led to the conclusion that a long growing season leads to large annual NEE (Campbell et al., 2014). However, it remains unclear how the vegetation in more characteristic 'wet' (high water table) New Zealand bogs responds to water table variations.

Table 2.1. Published estimates of peatland annual net ecosystem exchange (NEE), gross primary production (GPP), and ecosystem respiration (ER) using eddy covariance. For studies spanning more than two years, the mean annual values are given. Peatland type is listed as reported within the published study.

Reference	Location	Peatland Type	Measurement Years	Annual NEE (gC-CO ₂ m ⁻² yr ⁻¹)	Annual GPP (gC-CO ₂ m ⁻² yr ⁻¹)	Annual ER (gC-CO ₂ m ⁻² yr ⁻¹)	MAT (°C)	MAP (mm)
Arneth et al., 2002	Siberia	Bog	1999	-43.2 ^a	—	—	-3.9	552
Arneth et al., 2002	Siberia	Bog	2000	60.0 ^a	—	—	-3.9	552
Euskirchen et al., 2014	Alaska, USA	Pine bog	2011-2013	-18.7	564.3	545.3	-2.2	206
Euskirchen et al., 2014	Alaska, USA	Collapse scar bog	2011-2013	-39	530	491	-2.2	206
Humphreys et al., 2014	Canada	Bog	2011	-46	323	277	-1.3	699
Humphreys et al., 2014	Canada	Bog	2012	-53	299	246	-1.3	699
Humphreys et al., 2014	Canada	Bog	2011	-45	295	250	-1.1	682
Humphreys et al., 2014	Canada	Bog	2012	-55	298	243	-1.1	682
Alm et al., 1999	Finland	Open bog	1994	50	—	—	1.6 ^b	648
Arneth et al., 2002	Russia	Bog	1999	26.4 ^a	—	—	3.9	711
Lafleur et al., 2003	Canada	Raised bog	1999-2001	-58.2	528.5	460.9	5.8	910
Roulet et al., 2007	Canada	Raised bog	1999-2004	-40.8	—	—	6.0	943
Strilesky and Humphreys, 2012	Canada	Open bog	2007	-104	—	—	6.0	943
Humphreys et al., 2014	Canada	Raised bog	2011	-55	651	596	6.0	944
Humphreys et al., 2014	Canada	Raised bog	2012	-78	760	682	6.0	944
Strilesky and Humphreys, 2012	Canada	Treed bog	2007	-72	—	—	6.0	944
Lund et al., 2007	Sweden	Eccentric bog	2006	-21.5	—	—	6.2	700
Dinsmore et al., 2010	Scotland	Bog	2007	-136	—	—	8.0	1155
Dinsmore et al., 2010	Scotland	Bog	2008	-93.5	—	—	8.0	1155
Koehler et al., 2011	Ireland	Blanket bog	2003-2008	-47.8	—	—	10.0	1430

Table 2.1. continued

Reference	Location	Peatland Type	Measurement Year	Annual NEE (gC-CO ₂ m ⁻² yr ⁻¹)	Annual GPP (gC-CO ₂ m ⁻² yr ⁻¹)	Annual ER (gC-CO ₂ m ⁻² yr ⁻¹)	MAT (°C)	MAP (mm)
Sottocornola and Kiely, 2005	Ireland	Blanket bog	2003	-49	—	—	10.0	1430
Sottocornola and Kiely, 2005	Ireland	Blanket bog	2004	-61	—	—	10.0	1430
McVeigh et al., 2014	Ireland	Blanket bog	2003-2011	-58.7	287.7	232	10.0	1430
Campbell et al., 2014	New Zealand	Raised bog	1999	-218.2	1124.2	906	13.4	1188
Campbell et al., 2014	New Zealand	Raised bog	2000	-250.3	1148.3	897.8	13.4	1188
Aurela et al., 2009	Sweden	Rich fen	2006-2008	-31.9	—	—	-1.4	484
Aurela et al., 2004	Finland	Fen	1997-2002	-21.5	—	—	-1.2	470
Olefeldt et al., 2012	Sweden	Palsa mire	2008	-61.98	—	—	-0.5	308
Olefeldt et al., 2012	Sweden	Palsa mire	2009	-38.42	—	—	-0.5	308
Sagerfors et al., 2008	Sweden	Poor fen	2001-2003	-55	—	—	1.2	523
Nilsson et al., 2008	Sweden	Poor fen	2004	-55	—	—	1.2	523
Nilsson et al., 2008	Sweden	Poor fen	2005	-48	—	—	1.2	523
Peichl et al., 2014	Sweden	Poor fen	2001-2012	-58	336	278	1.2	523
Gazovic et al., 2013	Finland	Fen	2006	-92.5	—	—	2	667
Gazovic et al., 2013	Finland	Fen	2007	-154.6	—	—	2	667
Syed et al., 2006	Canada	Moderate rich fen	2004	-144	713	569	2.1	504
Adkinson et al., 2011	Canada	Poor fen	2004-2006	-108 ^a	—	—	2.1 ^b	504
Adkinson et al., 2011	Canada	Extreme rich fen	2004-2006	-77.7 ^a	—	—	2.1 ^b	504
Shurpali et al., 1995	USA	Poor fen	1992	-32	—	—	3 ^b	770
Olson et al., 2013	USA	Poor fen	2009-2011	-35.3	—	—	3 ^b	770
Aurela et al., 2007	Sweden	Fen	2004	-51.3	—	—	3.3	713
Aurela et al., 2007	Sweden	Fen	2005	-59.7	—	—	3.3	713
Lund et al., 2010	Poland	Rich fen	2005	-252	855	606	8.5 ^b	526

^a = estimated for growing season only^b = mean annual climate data taken from online climate records

2.5.3. Published peatland eddy covariance CH_4 fluxes

There are fewer published annual estimates of eddy covariance peatland CH_4 fluxes than NEE, and many only report growing season totals (Table 2.2). The earliest CH_4 eddy towers were closed-path systems equipped with fast response flame ionization detectors (Fan et al., 1992) but tunable diode laser spectrometers became the most common measurement approach (Billesbach et al., 1998; Long et al., 2010; Olson et al., 2013; Rinne et al., 2007; Riutta et al., 2007; Shurpali et al., 1993). More recently, a lower power, open-path CH_4 analyzer was developed, and has been successfully deployed at a number of sites (McDermitt et al., 2011; Nadeau et al., 2013; Sturtevant et al., 2012) and alternative cavity ring down and cavity output spectrometers for closed-path set-ups are also being utilized (Peltola et al., 2013). These advancements have led to a recent increase in the number of published eddy covariance CH_4 flux data sets from peatlands.

There is quite a large overall range of estimated annual CH_4 flux from bog and fen peatlands (Table 2.2). Fens are generally considered to be greater CH_4 source than bogs due to higher water tables and greater coverage of aerenchymous vegetation (see review by Lai, 2009). Published ecosystem-scale measurements provide some support for this. Bog CH_4 fluxes ranged $1.6 - 3.2 \text{ gC m}^{-2} \text{ yr}^{-1}$ (Table 2.2), although only two sites are represented and one of them collected only growing season observations. The average annual CH_4 flux from fens was higher ($9.7 \text{ gC m}^{-2} \text{ yr}^{-1}$) although estimates were variable, ranging $2.4 - 16.3 \text{ gC m}^{-2} \text{ yr}^{-1}$, including the growing season-only estimates (Table 2.2). The paucity of published annual integrated CH_4 fluxes from peatlands precludes a

definitive comparison between bogs and fens. Nevertheless, researchers have consistently found that, within both bogs and fens, arenchymous plant cover promotes higher CH₄ fluxes (Joabsson and Christensen, 2001; Noyce et al., 2014; Shannon and White, 1994), higher water tables increase emissions, although peak CH₄ fluxes occur at different water table depths for fens and bogs (Turetsky et al., 2014). This again highlights the importance of dry years and droughts in driving inter-annual differences in peatland CH₄ fluxes. Brown et al. (2014) presented the only eddy covariance CH₄ data covering a drought year, which resulted in low observed fluxes during the drought period and for an extended period afterward. Drought events clearly have important implications for peatland CH₄ fluxes in a changing climate, but more work is needed to describe drought response at ecosystem scales in different peatland types.

New Zealand bogs represent an interesting and unique case in that water tables may be relatively high compared to Northern Hemisphere bogs, and the dominant vegetation is arenchymous (Sorrell et al., 2002). In addition to quantifying its contribution to NECB, conducting the first ecosystem-scale CH₄ flux measurements from an unaltered restiad peatland will provide an invaluable comparison to Northern Hemisphere systems.

Table 2.2. Published estimates of peatland annual methane flux (F_{CH_4}) using eddy covariance. For studies spanning more than two years, the mean annual values are given. Peatland type is listed as reported within the published study.

Reference	Location	Peatland type	Measurement Years	Annual F_{CH_4} (gC m ⁻² yr ⁻¹)	MAT (°C)	MAP (mm)
Nadeau et al., 2013	Canada	bog	2012	3.2 ^a	-2.4	697
Brown et al., 2014	Canada	raised bog	2011	3.1	6	943
Brown et al., 2014	Canada	raised bog	2012	1.6	6	943
Hanis et al., 2013	Canada	eutrophic palsa fen	2008-2011	5.1 ^a	-7 ^b	412
Long et al., 2010	Canada	moderately rich treed fen	2007	2.4 ^a	2.1	504
Shurpali et al., 1993	USA	poor fen	1991	11.1 ^a	3	770
Olson et al., 2013	USA	poor fen	2009-2011	16.3	3	770
Shurpali and Verma, 1998	USA	poor fen	1991	10.4 ^a	3	770
Shurpali and Verma, 1998	USA	poor fen	1992	11.5 ^a	3	770
Rinne et al., 2007	Finland	oligotrophic fen	2005	9.4	3.3	713
Pypker et al., 2013	USA	poor fen	2011	12.7 ^a	5	810
Herbst et al., 2011	Denmark	fen/wet meadow	2008	8.1	7.5	781
Jackowicz-Korczyński et al., 2010	Sweden	palsa mire	2006	17.9	-0.9	305
Jackowicz-Korczyński et al., 2010	Sweden	palsa mire	2007	21.6	-0.9	305

^a = estimated for growing season only

^b = mean annual climate data taken from online climate records

2.5.4. Published peatland NECB

There have been only four published site estimates of the full peatland NECB where measurements for each component were obtained simultaneously at the same site. Roulet et al. (2007) reported a six year dataset of NECB from Mer Bleue bog in Ontario, Canada using eddy covariance CO₂ fluxes, manual chamber CH₄ fluxes, and measurements of DOC in stream outflow to estimate water-borne C losses. Annual NECB ranged from net C loss of 13.5 gC m⁻² yr⁻¹ to net C gain of 89.2 gC m⁻² yr⁻¹ (mean of 21.5 gC m⁻² yr⁻¹, net C sink). Roulet et al. (2007) found that NEE was the largest term in the C balance but also the most variable. Years with lowest summer and autumn water tables resulted in overall C loss from the peatland, largely resulting from reduced CO₂ sink strength. However, the peatland exhibited net annual CO₂ uptake in each year, meaning that C losses from CH₄ emission and DOC export can push the ecosystem from net annual C sink to net annual source.

Nilsson et al. (2008) reported two years of NECB measurements from a Swedish fen site, Degerö Stormyr, using eddy covariance CO₂ fluxes, manual chamber CH₄ fluxes, total C export from stream outflow (total organic C, dissolved CO₂ and CH₄), and total organic C inputs from rain water. Annual NECB exhibited net gains of 20-27 gC m⁻² yr⁻¹ with NEE constituting the largest term, although CH₄ fluxes and stream C export represented 53-61% of annual NEE, while rain water C inputs were 2-3% of annual NECB.

Koehler et al. (2011) presented 6 years of annual NECB measurements from an Irish blanket bog, Glencar, using eddy covariance CO₂ fluxes, manual chamber CH₄ fluxes, and DOC measurements in stream discharge. Annual NECB ranged

from a net loss of $8.6 \text{ gC m}^{-2} \text{ yr}^{-1}$ to a net gain of $65.6 \text{ gC m}^{-2} \text{ yr}^{-1}$ (mean of $29.7 \text{ gC m}^{-2} \text{ yr}^{-1}$, net C sink). Again NEE was the largest term while CH_4 emissions and DOC export constituted a slightly smaller percentage of NEE (38%) than found by Nilsson et al. (2008). Similar to Roulet et al. (2007), Koehler et al. (2011) found that annual C loss was greatest during the year with lowest summer water table. Olefeldt et al. (2012) reported NECB estimated from a permafrost palsamire, Stordalen, in Northern Sweden over two years. They used eddy covariance CO_2 fluxes, total hydrocarbon (sum of CH_4 and non- CH_4 volatile organic compounds) fluxes from automated chambers, and DOC measurements in runoff from an outflow weir. At Stordalen, the sum of CH_4 emissions and DOC export were only 12% of annual NEE, a smaller percentage than found at the abovementioned peatlands, although the range in annual NECB was similar ($33.0 - 55.8 \text{ gC m}^{-2} \text{ yr}^{-1}$).

Finally, Gažovič et al. (2013) measured NECB at a Finnish fen, Salmisuo, over two years using eddy covariance NEE measurements, manual chamber CH_4 fluxes, and DOC export in stream outflow. NECB estimates from this site were 85 and $136 \text{ gC m}^{-2} \text{ yr}^{-1}$ (net C gains), larger than the abovementioned estimates. This was due to the relatively large CO_2 uptake ($92 - 154 \text{ gC m}^{-2} \text{ yr}^{-1}$) and low CH_4 ($3.4 - 6.4 \text{ gC m}^{-2} \text{ yr}^{-1}$) and aquatic DOC fluxes ($4.2 - 11.3 \text{ gC m}^{-2} \text{ yr}^{-1}$). As expected however, lowered water tables in the first year of measurement at Salmisuo led to lower annual C sink strength.

Other studies have estimated peatland NECB by incorporating representative data from separate studies on individual C balance components or by combining

measurements of C flux components from different areas of a catchment.

Aurela et al. (2007) measured annual NEE at a Swedish fen, Siikeneva, with eddy covariance, and combined these data with previously published estimates of CH₄, non-CH₄ volatile organic C fluxes, and total organic C export in stream outflow, resulting in estimated annual C gain of 36 gC m⁻² yr⁻¹. Dinsmore et al. (2010) focused on aquatic C export pathways from a peatland catchment and used eddy covariance to estimate CO₂ flux. After incorporating CH₄ flux estimates from a parallel study, they estimated annual NECB of 38.2 – 101 gC m⁻² yr⁻¹.

Mean annual water table depth is clearly a strong driver of inter-annual differences in major C balance components, although the impact of dry years is variable among peatland types. Dry conditions may reduce peatland C sink strength or even cause systems to shift from C sink to source. Furthermore, the percentage contribution of non-CO₂-C fluxes to overall NECB is highly site dependent. In New Zealand, the only year-round peatland C flux estimate illustrated a large CO₂ sink at a dry restiad bog site, and incorporation of typical published non-CO₂-C losses still suggested an annual C sink > 200 gC m⁻² yr⁻¹ (Campbell et al., 2014).

From a peatland C balance perspective, average annual losses of CH₄ may contribute a small, albeit important, percentage of total NECB. However, the climate impact of CH₄ must be considered, given its greater global warming potential. The most recent estimate from the IPCC (2013) suggests that atmospheric CH₄ is 28.5 times as potent as CO₂, considering a 100-year time horizon. To account for this, many researchers convert CH₄ emissions into CO₂-equivalents in an effort to assess the overall climate impact of the peatland.

Using this approach, the atmospheric cooling effect of CO₂ uptake is sometimes offset by the warming effect of CH₄ emission (Herbst et al., 2011; Long et al., 2010; Olson et al., 2013; Rinne et al., 2007). However, Frolking and Roulet (2007) demonstrated that, throughout the Holocene, peatlands have had a net cooling effect on the atmosphere because of the cumulative nature of CO₂ sequestration and the shorter atmospheric lifetime of CH₄. Nevertheless, the magnitude of a peatland's cumulative radiative forcing over the long-term depends strongly on the ratio of CH₄ emission to CO₂ uptake (Frolking et al., 2006), necessitating a more complete understanding of the magnitudes and drivers of both fluxes.

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Chapter 3. High vapour pressure deficit constrains GPP and the light response of NEE at a Southern Hemisphere bog

3.1. Introduction

Peatlands store a large amount of carbon (C) globally (Yu et al., 2010), which has led to concern about potential feedbacks between peatland C cycling and climate change. The net ecosystem exchange of CO₂ (NEE) is comprised of two much larger component fluxes, gross primary production (GPP) and ecosystem respiration (ER), and these generally represent the largest terms of a peatland C budget (Koehler et al., 2011; Nilsson et al., 2008; Olefeldt et al., 2012; Roulet et al., 2007). Recent efforts have focused on characterizing variability in NEE between years (Teklemariam et al., 2010), comparisons of NEE between sites (Humphreys et al., 2006; Lund et al., 2010), and testing the utility of ecosystem models in different peatland types (Sulman et al., 2012). Although peatland photosynthetic rates are often low relative to other ecosystem types (Frolking et al., 1998), decomposition rates are also restricted, largely due to anaerobiosis associated with water-logged conditions (Clymo, 1984). This constraint on decomposition has led to lower variability of ER relative to GPP between sites, which emphasizes the importance of understanding the drivers of GPP among different peatlands (Lund et al., 2010). The majority of peatland C exchange research has focused on Northern Hemisphere temperate to arctic ecosystems, whereas measurements in Southern Hemisphere peatlands are sparse despite the need to provide insight into ecosystem exchange processes under different climatic, hydrologic, and biotic conditions (Campbell et al., 2014; Frolking et al., 2011; Limpens et al., 2008).

Land development for agricultural production has severely impacted on the areal extent of all New Zealand wetland types with only about 10% of their original area remaining (McGlone, 2009). However, large unaltered peatland remnants may serve as analogues to their Northern Hemisphere counterparts albeit in a comparatively warmer climate with unique dominant peat-forming vegetation (Hodges and Rapson, 2010). In ombrotrophic bogs on the North Island of New Zealand, the main peat-forming species is the vascular plant *Empodisma robustum* (Wagstaff and Clarkson, 2012), which forms root clusters with similar nutrient capture and water holding capacity functions to *Sphagnum* mosses in northern peatlands (Agnew et al., 1993; Clarkson et al., 2009). However, *E. robustum*-dominated systems are characterised by a dense canopy of interwoven live and dead stems, which limits evaporation rates through high stomatal resistance and a physical mulching effect (Campbell and Williamson, 1997), and little is known about canopy scale CO₂ exchange and, particularly, the controls on GPP.

Daytime NEE in terrestrial ecosystems is largely controlled by radiation, temperature, saturation vapour pressure deficit (VPD), and the fraction of diffuse incoming radiation (f_{diff}) (Law et al., 2002), while light-saturated NEE further depends on specific ecosystem characteristics such as canopy architecture, green plant area index (GAI), and plant functional group (Ruimy et al., 1995). When compared to the canopy light response of forests, grasslands, and crops, Northern Hemisphere peatlands form a distinct ecological class, characterised by low apparent quantum yield (α) and light-saturated photosynthetic capacity (P_{max}) (Frolking et al., 1998). The light response

characteristics of peatlands are also partly a function of nutrient limitation (Clymo, 1984), especially in ombrotrophic bogs where atmospheric deposition provides the sole nutrient input.

While studies in a range of ecosystems have shown that overcast conditions can enhance canopy scale α and $P_{\max}$ due to increased f_{diff} (Kanniah et al., 2012), the extent to which diffuse radiation may affect NEE is strongly related to canopy architecture, and particularly, GAI (Knohl and Baldocchi, 2008; Wohlfahrt et al., 2008). One of the main causes for this is the increase in effective leaf area when diffuse radiation penetrates to deeper canopy layers and illuminates otherwise shaded canopy elements (Gu et al., 2002). The importance of this mechanism has been demonstrated for ecosystems with relatively high GAI such as forests, shrub lands, and grasslands (e.g., Alton, 2008). In peatland ecosystems, vegetation is generally short-statured with relatively low GAI and, consequently, the influence of f_{diff} on canopy light penetration may not be important. A sole previous study of peatland NEE response to sky conditions concluded that NEE did not differ between overcast and clear sky periods at the *Sphagnum* – low shrub-dominated Mer Bleue bog in Ontario, Canada (Letts et al., 2005). However, it remains unclear whether this also applies to *E. robustum*-dominated bogs given the very different canopy architecture, albeit similar GAI.

Most short-statured canopies with low GAI would not benefit from diffuse light penetrating to subsurface vegetation during overcast conditions because self-shading within the canopy is minimal (Kanniah et al., 2012; Wohlfahrt et al., 2008). However, changes in temperature and VPD concurrent with changing sky conditions can affect peatland NEE through stomatal regulation or by

influencing ecosystem respiration (Kwon et al., 2006). Elevated VPD can cause plants to reduce stomatal aperture in order to avoid water loss but this also restricts CO₂ assimilation (Körner, 1995). High temperatures above an optimum can also lead to reduced photosynthetic rates (June et al., 2004) and contribute to reduced CO₂ uptake associated with clear-sky conditions (Cai et al., 2009).

Because f_{diff} is correlated with temperature and VPD, some portion of the canopy response to sky conditions will likely derive from these associated variables (Urban et al., 2007; Wohlfahrt et al., 2008). In a modelling study focused on a region of East Asia containing a mix of croplands, natural forest, and shrublands, Steiner and Chameides (2005) illustrated that temperature and VPD effects can be the dominant factor influencing GPP with an increase in f_{diff} . Furthermore, elevated VPD, often in concert with clear skies, has been recognized as a constraint to CO₂ uptake in a cool, temperate mountain peatland dominated by grasses and sedges (Otieno et al., 2012).

Increasingly dry summers in New Zealand have been related to large-scale atmospheric circulation modes (Ummenhofer et al., 2009) and a trend toward expanding high-pressure systems (MPI, 2013), while global shifts in precipitation and temperature due to greenhouse gas-induced warming are projected (Liu et al., 2013). Consequently, it is imperative to understand how future changes in f_{diff} , VPD, and temperature will affect peatland CO₂ uptake, and the mechanisms involved.

We used eddy covariance (EC) measurements of NEE in a warm-temperate Southern Hemisphere peatland to explore the major drivers of daytime ecosystem CO₂ uptake. Our objective was to determine the relative importance

of light, temperature, and VPD as drivers of GPP at Kopuatai bog. Given the mild climate and infrequent sub-zero temperatures in this region, we hypothesized that the seasonality of CO₂ uptake would depend more strongly on light than on temperature, in contrast to most Northern Hemisphere peatlands. We also expected VPD to play a strong role in driving day-to-day variability in GPP because of the exceptionally low canopy conductance to water loss previously demonstrated at Kopuatai (Campbell and Williamson, 1997).

3.2. Methods

3.2.1. Site description

Kopuatai is a raised ombrotrophic peat bog that covers approximately 96 km² in the Hauraki Plains of the North Island/ Te Ika-a-Māui, New Zealand, with peat depths reaching 14 m toward the domed bog crest (Newnham et al., 1995).

Jointed wire rush, *Empodisma robustum* Wagstaff & B.R.Clarkson, sp. nov., is the dominant vegetation around the EC tower site, forming a dense canopy 0.25 - 0.8 m high. This species of the family *Restonaceae* has narrow (~ 2 mm diameter) elongated stems with leaves reduced to sheaths on stem joints (Wagstaff and Clarkson, 2012). Sedges, *Machaerina teretifolia* and *Schoenus brevifolius*, are present especially in wetter zones, and clusters of small shrubs (1-2 m height), *Leptospermum scoparium* and *Epacris pauciflora*, are sparsely scattered throughout the study area.

The canopy structure is characterized by a large amount of standing dead plant litter relative to green biomass. In a parallel study, 15 randomly positioned plots (0.25 m²) were destructively sampled for biomass and green area, resulting in an average ($\pm$ standard deviation) of 0.39 ($\pm$ 0.09) kg green dry matter m⁻² and 1.33

(± 0.54) kg m⁻² brown and dead dry matter (Keyte-Beattie, 2014), all from standing vascular vegetation. The canopy architecture was thus relatively dense compared to typical *Sphagnum* – low shrub-dominated Northern Hemisphere bogs (e.g., Bubier et al., 2003). The profile of one-sided GAI was 0.63, 0.48, and 0.21 m²m⁻² in the top (~60 cm and above), mid (~40 – 60 cm above the surface), and sub-canopy (~10 – 30 cm above the surface) layers, respectively, resulting in average ($\pm$ standard deviation) total GAI of 1.32 ± 0.32 m²m⁻² with range 0.90 – 2.0 m²m⁻².

3.2.2. Eddy covariance measurements and calculations

A 4.5 m tall triangular lattice tower was erected on the northern dome of the bog (latitude: 37.388 S, longitude: 175.554 E). Instruments were mounted on a horizontal arm approximately 1.5 m from the face of the tower and 4.25 m above the surface. Uninterrupted fetch extended >500 m in all directions with relatively uniform canopy height and negligible slope over that distance. An open path infrared gas analyzer (LI-7500; LI-COR Inc., Lincoln, Nebraska, USA) and a sonic anemometer (CSAT3; Campbell Scientific Inc., Logan, Utah, USA) were used to acquire high frequency CO₂ and H₂O concentration, and three-dimensional wind data, respectively. The system was controlled with a CR3000 data logger (Campbell Scientific Inc.), and high frequency (10 Hz) data were stored on a memory card.

Raw data were processed to fluxes with an averaging interval of 30 minutes (missing samples allowance of 10%) using the EddyPro v5.1 software (LI-COR). A double axis rotation was applied for tilt correction and high frequency data were de-trended using block averaging. A fully analytic approach was taken for

spectral corrections of high-pass filtering (Moncrieff et al., 2004) and low-pass filtering (Moncrieff et al., 1997). The standard Webb et al., (1980) method was applied to account for air density fluctuations. Additional corrections for surface heating of the open-path gas analyser (Burba et al., 2008) were not applied. Following the convention of Chapin et al., (2006), negative NEE indicates net CO₂ uptake by the ecosystem.

Ancillary measurements included incoming total and diffuse photosynthetic photon flux density (PPFD) (BF5 Sunshine Sensor, Delta-T Devices Ltd., Cambridge, United Kingdom) just above the canopy (~1.2 m above peat surface) and air temperature (T_{air}) and vapour pressure (fully aspirated HMP 155, Vaisala, Helsinki, Finland) at 4.25 m above the surface. Water table depth (WTD) was measured within a 1.5 m dipwell using a submersible pressure sensor (WL1000W, Hydrological Services, NSW, Australia). Precipitation was recorded using a tipping bucket rain gauge (TB5, Hydrological Services). The diffuse fraction of incoming radiation (f_{diff}) was calculated as diffuse PPFD divided by total PPFD for each half-hour. The analyses in this study include data from the period 1 December 2011 – 28 February 2014.

3.2.3. Data quality control

We conducted tests for stationarity in the high-frequency CO₂ concentration time series for each 30-minute period by setting limits for the standard deviation of CO₂ molar density (0.15 and 0.25 mmol m⁻³ for day and night time data, respectively). We chose a threshold for insufficient atmospheric turbulence by calculating annual sums of NEE using a range of friction velocity (u_*) thresholds and determining the value at which annual NEE stabilized

(Loescher et al., 2006). Subsequently, data for periods in which $u^* < 0.15$ were removed from the analysis. We then removed remaining spikes in the CO₂ flux time series by calculating 30-day moving window statistics and testing each half-hourly flux against the median for the corresponding time period. Fluxes exceeding the median ± 2 (daytime) or ± 3 (night time) standard deviations were flagged and any half hours with more than 1 (daytime) or 4 (night time) flags were rejected.

3.2.4. Using light response models to disentangle controls on NEE

The Michaelis-Menten based rectangular hyperbolic function is often used to describe the light response of NEE (Thornley and Johnson, 1990) and this can be coupled to the Lloyd and Taylor (1994) model to account for the temperature dependence of respiration (Gilmanov et al., 2003; Lasslop et al., 2010):

$$NEE = \frac{\alpha Q P_{\max}}{\alpha Q + P_{\max}} + R_{10} e^{308.56 \left(\frac{1}{283.15 - 227.13} - \frac{1}{T_{\text{peat}} - 227.13} \right)} \quad (1)$$

where, α is apparent quantum yield, $P_{\max}$ is maximum light-saturated NEE, and Q is incoming PPFD. The last term on the right-hand side of Eq. 1 represents ecosystem respiration (ER_{LT}), where R_{10} is the fitted parameter describing ER at 10 °C, and the effective activation energy and the reference temperature were assumed to be fixed at 308.56 K and 227.13 K, respectively. However, we were interested in exploring modifications to Eq. 1 (referred to henceforth as MM) based on f_{diff} , T_{air} , and VPD to identify limitations and improvements in the model's ability to describe NEE for this ecosystem. We recognize the limitations of using simple empirical functions to elicit the response of ecosystem processes to environmental variables (see Lasslop et al., 2010). However, we can glean

information from comparisons of various functions for which theoretical justifications have been described previously.

We incorporated f_{diff} into MM following Cai et al., (2009):

$$\text{NEE} = \frac{\alpha(Q_{\text{diff}} + k_1 Q_{\text{dir}})P_{\text{max}}}{\alpha(Q_{\text{diff}} + k_1 Q_{\text{dir}}) + P_{\text{max}}} + \text{ER}_{\text{LT}} \quad (2)$$

where Q_{diff} and Q_{dir} are the diffuse and direct components of PPFD, respectively, and k_1 is a fitted parameter ranging from 0 to 1. Equation 2 (henceforth MM_{diff}) explicitly represents the effective radiation utilized by the canopy, which changes with f_{diff} and phase of canopy development (Cai et al., 2009). When $k_1 = 1$, MM_{diff} simplifies to the MM model, indicating that f_{diff} is not important for describing NEE.

We also incorporated modifications to P_{max} based on T_{air} and VPD. A temperature response of P_{max} was added to the MM model according to the equation proposed by June et al. (2004) (Eq. 3, henceforth MM_{temp}), who used a Gaussian function to approximate the reversible temperature stress induced on the rate of photosynthetic electron transport above a threshold:

$$\text{NEE} = \frac{\alpha Q P_{\text{max}} e^{-((T_{\text{air}} - T_0)/k_2)^2}}{\alpha Q + P_{\text{max}} e^{-((T_{\text{air}} - T_0)/k_2)^2}} + \text{ER}_{\text{LT}} \quad (3)$$

Here, T_0 represents the temperature at which P_{max} is optimal and k_2 is a curvature term. Finally, we used a function allowing VPD restrictions on P_{max} (Eq. 4, henceforth MM_{VPD}) following Lasslop et al. (2010) who showed improved light response predictions of NEE for a global dataset across a range of sites when an exponential decay term was added to modify P_{max} above $\text{VPD}_0 = 1$ kPa:

$$\text{NEE} = \frac{\alpha Q P_{\text{max}} e^{-k_3(\text{VPD} - \text{VPD}_0)}}{\alpha Q + P_{\text{max}} e^{-k_3(\text{VPD} - \text{VPD}_0)}} + \text{ER}_{\text{LT}} \quad (4)$$

where k_3 is the exponential term.

Each of the four light response models was fitted to NEE measurements for the full study period using a non-overlapping 14-day moving window to accommodate seasonal shifts in canopy development, yet include sufficient data for meaningful parameter estimation (e.g., Gu et al., 2002). The terms k_2 and k_3 in the MM_{temp} and MM_{VPD} models, respectively, were poorly constrained at times due to scatter in the NEE data. Therefore, we estimated P_{max} from the MM model using NEE data binned across T_{air} and VPD, then fit the Gaussian temperature response of P_{max} from Eq. 3 and the exponential VPD response of P_{max} from Eq. 4 to estimate the coefficients T_o , and k_2 (MM_{temp}), and VPD_o , and k_3 (MM_{VPD}). The results were then used to set fixed values for those coefficients in the moving window curve fitting.

The addition of these terms into the MM_{temp} and MM_{VPD} models change the meaning of α and P_{max} from the standard MM model so we have reported estimates of those parameters based only on the moving window fitting of MM for the sake of consistency with the literature. For each window, parameter sets, residuals, and fit statistics, including root mean squared error (RMSE), Akaike's Information Criterion (AIC) (Akaike, 1974), and coefficient of determination (R^2) were calculated.

Previous work has demonstrated that energy partitioning of *E. robustum* canopies is dominated by evaporation of intercepted water when the canopy is wet. When the canopy is dry, evaporation rates are constrained to low values relative to other published data for peatlands (Campbell and Williamson, 1997;

Lafleur, 2008). Thus, we modified a simple antecedent wetness index, based on time since rain (Woods and Rowe, 1996) to constrain our analysis to dry canopy conditions.

3.3. Results

3.3.1. Meteorological conditions during the study period

Mean annual T_{air} at Kopuatai bog was 13.3 °C and 14.0 °C for 2012 and 2013, respectively, compared to the long-term normal (1980-2010) of 13.7 °C measured at a nearby climate station. During the study period, minimum T_{air} dropped below 0 °C on 33 days, while maximum T_{air} was generally 25 – 30 °C during summer (Fig. 3.1). Total rainfall for 2012 and 2013 was 1153 mm and 1105 mm, respectively, compared to a long-term normal of 1232 mm. However, from January – March 2013, New Zealand experienced the most severe nationwide drought in the past 70 years (MPI, 2013), leading to total rainfall 75% below the long-term mean for those months and the lowest WTD of the study period (Fig. 3.1d). Despite the 2013 drought, the water table remained within 30 cm of the peat surface throughout the study period.

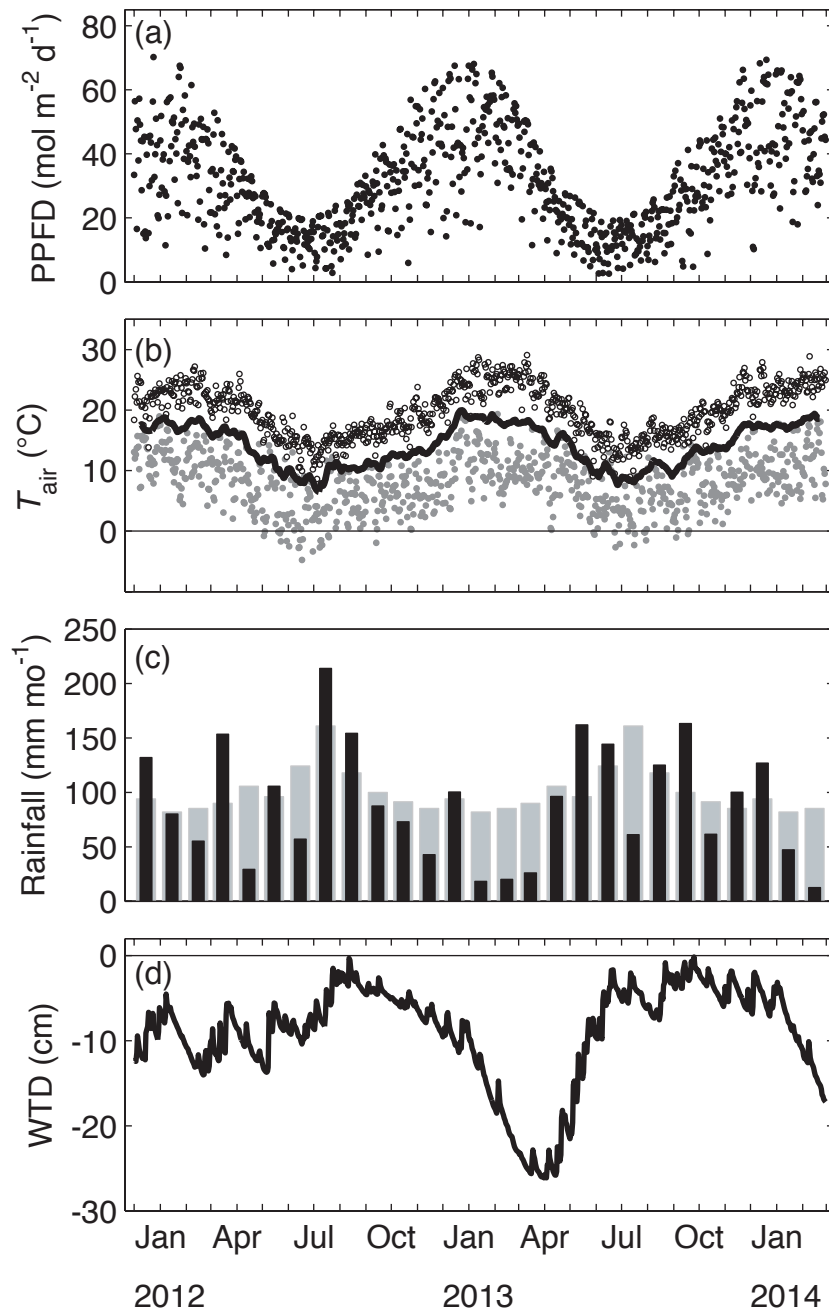


Figure 3.1 Meteorological and hydrological variables at Kopuatai bog, 1 Dec2011 – 28 Feb 2014: (a) daily total PPFD, (b) daily minimum (grey points) and maximum (open points) air temperatures (T_{air}), and the 15-day running mean of T_{air} (line); (c) monthly total rainfall (black bars) and monthly normals (1980-2010) taken from a nearby climate station (grey bars), (d) daily mean water table depth (WTD) (zero line is the peat surface).

In winter months (May – Aug), during dry-canopy conditions, T_{air} primarily ranged from $\sim 10 - 20$ °C (Fig. 3.2). During summer months (Nov – Feb) and shoulder seasons (Mar – Apr, Sep – Oct), T_{air} and VPD had similar ranges (summer: $5.5 - 27.5$ °C; $0 - 2.51$ kPa; shoulder: $3.1 - 29.1$ °C; $0 - 2.9$ kPa), although means were higher during summer (21.2 °C; 1.1 kPa) than in the shoulder season (18.6 °C; 0.9 kPa). Low values of f_{diff} were generally associated with high PPFD, although there was a large amount of variability in f_{diff} at any given PPFD level (Fig. 3.2c), likely related to cloud type and thickness, and solar zenith angle (Spitters et al., 1986).

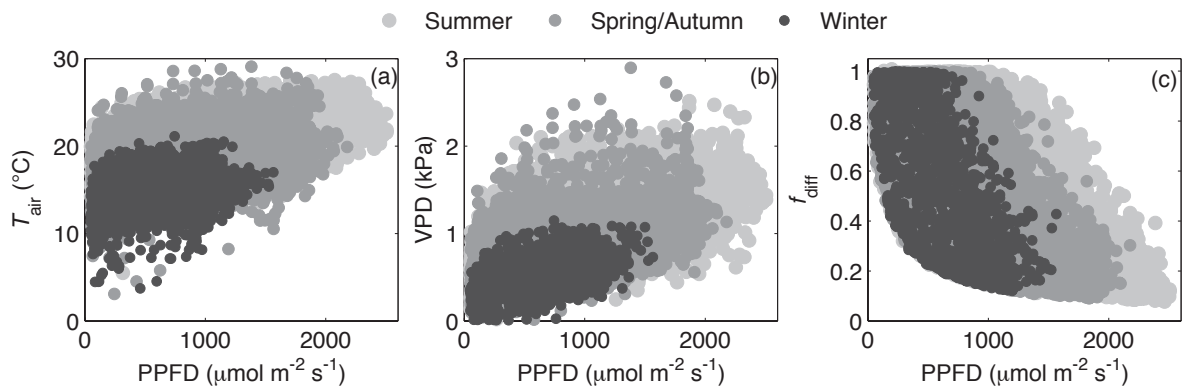


Figure 3.2. Scatter plots of half-hourly meteorological data used in the NEE light response models (dry canopy conditions only) for the period from 1 Dec 2011 – 28 Feb 2014: (a) air temperature (T_{air}) versus PPFD, (b) vapour pressure deficit versus PPFD, (c) fraction of diffuse incoming radiation (f_{diff}) versus PPFD. Summer months included Nov – Feb, spring/autumn included Mar, Apr, Sep, Oct, and winter included May – Aug.

3.3.2. Disentangling the drivers of NEE light response

The seasonality of light response parameters was estimated using the MM model (Eq. 1). The mild climate and year-round growing conditions allowed all light response parameter estimates to remain remarkably similar among

seasons (Table 3.1). Apparent quantum yield (α) was greatest (most negative) in summer and lowest in winter, but estimates of α from adjacent seasons had overlapping confidence intervals (Table 3.1). The range of $P_{\max}$ across seasons was small, varying from -6.4 to -6.7 $\mu\text{mol m}^{-2} \text{s}^{-1}$, indicating that this evergreen ecosystem had more-or-less constant photosynthetic capacity, likely related to the similar ranges in meteorological conditions among seasons (Fig. 3.2) and evergreen vegetation.

Table 3.1. Seasonal light response parameter estimates from the MM model (Eq. 1). Summer months included Nov – Feb, spring/autumn included Mar, Apr, Sep, Oct, and winter included May – Aug. Units of α are $\mu\text{mol } \mu\text{mol}^{-1}$, while units of $P_{\max}$ and R_{10} are $\mu\text{mol m}^{-2} \text{s}^{-1}$ and represent best fits ($\pm$ 95% confidence interval).

	Summer	Spring/Autumn	Winter
α	-0.019 ($\pm$ 0.003)	-0.013 ($\pm$ 0.003)	-0.008 ($\pm$ 0.002)
$P_{\max}$	-6.67 ($\pm$ 0.22)	-6.37 ($\pm$ 0.25)	-6.54 ($\pm$ 0.85)
R^2	0.46	0.56	0.55

After using the MM model to derive light response parameters from datasets of NEE binned across ranges of T_{air} , we modified the equation proposed by June et al. (2004) (used in MM_{temp}) to account for asymmetry in the temperature response of $P_{\max}$ (Fig. 3.3a) such that $T_o = 19.9$ °C, $k_2 = 9.1$ when $T_{\text{air}} < T_o$ and $k_2 = 3.2$ when $T_{\text{air}} > T_o$. In general, for $10.0 < T_{\text{air}} < 19.9$ °C, the magnitude of $P_{\max}$ increased from -5.9 to -7.7 $\mu\text{mol m}^{-2} \text{s}^{-1}$, then dropped to -5.6 $\mu\text{mol m}^{-2} \text{s}^{-1}$ when $19.6 < T_{\text{air}} < 25.0$ °C (Fig. 3.3a).

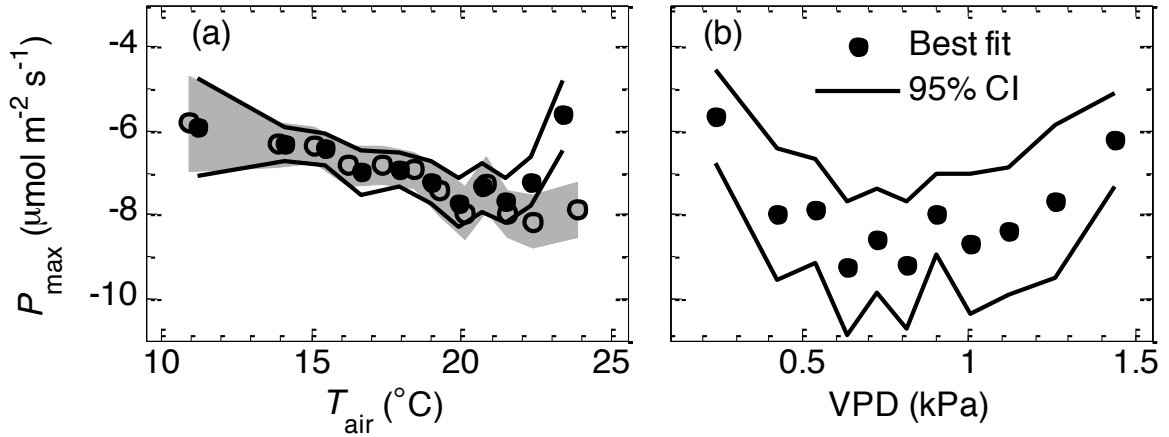


Figure 3.3. Light-saturated photosynthetic capacity ($P_{\max}$) was derived with the MM model (Eq. 1) using data binned by (a) T_{air} and (b) VPD. Points represent the best fit with solid lines delineating the 95% confidence interval around the estimate. The open points and shaded region in (a) represent parameter estimates obtained after excluding all data for VPD > 1.5 kPa, to illustrate the removal of an apparent temperature-induced inflection in $P_{\max}$ above 19.9 °C.

Similarly, high VPD led to reductions in $P_{\max}$ from -8.7 to $-6.2 \mu\text{mol m}^{-2} \text{s}^{-1}$, when VPD > 1 kPa (Fig. 3.3b), consistent with the threshold suggested by Lasslop et al. (2010) and we thus set VPD₀ to 1 kPa and the associated k_3 term to 0.73 in the MM_{VPD} model. For VPD < 1 kPa, $P_{\max}$ ranged from -5.6 to $-9.2 \mu\text{mol m}^{-2} \text{s}^{-1}$ with an increasing trend (Fig. 3.3b), likely related to the coincident increase in PPFD for that range in VPD (Fig. 3.2). We also found that $P_{\max}$ was generally enhanced by increasing f_{diff} , however the estimation of $P_{\max}$ became problematic at high f_{diff} because the light response of NEE did not saturate fully, leading to very high $P_{\max}$ estimates (data not shown). However, the relationships between $P_{\max}$ and these three driver variables are somewhat confounded by the correlations

among them. For instance, VPD is inherently related to T_{air} , and both generally change with a change in f_{diff} .

Our approach to disentangling the drivers of variability in daytime NEE, in particular P_{max} , was to investigate the statistical results (Table 3.2) and residual behaviour (Fig. 3.4) of the moving window fits of Eqs. 1-4. MM_{VPD} yielded the lowest AIC (Table 3.2), which not only computes a cost function (as in the case of RMSE and R^2) but also applies a penalty for added parameters to discourage over-fitting (Akaike, 1974). Having the lowest AIC thus suggests that MM_{VPD} is the most appropriate function of the four we considered to estimate NEE (Table 3.2). However, we were also interested in using the results from these models to separate out the effects of T_{air} , VPD, and f_{diff} on NEE. In order to compare the models, we examined the mean residuals binned by each meteorological driver (Carrara et al., 2004; Powell et al., 2006; Teklemariam et al., 2009; Tong et al., 2014). In this approach, any consistent pattern in the model residuals indicates a bias with respect to the given variable. The MM and MM_{diff} models consistently underestimated NEE at both high and low values of PPFD, T_{air} , and VPD, and resulted in over-estimates for mid-ranges of those variables (Fig. 3.4a,c,d). With respect to f_{diff} , there was essentially no bias in the MM_{diff} estimates of NEE, likely due to the explicit inclusion of direct and diffuse light components in that model (Eq. 2). However, the MM model consistently under-estimated NEE at low f_{diff} and over-estimated NEE at high f_{diff} (Fig. 3.4b).

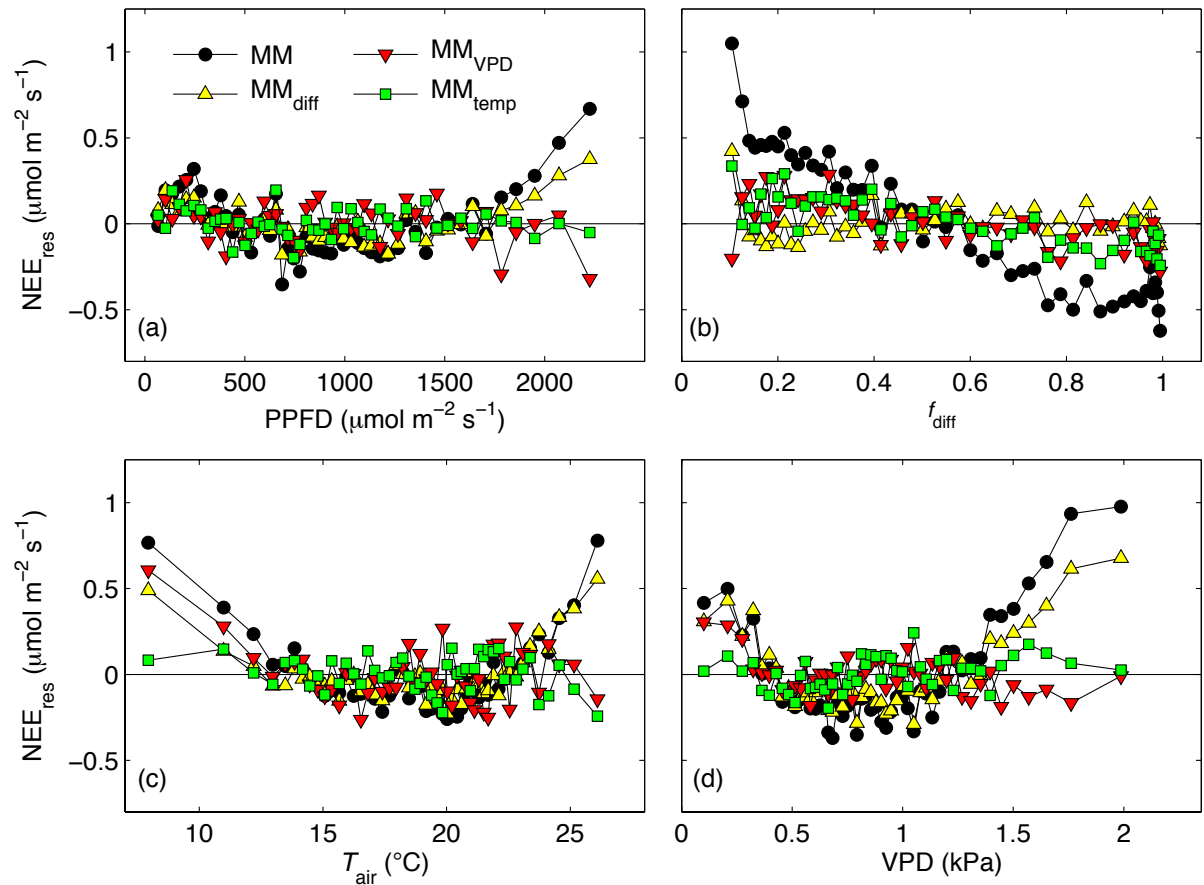


Figure 3.4. Residuals (measured NEE – modelled NEE) from the four light response models gathered during the moving window fitting routine were binned by (a) PPFD, (b) f_{diff} , (c) T_{air} , and (d) VPD. Any trend in residuals associated with these variables indicates a systematic bias in the model estimates of NEE.

Table 3.2. Statistics gathered from the 14-day non-overlapping moving window light response curve fitting approach for the four light response models (Eqs. 1-4) describing daytime NEE for the period from 1 Dec 2011 – 1 Mar 2014.

Model	RMSE	AIC	R^2
MM	0.969	966.5	0.63
MM _{diff}	0.818	905.5	0.73
MM _{temp}	0.919	947.7	0.67
MM _{VPD}	0.949	854.5	0.58

In general, the estimates of NEE produced by MM_{temp} and MM_{VPD} were less biased with respect to PPFD, T_{air} , and VPD than those of MM and MM_{diff} (Fig. 3.4a,c,d). The MM_{temp} and MM_{VPD} models also produced less biased estimates of NEE with respect to f_{diff} than MM (Fig. 3.4b). Considering the reduction in model bias with respect to all driver variables, we concluded that MM_{temp} and MM_{VPD} better represented the variability in NEE than MM and MM_{diff} .

The asymmetric temperature response of P_{max} , with a more rapid decline above T_o than below (Fig. 3.3a), is unusual and contrary to results from June et al. (2004). The authors of that study found that the peak rate and curvature of electron transport response to temperature varied with growth conditions, but the curve was generally symmetric (June et al., 2004). To investigate this further, we excluded data for which VPD > 1.5 kPa and re-fit MM to NEE binned by T_{air} (Fig. 3.3a). The low-VPD data resulted in more negative P_{max} estimates for values above what would have otherwise been deemed T_o than when the full data set was used. This suggested that VPD effects were more important to the observed restrictions to P_{max} (and associated reductions in daytime NEE) than high temperatures. We thus chose to fill gaps in daytime NEE using MM_{VPD} . The low AIC found here (Table 3.2) as well as the widespread applicability of this function and the consistent threshold VPD across ecosystem types (Lasslop et al., 2010), provided further confidence in this choice.

After filling gaps in the half-hourly daytime NEE time series using the MM_{VPD} parameter sets from the corresponding time windows, we partitioned the fluxes into ER and GPP using night time ($PPFD < 50 \mu\text{mol m}^{-2} \text{s}^{-1}$) data to parameterize ER_{LT} , and GPP was then calculated as: $GPP = -NEE + ER$. Drivers of daytime GPP

were investigated using cubic spline interpolation within each data space (Fig. 3.5) and mean middle-of-day (1000 – 1600 hr) GPP was compared directly to PPFD, f_{diff} , T_{air} , and VPD (Fig. 3.6).

3.3.3. Controls on mid-day GPP

Mid-day GPP was controlled by interactions among PPFD and T_{air} , VPD, and f_{diff} (Fig. 3.5) but these driver variables were also correlated to each other. Mean VPD was most strongly correlated to total PPFD ($r(\text{PPFD}, \text{VPD}) = 0.87$, $p < 0.001$), whereas the correlations were weaker with f_{diff} ($r(\text{PPFD}, f_{\text{diff}}) = -0.68$, $p < 0.001$) and mean T_{air} ($r(\text{PPFD}, T_{\text{air}}) = 0.71$, $p < 0.001$). As expected, light limitation of GPP was strongest in winter, whereas there was very little variation in mid-day GPP with changes in PPFD during summer (Fig. 3.6). For $\text{PPFD} > \sim 1500 \mu\text{mol m}^{-2} \text{s}^{-1}$, maximum GPP generally occurred at highest daily T_{air} and f_{diff} , but mid-range VPD (Fig. 3.5).

The seasonal breakdown revealed that, during winter, GPP increased with both temperature and light (Fig. 3.6a,c), which indicates a dual limitation. The slight reduction in GPP with increasing f_{diff} during winter and shoulder seasons (Fig. 3.6b) was also likely a result of light limitation since higher f_{diff} was generally associated with decreasing PPFD (Fig. 3.2c). High VPD was the only condition to which mid-day mean GPP seemed to respond negatively above a threshold during summer (Figure 3.6d), although means were not significantly different. However, mid-day mean T_{air} during summer was significantly, and positively, correlated to mid-day mean GPP ($r(T_{\text{air}}, \text{GPP}) = 0.29$, $p < 0.001$) indicating that high temperature was not a constraint to photosynthesis during those periods.

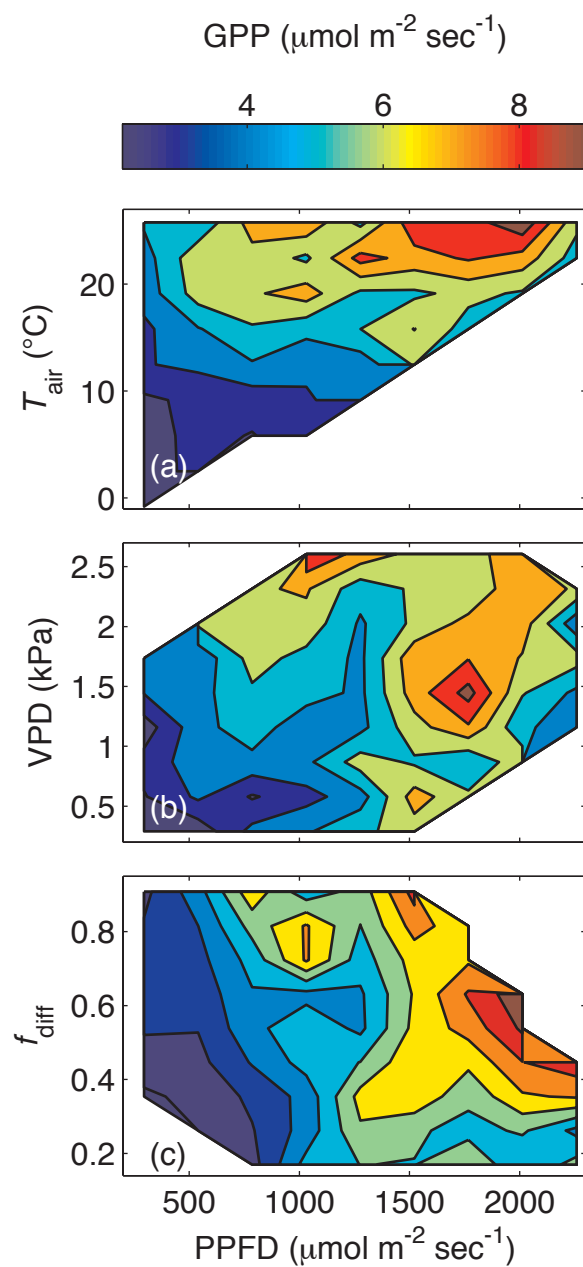


Figure 3.5. Relationships between 30-minute mid-day (1000 – 1600 hrs) PPFD (a) T_{air} , (b) VPD, and (c) f_{diff} . Coloring indicates 30-minute mid-day GPP, while contours were obtained via cubic spline interpolation.

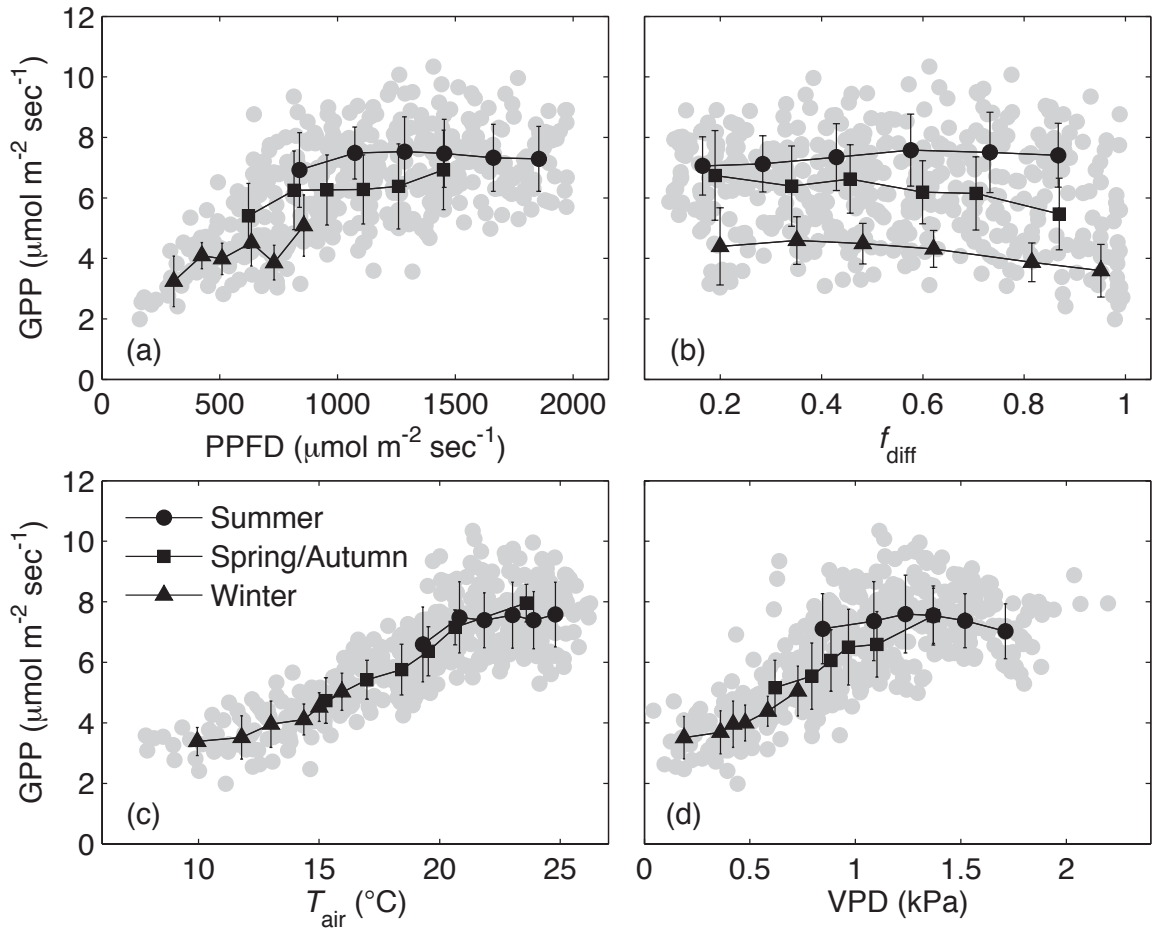


Figure 3.6. Relationships between mid-day (1000 – 1600 hrs) mean GPP and means of (a) PPFD, (b) f_{diff} , (c) T_{air} , and (d) VPD. Solid black points are means binned by each variable for individual seasons, where Summer months included Nov – Feb, Spring/Autumn included Mar, Apr, Sep, Oct, and winter included May – Aug. Error bars represent ± 1 standard deviation.

3.4. Discussion

3.4.1. Canopy response to light and temperature

The mild maritime climate at Kopuatai bog allowed for $GPP > 0$ in all seasons.

Although our estimate of overall summer P_{max} at Kopuatai was similar to growing season P_{max} values reported for northern peatlands (Frolking et al., 1998), we found that winter P_{max} did not differ significantly from the summer estimate here (Table 3.1). In Northern Hemisphere peatlands, photosynthetic activity is generally halted by freezing temperatures and snow cover, and plants

then require sufficient accumulation of growing degree-days before becoming active again in spring (Adkinson et al., 2011; Syed et al., 2006). Thus, while the estimates of peak GPP and canopy light response parameters at Kopuatai compare well to Northern Hemisphere counterparts, transitions in New Zealand peatland CO₂ uptake are less dramatic between seasons. At an Irish, maritime blanket bog, year-round positive GPP was also demonstrated, although lower GAI and higher latitude (lower insolation) of that site led to a much shorter season of net CO₂ uptake than we found at Kopuatai (Sottocornola and Kiely, 2010).

Light and temperature were the primary drivers of seasonality in mid-day mean GPP (Fig. 3.6), while the near-linear relationship between T_{air} and P_{max} (Fig. 3.3a) further suggested a temperature driven component to the seasonality of CO₂ uptake. However, the evergreen plants that dominate ecosystem photosynthesis, along with T_{air} that routinely ranged from 5 – 20 °C during winter months, allowed winter-time P_{max} to approach summer values (Table 3.1). Since winter GPP at this site is dependent on both daily variations in light and temperature, future increases in mean winter temperatures may lead to increased GPP.

In contrast to the temperature limitation of GPP during winter and shoulder seasons, CO₂ uptake was reduced during clear days when temperature and VPD were highest. We investigated the role of temperature using the Gaussian function suggested by June et al. (2004). This function (Eq. 3) adequately represented the peaked temperature response of MM-derived P_{max} until data with high VPD were removed and the inflection of P_{max} was no longer apparent

(Fig. 3.3a). Nonetheless, this function has been implemented in other peatland studies (albeit without accounting for potential VPD effects) to parameterize seasonal plot-scale (Bortoluzzi et al., 2006) and inter-annual ecosystem-scale data (Flanagan and Syed, 2011). Furthermore, in peatlands where *Sphagnum* mosses contribute a large proportion of ecosystem photosynthesis, a temperature optimum independent of VPD may be expected (Harley et al., 1989) because mosses do not have true stomata (Duckett et al., 2009), potentially making them less responsive to changes in atmospheric demand *per se*. The expression of a temperature optimum for CO₂ assimilation by plants is also well supported by theoretical and leaf-level studies (Farquhar et al., 1980; Medlyn et al., 2002). Indeed, Duursma et al. (2014) recently suggested that the apparent stomatal response to VPD, enacted to reduce transpiration, may include (or be preceded by) a temperature response of assimilation. However, in the field at the ecosystem scale, this behaviour is very difficult to disentangle and our results suggested that high VPD (not high temperature) was the primary restriction to CO₂ uptake when light was not limiting in the vascular plant-dominated peatland studied here.

3.4.2. Canopy response to VPD

Our results suggest that VPD-induced stomatal closure is more likely the driver responsible for NEE reduction during the often coinciding periods of high T_{air} and VPD than temperature-induced stress on photosynthetic capacity (Fig. 3.3). Summer mid-day mean GPP was positively correlated with T_{air} and although no significant relationship was found with VPD, GPP seemed to decline as VPD increased (Fig. 3.6d). This result was consistent with analysis of NEE light

response using half-hourly data. The modification of $P_{\max}$ above $\text{VPD} = 1 \text{ kPa}$ (MM_{VPD} , Eq. 4) resulted in better AIC (Table 3.2) and reduced residual bias relative to the MM and MM_{diff} models (Fig. 3.4). This is also in agreement with the analysis of Lasslop et al. (2010), who showed that high VPD caused asymmetric diel cycles of NEE in various ecosystem types globally. Such VPD effects are also supported by previous work at Kopuatai bog that revealed latent heat flux plateaued above $\text{VPD} \sim 1 \text{ kPa}$, which generally occurred on clear-sky days when the canopy was dry, leading to exceptionally high Bowen ratios since sensible heat dominated the energy balance (Campbell and Williamson, 1997). In addition to a physical mulching effect provided by the standing dead litter, Campbell and Williamson (1997) demonstrated a physiological restriction to canopy conductance by VPD. Our results suggest that GPP is also constrained by that physiological response.

Studies in other peatland types have also suggested that high VPD leads to reductions in NEE. For example, Otieno et al. (2012) found that stomatal sensitivity to low root-to-shoot hydraulic conductance in fen sedge and grass species led to reduced leaf CO_2 assimilation and overall NEE during dry summer months when VPD exceeded 1 kPa. Takagi et al. (1998) found strong stomatal regulation of leaf transpiration in a Japanese peatland complex (vascular plant-dominated), dependent on the magnitude of VPD regardless of peat water content. Aurela et al. (2007) described a linear reduction in NEE above VPD of approximately 1.5 kPa at a sedge fen in southern Finland. Each of these studies found that the response of NEE (or stomatal conductance) to elevated VPD was apparent regardless of peat WTD but others have shown that dry conditions can

cause plant stress and lowered stomatal conductance (Sonnentag et al., 2010). During our study period, there was a substantial drought from January to April, 2013 (Fig. 3.1d), although we found no evidence that WTD changed the relationship between VPD and CO₂ uptake, probably because access to water was not an issue for *E. robustum* roots that typically extend well below 30 cm depth (Clarkson et al., 2009).

3.4.3. Implications with respect to sky conditions

At Kopuatai bog, the highest GPP at moderate to high-light levels occurred during cloudy conditions (i.e., high f_{diff}) (Fig. 3.5c) and estimates of P_{max} became exceptionally high with increasing f_{diff} . This occurred because during the most overcast conditions, NEE did not saturate as quickly as during clear conditions. However, the mechanism responsible for this behaviour was most likely plants' direct response to VPD, given the reduction in GPP above a threshold (VPD_0) and the correlations amongst PPFD, f_{diff} , and VPD (Figs. 3.2 and 3.5). Although incorporating diffuse and direct components of incoming radiation (MM_{diff}) removed the bias that was apparent in the MM-derived estimates of NEE related to f_{diff} , MM_{VPD} provided a similar improvement (Fig. 3.4b). This suggests that the addition of either f_{diff} or VPD into the light response parameterization compensated almost equally well for whatever process is not adequately represented by MM. Further considering the VPD constraint to mid-day GPP (Fig. 3.6d), serves to bolster the conclusion that high VPD is the critical restriction to plant CO₂ uptake in this system.

The importance of sky conditions in driving NEE has been demonstrated for forests, crops and grasslands in numerous studies (Kanniah et al., 2012),

whereas the response of peatland ecosystems has only been explicitly explored once before. At Mer Bleue bog in Ontario, Canada, Letts et al. (2005) examined mean half-hourly NEE binned by clearness index, defined as the measured solar radiation at the canopy surface divided by a computed top-of-atmosphere flux. The authors found no significant differences between mean NEE at full sun and mean NEE at intermediate intervals of the clearness index and argued that the sub-canopy was nearly always light saturated regardless of f_{diff} and that the short statured overstory shrubs did not benefit from increased diffuse light penetration. Our data also indicated no direct response of CO_2 uptake to f_{diff} , which would be expected if diffuse light penetration through the canopy were enhancing light use efficiency or photosynthetic capacity (Farquhar and Roderick, 2003; Gu et al., 2002). However, implications still exist for potential future changes in sky conditions regardless of the mechanism for the response in GPP (Steiner and Chameides, 2005). In New Zealand, mean sea-level pressure during summer months is increasing at a rate of approximately $0.2 \text{ kPa century}^{-1}$ as a result of the expanding sub-tropical high-pressure belt (MPI, 2013). Our results suggest that peak growing season GPP could be reduced if this trend leads to more frequent slow moving high pressure weather systems with associated clear skies and elevated VPD.

3.5. Conclusions

GPP at a New Zealand bog dominated by the vascular plant *E. robustum* was > 0 for all seasons in contrast to most high-latitude, Northern Hemisphere bogs for which plant production shuts down in winter. The magnitude and daily variation

in GPP during winter was limited by both incoming solar radiation and air temperature, whereas in summer months, GPP was often light-saturated, with maximum values determined by a VPD threshold. The canopy response to VPD was important for determining the light response of half-hourly NEE as well as daily scale variability. In addition, mid-day GPP was generally highest during periods of high f_{diff} given the same amount of total light. The mechanism for this behaviour is most likely VPD-induced stomatal closure. As a result, future summertime GPP may be reduced given the trend toward increasing frequency and duration of summertime high pressure systems in the region, associated with extended clear sky periods.

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Chapter 4. Overriding control of methane flux temporal variability by water table dynamics in a Southern Hemisphere raised bog

4.1. Introduction

Methane (CH_4), is a greenhouse gas that plays a key role in atmospheric chemistry and radiative forcing (Forster et al., 2007; Kirschke et al., 2013). Although it has become clear that peatlands influence global trends in atmospheric CH_4 concentration (Bousquet et al., 2006; Bousquet et al., 2011; Chen and Prinn, 2006), there are large uncertainties regarding their future role as CH_4 sources in the Earth system. Some of these uncertainties stem from the large inherent spatial and temporal variability within and across peatland types (Christensen, 2014; Lai, 2009; Turetsky et al., 2014). Additional knowledge gaps also remain in our understanding of how well-established process-level drivers of CH_4 production and consumption manifest at larger scales, such as whole ecosystems or regions (Baird et al., 2009). These issues emphasize the need for long-term, continuous flux measurements across the global spectrum of peatland types to test how our ideas of methane biogeochemistry generalize at larger scales across these diverse ecosystems.

The broad spectrum of peatland types is delineated by site hydrology, nutrients, and pH, which give way to differences in vegetation and peat properties (Rydin and Jeglum, 2013). The majority of peatland research has been conducted in Northern Hemisphere systems, whereas there are no continuous ecosystem scale methane flux measurements from Southern Hemisphere peatlands and therefore there is a limited basis for predicting how these may be affected by a

changing climate. Furthermore, we can obtain new insights from Southern Hemisphere peatland systems, which differ in climatic settings and considerably in vegetation composition from their Northern Hemisphere counterparts. For example, in the first study of methane fluxes from a Southern Hemisphere bog in Patagonia, Fritz *et al.* (2011) used chambers and pore water measurements to show that oxygenation in the rhizosphere of cushion plants was sufficient to restrict methane production and enhance oxidation. In sites dominated by these plants, the authors observed near-zero methane fluxes despite their long aerenchymous roots. Aerenchyma are more commonly associated with elevated fluxes because they provide a conduit for CH₄ release to the atmosphere, bypassing much of the surface oxidation zone (Whalen, 2005).

In northern New Zealand, bogs and fens are dominated by the vascular evergreen 'wire rush', *Empodisma robustum* (Wagstaff and Clarkson, 2012), which is aerenchymous (Sorrell *et al.*, 2002) and is the primary peat-forming material through its root clusters (Agnew *et al.*, 1993). Northern New Zealand raised bogs have developed under warm annual temperatures and summer water deficits, climatic conditions that would generally be considered unfavorable for bog formation and persistence (McGlone, 2009). However, even in periods of summer water deficit, water tables in these bogs are generally higher than in Northern Hemisphere bogs during summer (Hodges and Rapson, 2010). These peatlands display similar morphology to Northern Hemisphere ombrotrophic raised bogs (Agnew *et al.*, 1993; Hodges and Rapson, 2010), but water table range and mean depth more closely resemble those of fens (Turetsky *et al.*, 2014) and blanket bogs (e.g., Sottocornola and Kiely, 2010). No

methane flux measurements have been made in this kind of Southern Hemisphere bog. Comparing Northern Hemisphere peatlands to New Zealand systems, with their unique combination of climate, hydrology, and vegetation, provides an opportunity to identify commonalities or differences with respect to methane flux magnitudes and the response to environmental drivers.

In general, water table depth (WTD) has been recognized as one of the most important controls on methane fluxes from peatlands because of its influence on redox conditions (Knorr et al., 2009; Roulet et al., 1993) and physical constraints on CH₄ transport (Romanowicz et al., 1995; Windsor et al., 1992). Moore and Roulet (1993) showed that methane fluxes were temporally controlled by WTD using peat columns from a range of Northern Hemisphere wetland types. However, most ecosystem-scale studies suggest that temporal variations in methane fluxes are better explained by peat temperature, particularly when water tables vary within a small range (10 – 30 cm) near the surface (Jackowicz-Korczynski et al., 2010; Olson et al., 2013; Rinne et al., 2007). The observed temperature response of methane fluxes is partly due to the higher temperature sensitivity of CH₄ production than consumption (Dunfield et al., 1993). However, temporal control may shift in favor of WTD below some (site dependent) critical depth where methane fluxes are less responsive to temperature variations (Herbst et al., 2013; Lai et al., 2014a).

At longer timescales, differences in mean annual WTD are important drivers of inter-annual variability in cumulative CH₄ release from peatlands (Moore et al., 2011). In particular, droughts can lead to large inter-annual variations in methane fluxes because sustained low water tables can impact activity of

methanogen populations beyond the drought period itself (Yavitt, 2013). Until recently, studies of peatland methane flux response to drought have been limited to manipulation studies, incubations, or plot-scale measurements. However, Brown *et al.* (2014) reported eddy covariance methane flux data from Mer Bleue bog in Ontario, Canada over a meteorological drought that led to the lowest water table in a 14-year record at that site. The authors described a non-monotonic (Gaussian) relationship between WTD and methane fluxes at the ecosystem scale, suggesting there was a critical zone for the water table above and below which methane fluxes declined (Brown *et al.*, 2014). Characterizing and comparing the drought effects on ecosystem methane fluxes in other peatland types and regions is valuable in reducing uncertainties around future peatland CH₄ emissions across the globe given the potential for increased severity of drought as a consequence of climate change (Trenberth *et al.*, 2014). Furthermore, the range of climatic conditions experienced during drought, well outside the long-term normal, provide an opportunity to determine the relative importance of temperature versus water table in driving temporal methane flux variability.

We measured ecosystem-scale methane fluxes using eddy covariance to estimate seasonal and annual sums in a warm-temperate New Zealand peatland. During this study New Zealand experienced one of the worst meteorological droughts in the past 75 years (MPI, 2013), which allowed us to explore the interacting controls of WTD and temperature in driving temporal methane flux variability given the relatively large range in these variables for this site. We were particularly interested in exploring the ecosystem-scale flux implications of

the hypothesized 'critical zone' for methane production. The critical zone (or specific peat profile section) where production is highest has been associated with site-specific characteristics such as mean WTD (e.g., Brown et al., 2014; Kotiaho et al., 2010), or the rhizosphere of the dominant vegetation (e.g., Ström and Christensen, 2007). The critical zone location and bounds will have important implications for the overarching WTD control on methane fluxes given that the movement of the water table ultimately determines access of both aerobic and anaerobic microbial communities to that zone.

4.2. Methods

4.2.1. Site description

Kopuatai bog is located in the Hauraki Plains of the North Island/Te Ika a Māui, New Zealand (37°55.5' S, 175°22.2' E). This ombrotrophic, raised bog has peat depths up to 14 m [Newnham et al., 1995] and is the largest remaining unaltered peatland (~90 km²) in the country since the majority of New Zealand wetlands have been drained, primarily for agriculture (McGlone, 2009). The vegetation at the site is dominated by the jointed wire rush, *Empodisma robustum* (Wagstaff and Clarkson, 2012), which forms a dense canopy of interwoven live and dead stem material. This mulch-like layer results in very conservative evaporation rates, limiting water losses during dry conditions (Campbell and Williamson, 1997). *Sphagnum* mosses appear sporadically throughout the peatland where coverage of the dominant vegetation is sparse and light penetrates to the surface, however the primary peat forming material is *E. robustum* roots (Agnew et al., 1993). These roots form negatively geotropic clusters covering the surface and serve a similar nutrient capture and water holding capacity role as *Sphagnum* in Northern Hemisphere peatlands (Agnew et

al., 1993; Clarkson et al., 2009). The deeper, adventitious roots of *E. robustum* are aerenchymous and extend below the water table (Sorrell et al., 2002). Other species found within the study area include sedges, *Machaerina teretifolia* and *Schoenus brevifolius*, especially in wetter zones, and clusters of small shrubs (1-2 m height), *Leptospermum scoparium* and *Epacris pauciflora*, sparsely scattered throughout the study area. Kopuatai bog's surface is generally planar, lacking the hummock-hollow microtopography characteristic of many Northern Hemisphere, high-latitude bogs.

4.2.2. Flux measurements

We measured ecosystem-scale methane fluxes (F_{CH_4}) and net ecosystem exchange of CO₂ (NEE) using the eddy covariance (EC) technique from 4 February 2012 to 4 August 2014. Our EC instrumentation was mounted on a 4.5 m tall triangular lattice tower and included a sonic anemometer (CSAT3, Campbell Scientific Inc., Logan, Utah, USA), an open-path CH₄ analyzer (LI-7700, LI-COR Inc., Lincoln, Nebraska, USA) and an open path H₂O/CO₂ analyzer (LI-7500, LI-COR Inc.). Sensors were mounted on a horizontal boom approximately 1.5 m from the face of the tower with an uninterrupted fetch extending >500 m in all directions with relatively uniform canopy height and negligible slope over that distance. Data were collected at 10 Hz using a CR3000 datalogger (Campbell Scientific Inc.) and stored on a memory card.

Fluxes were processed with an averaging interval of 30 minutes using EddyPro software (v5.1.1, LI-COR Inc.). A double-axis rotation was applied for sonic tilt correction and the concentration time series were de-trended by block averaging. Spikes in the high frequency data were removed according to Vikers

and Mahrt (1997). Time lags between the wind and scalar concentration time series were removed by covariance maximization. A fully analytic approach was chosen for correction of low-pass (Moncrieff *et al.*, 1997) and high-pass filtering (Moncrieff *et al.*, 2005) and the standard Webb *et al.* (1980) method was applied to compensate for air density fluctuations. More details associated with calculation and quality control of NEE fluxes are given in Goodrich *et al.* [2015].

Ancillary measurements included incoming photosynthetic photon flux density (PPFD) (BF5 Sunshine Sensor, Delta-T Devices Ltd., Cambridge, United Kingdom) just above the canopy (~1.2 m above peat surface) and air temperature and vapour pressure (fully aspirated HMP 155, Vaisala, Helsinki, Finland) at 4.25 m above the surface. Thermistors inserted 50, 100, and 150 mm below the peat surface measured peat temperature (T_{peat}). Water table depth (WTD) was measured within a 1.5 m dipwell using a submersible pressure sensor (WL1000W, Hydrological Services, NSW, Australia) and precipitation was recorded using a tipping bucket rain gauge (TB5, Hydrological Services).

4.2.3. Data filtering and gap filling

Gaps in the F_{CH_4} data resulted from reduced signal strength of the LI-7700 open path analyzer during precipitation events or when dew accumulated on the sensor mirrors. During EddyPro flux processing and computation, we implemented the Göckede *et al.* (2006) method to assign quality control (QC) flags to each 30-min flux, based on tests for well-developed turbulence and steady state conditions (flags 1 – 5 with 1 being best quality). Only fluxes deemed highest quality were used in this study (QC flag = 1). It was clear after carefully inspecting the raw data, that negative and unrealistically high F_{CH_4}

values ($>250 \text{ nmol m}^{-2} \text{ s}^{-1}$) represented spikes and we removed these ($< 0.2\%$ of data removed). To determine an appropriate turbulence threshold, we followed the Reichstein *et al.* (2005) approach, leading us to reject data for periods when friction velocity (u_*) was below 0.14 m s^{-1} .

We compared two approaches to filling gaps in the half-hourly F_{CH_4} time series. First, a model incorporating an exponential temperature response to T_{peat} and an asymmetric Gaussian function describing the non-monotonic F_{CH_4} response to WTD (Brown *et al.*, 2014) was fitted using the full time series,

$$F_{\text{CH}_4} = a^{((T_{\text{peat}} - 10)/10)} b \exp(-(WTD - WTD_0)^2/2c^2) \quad (1)$$

where WTD_0 is the WTD at which F_{CH_4} was maximal, a , b , and c are fitted parameters. To account for asymmetry in the WTD response of F_{CH_4} , $c = c_1$ when the water table was below WTD_0 and $c = c_2$ when the water table was above WTD_0 (Brown *et al.*, 2014). Best-fit estimates of the model parameters were: $WTD_0 = -89.4 \text{ mm}$, $a = 2.1$, $b = 46.5$, $c_1 = 96.6$, and $c_2 = 91.5$, which were applied to the full dataset.

Recently Dengel *et al.* (2013) detailed the utility of artificial neural networks (ANN) for gap-filling eddy covariance F_{CH_4} and this approach is also increasingly being implemented for CO_2 flux data (Moffat *et al.*, 2007; Papale and Valentini, 2003). For our second gap filling approach, an ANN was developed, consisting of 13 input nodes including air temperature, peat temperature at 150 mm depth, WTD, WTD lagged by 10 days (see Section 3.3), PPFD, wind direction, barometric pressure, four fuzzy datasets representing seasonality of the data (Papale and Valentini, 2003), one fuzzy dataset representing the year of the study period,

and a bias node to allow an offset in the transfer function. The hidden layer was assigned four nodes, and sigmoid transfer functions were applied to the weighted sums from the hidden and output layers (Dengel et al., 2013; Papale and Valentini, 2003). The Levenberg-Marquardt back-propagation algorithm was implemented for training the network (Hagan and Menhaj, 1994), using 70% of the full dataset taken randomly for each run while the remaining data were used for testing (15%) and validation (15%). Our final choice of ANN structure was based on evaluating several model performance statistics including mean squared error, Akaike's information criterion (AIC), and R^2 , calculated during the validation and testing phases of the procedure.

One of the drawbacks of the ANN approach is that each time the network is trained, the resulting weights are unique, producing slightly different outputs with each run (Smith, 1997). To account for this variation in output values, we trained and fitted the ANN 20 times, and filled gaps using the median simulated flux for each missing half hour (Knox et al., 2014). We also compared the time series of daily F_{CH4} sums based on the two gap-filling approaches to daily mean F_{CH4} (means were converted to daily units) based on available data for each day when at least eight half-hourly F_{CH4} remained after filtering.

4.2.4. Data analysis

To investigate the role of water table depth in regulating the relationship between methane fluxes and peat temperature, we followed an approach similar to Lai et al. (2014a), where correlation coefficients between T_{peat} and F_{CH4} were estimated for data binned by WTD. Here, the daily means of F_{CH4} and T_{peat} were divided into equal-sized bins of WTD. We then estimated the linear regression

slopes of F_{CH_4} by T_{peat} with associated p -values and 95% confidence intervals for each WTD bin. The range in WTD within each bin was restricted to 15 mm to control for WTD changes within the bin. Thus we excluded data for the deepest water tables since many of the changes in WTD occurred rapidly and there were less data available for progressively deeper intervals (Fig. 4.1c).

We also analyzed the relative importance of water table depth and peat temperature in driving methane flux variability over the timescale of days to weeks, using cross correlation analysis following the approach of Kettunen et al. (1996). We thus, isolated a period from 1 October 2013 to 15 January 2014 when there were relatively few gaps in F_{CH_4} , and WTD remained within 100 mm of the peat surface with several rainfall events providing discrete ramping and subsequent lowering of the water table (Fig. 4.1c). The cross correlations between F_{CH_4} and both T_{peat} and WTD were calculated by estimating Pearson's correlation coefficient between the two pairs of daily time series, then shifting the F_{CH_4} series one day at a time and re-calculating the correlation until a maximum lag of 20 days. Cross correlation of two time series can be confounded if one of them is significantly auto-correlated, resulting in spurious results (Kettunen et al., 1996). To avoid this issue, we used the differenced WTD (ΔWTD) and T_{peat} (ΔT_{peat}) time series calculated as $\Delta X_i = X_i - X_{i-1}$ (Kettunen et al., 1996) where i is the current day of the time series and X is the variable of interest. All gap-filling and data analyses were conducted with Matlab (vR2013b, MathWorks, MA, USA).

4.3. Results

4.3.1. Meteorological conditions

Rainfall totals for 2012 and 2013 were 1153 mm and 1105 mm, respectively, compared to the long-term average (1980-2010) of 1232 mm (taken from a nearby climate station). However, a severe nationwide drought (MPI, 2013) reduced the total rainfall during January – March 2013 (the Southern Hemisphere summer) to 25% of the long-term average for those months (Fig. 4.1b). As a result, the late summer to autumn WTD contrasted strongly between 2012 and 2013 (Fig. 4.1c). In 2012, the water table remained within 120 mm of the surface even during the driest periods. However, in 2013 the water table dropped to approximately 250 mm below the surface in March (Fig. 4.1c). Following the 2013 summer drought, WTD recovered quickly from May to mid-June when it rose to 20 mm below the surface and varied between 0 and -100 mm until January 2014. Rainfall totals from January to March 2014 were again lower than the long-term average (40% of the long-term average), causing a drop in WTD to ~200 mm below the surface (Fig. 4.1c).

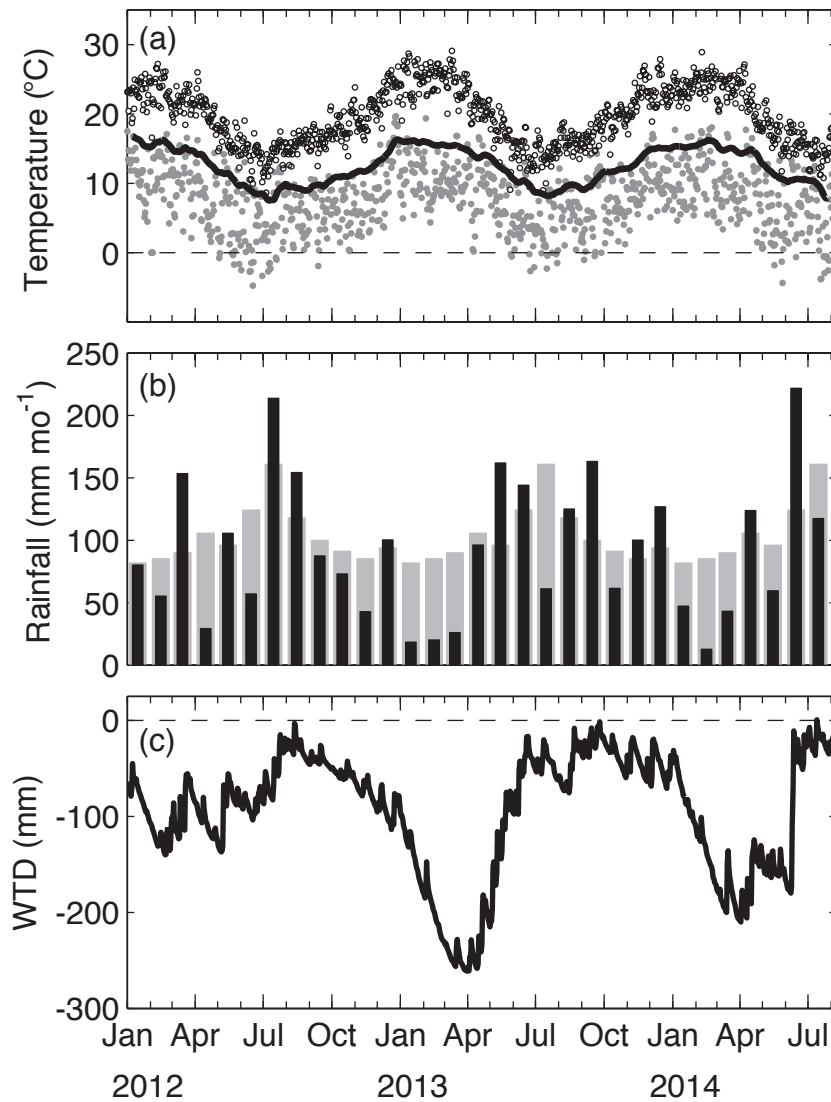


Figure 4.1. Meteorological and hydrological variables at Kopuatai bog, 1 January 2012 – 4 August 2014: (a) daily minimum (grey points) and maximum (open points) air temperatures, and the 15-day running mean 50 mm depth peat temperature (line); (b) monthly total rainfall (black bars) and monthly normals (1980-2010) taken from a nearby climate station (grey bars), (c) daily mean water table depth (WTD) (horizontal zero line is the peat surface).

Mean annual air temperature at Kopuatai was 13.3 °C and 14.0 °C for 2012 and 2013, respectively, compared to the long-term average of 13.7 °C. Mean T_{peat} at 50 mm depth typically ranged from 7 °C in winter to 18 °C in summer (Fig. 4.1a), leading to relatively subtle seasonality compared to high-latitude Northern Hemisphere peatlands that typically freeze during winter.

4.3.2. Methane flux magnitudes

In 2012, mean daily F_{CH_4} followed a simple seasonal pattern with maximum fluxes ($\sim 150 \text{ mg m}^{-2} \text{ d}^{-1}$) in summer and minimum fluxes ($40\text{-}60 \text{ mg m}^{-2} \text{ d}^{-1}$) in winter (Fig. 4.2). After the onset of the drought in January 2013, summer F_{CH_4} declined rapidly until reaching a minimum of $< 20 \text{ mg m}^{-2} \text{ d}^{-1}$ in autumn and remained lower than the 2012 winter minimum until late August 2013 (Fig. 4.2) despite full recovery of the water table by June 2013 (Fig. 4.1c). Summer 2013/2014 (December - March) peaks in F_{CH_4} then ranged from $140\text{-}170 \text{ mg m}^{-2} \text{ d}^{-1}$, similar to the summer before the drought (2011-12), indicating full recovery from the drier conditions.

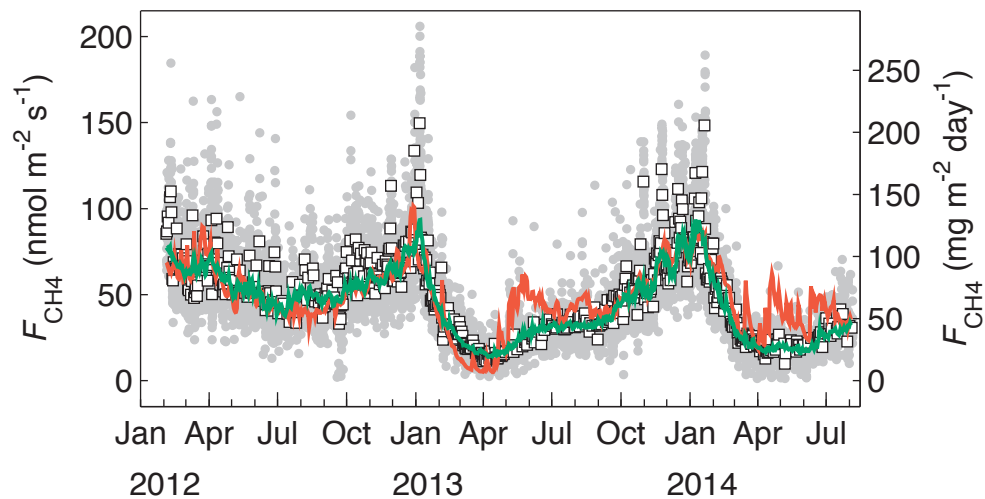


Figure 4.2. Half-hourly measurements of F_{CH_4} (grey points) with daily means of available observations (white squares); daily sums based on gap-filled time series using temperature and water table relationship described by Eq. 1 (red line), and daily sums based on gap-filled time series using the artificial neural network (green line).

The time series of daily F_{CH_4} sums based on the two gap filling approaches showed similar behavior in 2012 and compared well with the daily means calculated from the available half-hourly data (Fig. 4.2). However, during water

table recharge from May to August 2013 and from April to June 2014 (Fig. 4.2), the gap-filled daily sums based on Eq. 1 deviated substantially from both the daily means and half-hourly measurements. In contrast, the time series of daily sums based on the ANN captured the slow recovery of methane flux during the water table recharge periods, therefore we based our annual estimates on the ANN gap-filled time series.

For the year 4 February 2012 to 3 February 2013, we estimated total methane flux of $29.1 \text{ g CH}_4 \text{ m}^{-2} \text{ yr}^{-1}$ from the EC tower footprint, 28% of which was released during the drier season (i.e., February – April) (Table 4.1). From 4 February 2013 to 3 February 2014, the total methane flux was $20.6 \text{ g CH}_4 \text{ m}^{-2} \text{ yr}^{-1}$ (13% released during the drier season). The lower annual methane flux in 2013 was primarily driven by the >50% reduction in summer and autumn emissions relative to 2012 (Table 4.1).

Table 4.1. Seasonal and annual total methane fluxes ($\text{g CH}_4 \text{ m}^{-2} \text{ period}^{-1}$), gap-filled with the ANN approach for 2012 and 2013. Values for both years span 4 February to 3 February.

Year	Feb-Apr	May-Jul	Aug-Oct	Nov-Jan	Annual
2012	8.2	6.1	6.6	8.2	29.1
	(28%)	(21%)	(23%)	(28%)	(100%)
2013	2.6	3.7	5.2	9.1	20.6
	(13%)	(18%)	(25%)	(44%)	(100%)

4.3.3. Interacting controls on methane flux

We explored the delayed recovery in methane flux following water table recharge after the drought by examining plots of daily mean F_{CH_4} versus both T_{peat} and WTD (Fig. 4.3). To reduce noise in the daily means and to clarify

patterns through time, we calculated 30-day averages with a moving window that advanced seven days at a time, and included these in the scatter plots separately for each year. In 2012, F_{CH_4} followed a seasonal temperature response path with both increasing and decreasing T_{peat} (Fig. 4.3b). However, as the water table fell during the drought in 2013, F_{CH_4} decreased steadily according to WTD (Fig. 4.3c) and was no longer dependent on temperature (Fig. 4.3d). During the water table recovery phase (May to mid-June 2013), F_{CH_4} showed very little response to either WTD or T_{peat} (Fig. 4.3c,d), suggesting some other limitation or restriction of methane production or flux. By August 2013, F_{CH_4} became more responsive to temperature, similar to 2012. However, drier conditions returned in summer 2013/14, and again F_{CH_4} was unresponsive to temperature but rather decreased with falling water table (Fig. 4.3e,f).

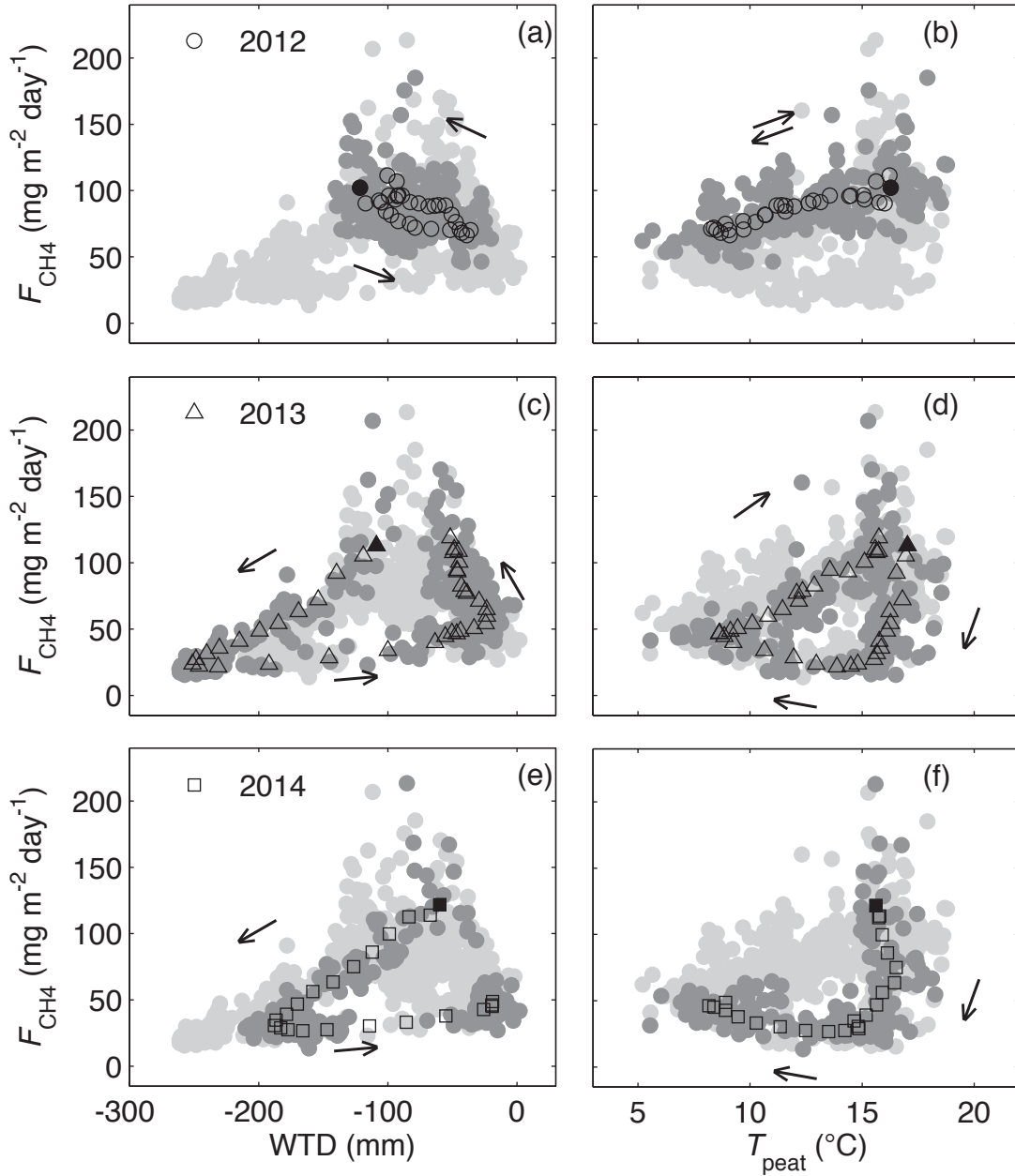


Figure 4.3. Daily mean F_{CH_4} based on available measurements (non-gap-filled) against daily mean water table depth (WTD) and peat temperature at 50 mm depth (T_{peat}). Light grey dots are all available daily means from the full measurement period and darker grey dots correspond to the given measurement year. 30-day averages were plotted as hollow symbols to illustrate the direction of hysteresis with respect to (a,c,e) WTD and (b,d,f) T_{peat} for data from 2012, 2013, and 2014. The black symbol in each panel indicates the first available 30-day average for the given measurement year.

A linear regression analysis between F_{CH_4} and T_{peat} for data grouped by WTD provided further insight into the collapse of the methane flux temperature dependence. When the water table was within ~100 mm of the peat surface, daily mean F_{CH_4} exhibited significant ($p < 0.05$) positive linear relationships with mean T_{peat} measured at 50mm depth (slopes ranged from $1.8 - 5.5 \text{ mg CH}_4 \text{ m}^{-2} \text{ day}^{-1} \text{ }^{\circ}\text{C}^{-1}$), and the maximum slope was associated with WTD centered at approximately -70 mm. However, as the water table dropped below -100 mm, the slope of F_{CH_4} versus T_{peat} was no longer significantly different from zero ($p > 0.05$). To explore the regression slopes' sensitivity to the depth of temperature measurement, we repeated the above analysis using temperature measured at 100 mm and 150 mm depth. We found similar trends in regression slopes with WTD and comparable R^2 values but given that methane fluxes become decoupled from temperature with deeper water tables (Fig. 4.3), we used T_{peat} from 50 mm depth.

Linear regression between daily mean F_{CH_4} and daytime (1000 – 1400 local time) mean NEE indicated that increasing CO_2 uptake related to increased methane fluxes when the water table was within 150 mm of the surface (Fig. 4.4).

However, there was no significant relationship for deeper water tables. We found that F_{CH_4} increased $10.5 \text{ nmol m}^{-2} \text{ sec}^{-1}$ for every unit $\mu\text{mol CO}_2$ increase in mean daytime NEE during higher water tables (Fig. 4.4). Although the linear regressions with NEE for both high and low water tables explained only a small proportion of the variance in F_{CH_4} ($R^2 = 0.11$ and 0.02 , for high and low water tables, respectively), the former was highly significant ($p < 0.001$) whereas the slope of the latter was not significantly different from zero ($p = 0.12$). A large

degree of scatter is expected when comparing fluxes of CO₂ and CH₄ given the spatial integration of the EC fluxes over a surface that is not perfectly homogeneous and the complex set of drivers associated with both gas fluxes, but the high degree of significance in the higher water table relationship is consistent with the break-down in the methane flux versus temperature relationship at deeper water tables described above.

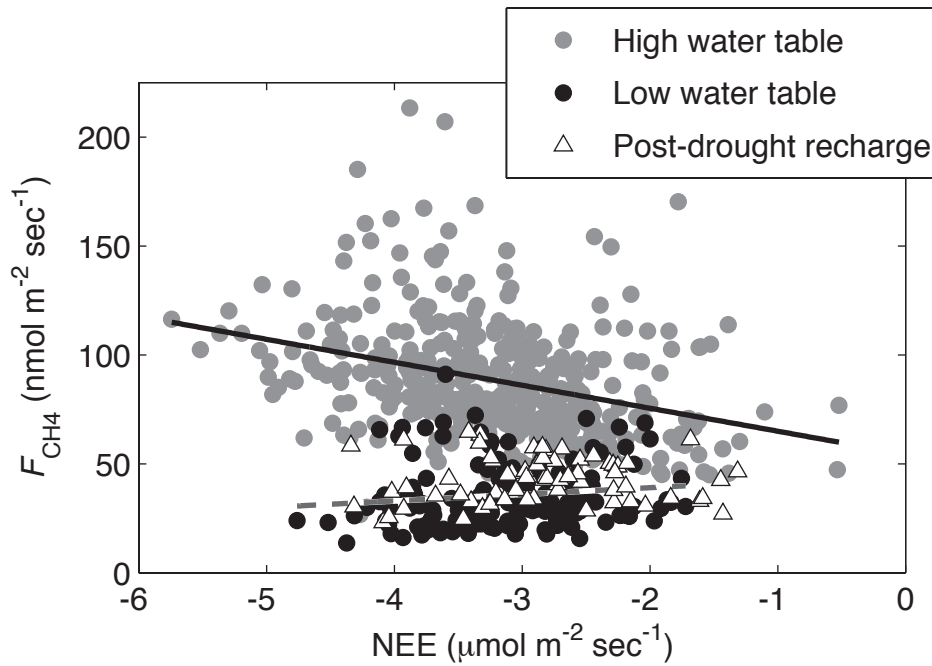


Figure 4.4. Daily mean F_{CH_4} versus daytime (1000 – 1400 local time) mean NEE for high (≤ 150 mm from the surface) and low (> 150 mm from the surface) water table conditions. Solid line indicates regression for high water table conditions ($y = -14.0x + 35$; $p < 0.001$; $R^2 = 0.15$) and dashed line indicates regression for low water table conditions ($y = 3.04x + 45$; $p < 0.124$; $R^2 = 0.02$). Post-drought recharge (open triangles) refers to periods when water tables rose to within 150 mm of the surface after the extended dry periods for 2013 and 2014 (1 May 2013 – 1 September 2013 and 15 April – 4 August 2014).

Finally, we compared the direct impacts of both water table depth and peat temperature on the temporal variability in methane flux using a lagged cross-correlation analysis. The period isolated for cross correlations (1 Oct. 2013 – 15

Jan. 2014) had relatively few gaps in daily mean F_{CH_4} and the water table remained within 100 mm of the surface (Fig. 4.5 a,b). There were several isolated rainfall events that led to rapidly rising water table (20-50 mm change in a single day) followed by extended rainless periods and associated steady drops in water table (Fig. 4.5b). T_{peat} varied from 11 – 16 °C, with a steady increase from November to December (Fig. 4.5c). Methane fluxes seemed to be suppressed during rain events then rose steadily as the water table receded until there were a few days of typically elevated fluxes, two to three times larger than immediately following the water table rise (Fig. 4.5a). The maximum correlation coefficient between F_{CH_4} and ΔWTD occurred at a lag of 10 days after the water table rise (Fig. 4.6). The positive correlation indicates that increases in F_{CH_4} were correlated with rises in water table caused by rainfall. The correlations between F_{CH_4} and ΔWTD at lags of 10 and 11 days were significant ($p < 0.05$), suggesting there may be some variation in the lagged response of methane flux to water table based on the WTD at the start of rain or on rates of evapotranspiration and subsequent post-rain water table drawdown. There were no significant correlations between F_{CH_4} and ΔT_{peat} for any lag up to 20 days during the time period analyzed (Fig. 4.6).

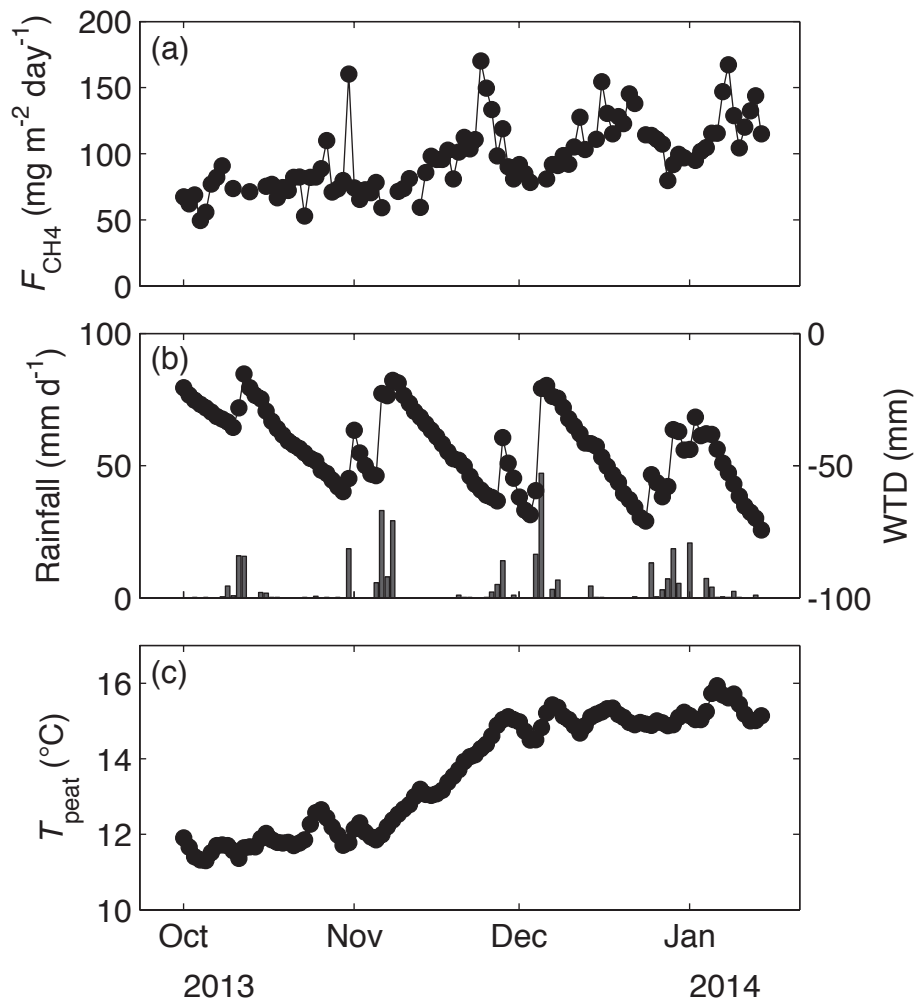


Figure 4.5. Time series of daily mean (a) F_{CH_4} , (b) WTD, and (c) T_{peat} from 1 October 2013 to 15 January 2014, a period illustrating several isolated rain events with associated rises and steady drawdown of water table with few gaps in F_{CH_4} .

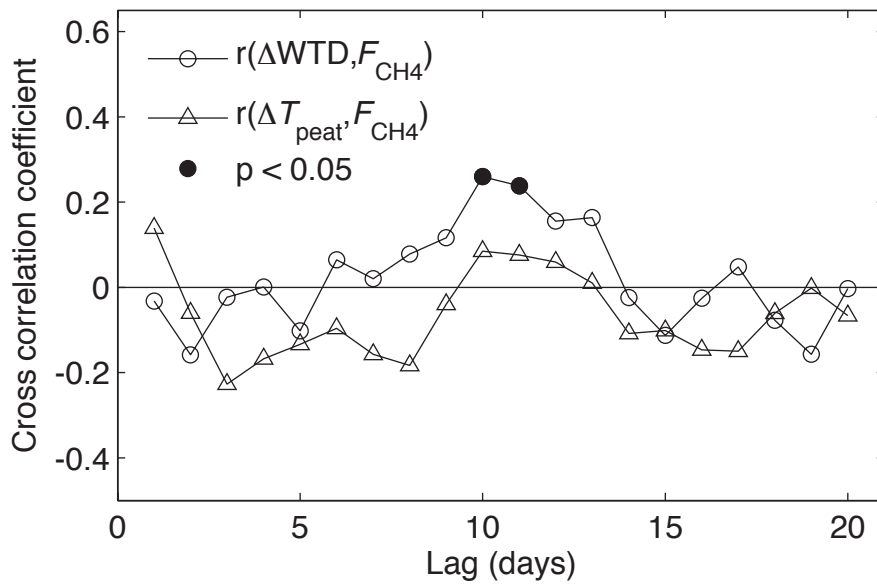


Figure 4.6. Lagged cross correlations between daily mean F_{CH_4} , daily change in water table depth (ΔWTD) and daily change in peat temperature (ΔT_{peat}) for the period from 1 October 2013 to 15 January 2014 shown in Fig. 4.5.

4.4. Discussion

4.4.1. Annual and daily F_{CH_4} magnitudes

Annual total methane flux at Kopuatai was $29.1 \text{ g CH}_4 \text{ m}^{-2} \text{ yr}^{-1}$ in 2012 and $20.6 \text{ g CH}_4 \text{ m}^{-2} \text{ yr}^{-1}$ in 2013 (Table 4.1), both of which are at the higher end of the range of annual methane flux reported for Northern Hemisphere peatlands where annual sums are generally $< 15 \text{ g CH}_4 \text{ m}^{-2} \text{ yr}^{-1}$ but can exceed $40 \text{ g CH}_4 \text{ m}^{-2} \text{ yr}^{-1}$ (Baldocchi, 2014; Godwin et al., 2013). For example, our annual estimates were similar to those reported for a poor fen in Minnesota, USA, where total methane flux ranged from $15.7 - 33.2 \text{ g CH}_4 \text{ m}^{-2} \text{ yr}^{-1}$ although the majority of methane from that site was released within a ~ 5 month growing season (Olson et al., 2013). The peat temperature at Kopuatai bog was never below freezing, which led to less pronounced seasonality in methane fluxes. Up to 21% of the annual total was released during the lowest emission season (Table 4.1). This is a key

distinction between peatlands in northern New Zealand and continental peatlands in the Northern Hemisphere when considering annual sums. Such dampened seasonality has also been demonstrated for CO₂ fluxes in a drainage-impacted New Zealand peatland due to year-round growing conditions that also result in large annual net ecosystem exchange relative to Northern Hemisphere bogs (Campbell et al., 2014). However, in a study from an Irish maritime blanket bog (Glencar), where seasonality in peat temperature was comparable to Kopuatai and the surface was also dominated by vascular aerenchymous vegetation, annual methane flux was much lower than we estimated for our site (Laine et al., 2007). The authors speculated that elevated sulphate concentrations may have suppressed methane production, and ebullition fluxes may have been under-represented in their chamber measurements (Laine et al., 2007). In addition, Glencar is approximately 14° of latitude farther from the equator than Kopuatai and has a lower leaf area index, leading to fewer months of net CO₂ uptake than has been demonstrated for NZ peatlands (Sottocornola and Kiely, 2005, Campbell et al., 2014) and this is an important distinction if methanogen substrate supply through root exudation controls methane fluxes.

The magnitude of daily methane fluxes at Kopuatai during November to January (i.e., summer; Fig. 4.2) was 100 – 200 mg CH₄ m⁻² day⁻¹; within the range of peak ecosystem-scale values reported for Northern Hemisphere fens (Olson et al., 2013; Pypker et al., 2013), but generally higher than Northern Hemisphere bogs (Brown et al., 2014; Nadeau et al., 2013). At Kopuatai, litter decomposition rates are comparable to Northern Hemisphere bogs (Clarkson et al., 2014) and the peat is also acidic (pH ~4) (Agnew et al., 1993; Clarkson et al., 2004), suggesting

these factors do not contribute to the observed differences between fluxes at Kopuatai and those of Northern Hemisphere bogs. However, the water table at Kopuatai remained within 300 mm of the peat surface even during drought, in contrast to many Northern Hemisphere bogs where water tables routinely reach depths from 300 – 500 mm below the surface, particularly during dry meteorological years (Brown et al., 2014; Turetsky et al., 2014). The hydrology of Kopuatai bog is quite different than that of Northern Hemisphere bogs because the water table remains much closer to the peat surface and this generally encourages the growth of sedge and grass species that can facilitate the flux of CH₄ through aerenchyma in northern systems (Lai, 2009; Noyce et al., 2014). The plant canopy at Kopuatai is also dominated by the vascular *E. robustum*, which possesses aerenchyma for transporting oxygen to its rooting zone (Sorrell et al., 2002). While the rhizosphere of aerenchymous plants can promote elevated oxygen levels, which may inhibit methanogenesis and enhance methanotrophy (Fritz et al., 2011), aerenchymous tissue also provides a direct conduit for CH₄ transport to the atmosphere. This plant-mediated pathway most often dominates over any enhancement of oxidation in the rooting zone, leading to higher net fluxes at sites with aerenchymous vegetation (Joabsson et al., 1999). Therefore the relatively high daily methane fluxes reported here for Kopuatai compared to Northern Hemisphere bogs may be the result of generally wetter conditions and higher density of aerenchymous vegetation.

4.4.2. Drought-induced inter-annual variation

The $8.5 \text{ g CH}_4 \text{ m}^{-2}$ (~30%) difference between annual total methane flux from Kopuatai in 2012 and 2013 (Table 4.1) was mostly due to a lower water table during the drought from January to April 2013 (Fig. 4.1), which led to a rapid initial decline in methane fluxes as well as a delayed recovery after water table recharge (Fig. 4.2). From February to July 2013, total methane flux was >50% lower than the same period in 2012. Mean annual WTD is generally one of the main drivers of inter-annual variability in total peatland methane flux (Moore et al., 2011) because of its control over redox conditions whereby a lowered water table reduces the anaerobic zone. Furthermore, when the water table remains deeper than average or below the main production zone for extended periods, it may change the size and structure of the peatland methanogen community (Tian et al., 2012), which can also influence CH_4 production rates. We explored the delayed recovery of methane flux following water table recharge after drought by comparing daily mean F_{CH_4} to estimated daily F_{CH_4} sums based on a non-linear regression incorporating temperature dependence and a non-monotonic WTD relationship (Eq. 1; Brown et al., 2014) and also based on estimates from the ANN approach that incorporated a larger suite of drivers (Fig. 4.2). Similar to the results of Brown et al. (2014), we found that Eq. 1 consistently over-estimated F_{CH_4} when compared to daily means for a period of several months post-drought, indicating a breakdown in the relationship between methane fluxes and both peat temperature and water table depth. This breakdown was consistent with changes to/or restrictions on the methanogenic population during that time. Interestingly, daily mean F_{CH_4} actually increased gradually during the post-drought recovery period despite

seasonally decreasing temperatures in both 2013 and 2014 (Fig. 4.3d, f). Estop-Aragonés and Blodau (2012) showed that higher temperatures sped up the recovery of CH₄ production rates after drying and re-wetting peat cores, likely related to low growth rates of methanogens and their competitors at low temperatures (Van Hulzen et al., 1999). At Kopuatai, the recovery period for methane fluxes was likely prolonged because the drought ended in autumn as temperatures were decreasing (Fig. 4.1). This was also the case in the Brown et al. (2014) study and may be a relatively common occurrence for temperate zones where extended dry periods resulting in deep water tables are typically associated with persistent mid to late summer high pressure weather systems.

The timescale for methanogenesis and methane flux recovery after drought can also be a function of drought intensity (Estop-Aragonés et al., 2013) and peatland characteristics such as mean WTD (Yavitt, 2013). Labile C substrate below the mean WTD is generally well protected from aerobic decomposition (Estop-Aragonés and Blodau, 2012). As the water table drops during dry conditions, these labile substrates likely become available to aerobic microbial communities and are rapidly depleted (Knorr and Blodau, 2009). Therefore, the delayed recovery in methane fluxes following water table rise may be partly due to the time required for fresh substrate to accumulate below the surface. In addition, a deeper water table leads to enhanced oxygenation of the surface peat (Blodau and Moore, 2003), which can serve to regenerate alternate electron acceptors in this zone (Knorr and Blodau, 2009). After water table recharge, these alternate electron acceptors are then available to competitive

anaerobes, which can further delay the recovery of methanogenesis to pre-drought rates (Yavitt and Seidman-Zager, 2006).

4.4.3. Importance of water table depth in controlling methane flux

Water table depth appeared to provide an over-riding correlate on the relationship between methane fluxes and peat temperature at Kopuatai. We illustrated this by fitting simple linear regressions within various bins of WTD. There were significant positive regression slopes ($p < 0.05$) between F_{CH_4} and T_{peat} when the water table was within 100 mm of the peat surface, whereas regression slopes were not significantly different from zero for deeper water tables. Similarly, Lai et al. (2014a) showed that the strength of correlations between methane fluxes and peat temperature became weaker as the water table dropped further below the surface and became insignificant when the water table was below the rooting zone of the dominant vegetation. Lai et al. suggested that when the aerobic zone extended beneath the rooting zone, methanogens no longer had access to labile root exudates and the plant transport flux pathway was also cut-off. The rhizomes and anchor roots of *E. robustum* generally extend to depths of 300 mm, however the main cluster root mat is primarily contained within 50 mm of the surface (Clarkson et al., 2009). Although root exudation research is lacking for *E. robustum*, cluster roots of various other plants are known to exude large amounts of labile carbon substrates (Lambers et al., 2012). Therefore, at Kopuatai the observed sensitivity of methane fluxes to water table fluctuations relatively close to the surface may be tightly coupled to the ability of methanogens to access labile substrates from cluster root exudation.

The relationship between F_{CH_4} and NEE when the water table was within 150 mm of the surface is also consistent with root exudation as an important supply of substrate for methanogenesis, since this relationship was no longer significant for deeper water tables (Fig. 4.4). Additional measurements would be needed to determine whether production is suppressed due to restricted access to substrate or oxidation enhanced due to increased aeration. However, a relationship between CO_2 uptake and methane fluxes is expected in vascular-dominated peatlands where assimilated CO_2 -C has been detected in CH_4 emitted within hours (Lai et al., 2014b; Olson et al., 2013; Ström et al., 2003; Whiting and Chanton, 1992). The contribution of root exudates as labile substrates for methanogenesis at our site could potentially be explored using isotopic pulse labeling of mesocosms with varied degrees of saturation (e.g., Crow and Wieder, 2005; Ström et al., 2005) or analysis of peat from profile increments to determine CH_4 production potential and substrate quality (acetate concentration) with depth (Ström et al., 2003).

The maximum potential for CH_4 production is also generally associated with the mean WTD at a site (Brown et al., 2014; Kotiaho et al., 2010). We do not have long-term measurements of WTD at our site, but given that total summer precipitation in 2012 was close to the long-term mean (Fig. 4.1), the 2012 WTD may reasonably approximate average values. Mean WTD for 2012 was -76.5 mm, coincident with the steepest slopes of the regressions between F_{CH_4} and T_{peat} , further supporting this as the zone of maximum production.

At times, the water table also exhibited a direct control over variability in methane fluxes at Kopuatai. Rises in water table (positive ΔWTD) during rainfall

events led to concurrent depressions in F_{CH_4} followed by steadily increasing fluxes as the water table fell (Fig. 4.5). We also observed lagged pulses of particularly high methane fluxes 10 – 11 days after rain, whereas changes in daily mean peat temperature did not correlate to F_{CH_4} for any time lag up to 20 days (Fig. 4.6). This suggests that, at sub-seasonal time-scales, WTD was a more important temporal control on methane fluxes than temperature for periods when the water table was close to the peat surface despite relatively small variations ($\Delta\text{WTD} \sim 50$ mm), because it regulated aerobic exposure of the critical zone. Brown et al. (2014) also observed delayed increases in methane fluxes with a falling water table after rain events at Mer Bleue bog in Ontario, Canada. They showed that methane fluxes peaked as the water table descended through the zone of maximum production, associated with the rooting zone of the dominant shrub species that provided labile substrates for methane production via root exudates (Brown et al., 2014). Kettunen et al. (1996) also used cross correlation analysis to show that, for some plant communities within a Finnish mire complex, rain events suppressed methane fluxes for a few days before there was an associated increase in fluxes.

Rising water tables had previously been shown to suppress diffusive fluxes (Moore and Roulet, 1993), which then increase as the water table falls because of the shorter distance to the water-air interface and the higher diffusivity of non-saturated peat (Brown et al., 2014; Walter and Heimann, 2000). Therefore, it is likely that increased methane fluxes following rain events is most pronounced when the water table fluctuates within the critical production zone where dissolved CH_4 concentrations will be highest. We confirmed this by

identifying rain events that occurred when the water table was below 100 mm and found little or no increase in methane fluxes as the water table declined (not shown). Dengel et al. (2013) suggested that the delayed increase in methane fluxes following rain events deserved further investigation and confirmation using continuous EC fluxes, after finding that ANN gap-filling improved when this effect was included, similar to our findings. Our results (Figs. 4.5 and 4.6), like those of Brown et al. (2014), suggest that lagged increases in methane fluxes after rain events are common in bogs. However, the importance of this mechanism may be restricted to when the water table is within a site-specific critical CH₄ production zone. Furthermore, the contribution to annual or seasonal totals is not yet clear and temperature still seemed to drive the seasonality of fluxes during the wetter 2012 year (Fig. 4.3b).

4.5. Conclusions

In general, the annual methane flux at Kopuatai for two full years was at the high end of the range reported for Northern Hemisphere peatlands because the mild New Zealand climate resulted in relatively large winter flux contributions. Peak daily methane fluxes at Kopuatai bog were relatively high compared to Northern Hemisphere bogs but similar to Northern Hemisphere fens, possibly because of the aerenchymous dominant vegetation and relatively high water tables at Kopuatai.

Our findings highlight the importance of the water table in driving temporal dynamics of methane fluxes across a range of timescales at this Southern Hemisphere raised bog. Although peat temperature drove seasonality of methane fluxes during the wetter year (2012), WTD ultimately regulated the

temperature response of methane fluxes as well as the relationship with NEE. Changes in water table depth also exhibited direct control over temporal variations in methane fluxes at sub-seasonal timescales during periods when the water table was close to the surface and varied within a relatively small range. This emphasized the importance of a well-constrained critical zone for CH₄ production corresponding with the dominant vegetation's rhizosphere and mean long-term water table depth. Drought-induced water table drawdown well below this critical zone for an extended period caused a large decrease in late summer and autumn methane fluxes in both 2013 and 2014 as well as the delayed recovery of fluxes after water table recharge.

In addition to temperature and water table depth effects, ecosystem methane flux modeling should take into account drought-induced lags in methane flux recovery that depend on drought timing and severity, and location of the site-dependent critical zone, which dictates aerobic and anaerobic microbial access to labile carbon substrates. Without including these effects, there is a risk that annual methane fluxes will be over-estimated, particularly given the potential for increased drought frequency in a changing climate.

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Chapter 5. Drought resilience allows a Southern Hemisphere raised bog to persist as a strong carbon sink

5.1. Introduction

Peatlands occupy a relatively small proportion of the global land area but store a large proportion of soil carbon (Gorham, 1991; Yu et al., 2010). Fluxes of carbon (C) in peatlands are sensitive to variations in weather and climate, but large uncertainties are associated with scaling process knowledge to landscapes or regions (Baird et al., 2009), with high variability within and between sites (Bubier et al., 2003; Mastepanov et al., 2008; Treat et al., 2007), and with a relative paucity of *in-situ* measurements (Christensen, 2014). The majority of global peatland area is located in boreal to Arctic regions of the Northern Hemisphere, which has led most of the research on peatland C exchange to focus on these regions (Lafleur, 2009). However, peatlands also make up an important component of the landscape in other regions where much less is known about the size of C stocks, rates and variability of C fluxes, and sensitivity of those fluxes to environmental and climatic change (Frolking et al., 2011; Lafleur, 2009; Limpens et al., 2008). Given the amount of C stored in peatland ecosystems and the potential for positive feedbacks between peatland C fluxes and changing climate, a better understanding of C exchange processes along the full spectrum of peatland types is needed.

In the Waikato Region of New Zealand, peatlands occupy about 5% of the land area, the majority of which has been drained for dairy pasture (McGlone, 2009; Pronger et al., 2014). The draining of peat leads to subsidence associated with enhanced mineralization and compaction (Pronger et al., 2014; Schipper and

McLeod, 2002) both of which result in large C losses of the affected area. However, intact peatland remnants adjacent to drained pastures seem to remain strong annual sinks for CO₂ despite un-naturally lowered water tables (Campbell et al., 2014). The dominant vegetation in New Zealand peatlands has very conservative evaporation rates and high canopy resistance to water vapour exchange during dry sunny periods (Campbell and Williamson, 1997). This behaviour also constrains gross primary production (GPP) when vapour pressure deficit is high (Goodrich et al., 2015). Lowered water tables during drought conditions also lead to reduced methane fluxes, which remain low for months after water table recovery, substantially reducing annual CH₄ emissions during drought years (Goodrich et al., accepted). However, we do not know the full extent of the net C balance (and its components) response in unaltered New Zealand peatlands to dry vs. wet conditions on seasonal to annual scales. Therefore we have little basis for understanding and predicting C balance changes in these systems when considering the increased pressure of intensifying agricultural demand (Fetzel et al., 2014) and the potential for increasing severity of summer droughts due to climate change (Dai, 2013; Trenberth et al., 2014).

Schwalm et al. (2010) synthesized data from 238 global FluxNet sites to show that drought events reduced the CO₂-C sink strength of terrestrial ecosystems. They found that drought effects were dominated by photosynthetic response, suggesting that respiration is less sensitive to drought. However, the response of peatland C balance components is complicated by the inherent hydrological setting, whereby water table depth determines redox boundaries (Moore and

Knowles, 1989) and thus plays an important role in driving many aspects of the C cycle. Northern Hemisphere peatlands can shift from annual sinks to sources of CO₂ in response to drought (Arneeth et al., 2002) and drought-induced lowering of the water table in peatlands is generally the most important driver of inter-annual variability in peatland C exchange (Gažovič et al., 2013; Herbst et al., 2011; Olson et al., 2013). Drought response of peatlands is also complicated by the potentially different effects on bogs versus fens. For example, the sensitivity of NEP and its components to water table depth under relatively normal ranges has been shown to be higher in bogs than fens (Lindroth et al., 2007). The importance of dry periods to annual peatland NEP is clear but the relative effects on ecosystem respiration and gross primary production is less so (Lafleur, 2009). The relative impact of drought on each C balance component may vary by dominant vegetation, peatland hydrology, growing season length, nutrient status, or timing of drought (Bubier et al., 2003; Lafleur, 2009; Lund et al., 2012; Sulman et al., 2010). Expanding the coverage of peatland C flux observations during drought to globally distinct vegetation types may aid our ability to determine common features and responses that lead to increased C losses or those that minimize drought effects.

We estimated the net ecosystem C balance (NECB) at a raised ombrotrophic bog in New Zealand over 2.5 years that included one of the most extreme meteorological droughts in the past 100 years (MPI, 2013). We used continuous eddy covariance (EC) measurements of CO₂ and CH₄ flux and a water balance approach to estimating DOC export in order to calculate monthly and annual budgets of each C flux component and to determine the main drivers of

variability among years. Carbon flux measurements from this site extend the range of climatic zones represented in peatland flux literature as well as add information on the response of a unique plant functional type to a wide range of environmental conditions. We also aim to highlight some useful parallels and contrasts between this globally unique system and the much better represented Northern Hemisphere peatlands with respect to drought effects on C fluxes.

5.2. Methods

5.2.1. Site description

Kopuatai bog is located in the Hauraki Plains of the North Island/Te Ika a Māui, New Zealand (-37.387S Latitude, 175.459E Longitude). The vegetation at the site is dominated by the jointed wire rush, *Empodisma robustum* (Wagstaff and Clarkson, 2012), which forms a dense canopy of interwoven live and dead stem material. Total green plant area index (GAI) at the site is $1.32 \text{ m}^2 \text{ m}^{-2}$ (Goodrich et al., 2015), primarily contributed by *E. robustum*, while other vegetation cover included sedges, *Machaerina teretifolia* and *Schoenus brevifolius*, especially in wetter zones, and clusters of small shrubs (1-2 m height), *Leptospermum scoparium* and *Epacris pauciflora*, sparsely scattered throughout the study area. *Sphagnum* mosses appear sporadically throughout the peatland where coverage of the dominant vegetation is sparse and light penetrates to the surface, however the primary peat forming material is *E. robustum* roots (Agnew et al., 1993). These roots form negatively geotropic clusters covering the surface and serve a similar nutrient capture and water holding capacity role as *Sphagnum* in Northern Hemisphere peatlands (Agnew et al., 1993; Clarkson et al., 2009a). Kopuatai is an ombrotrophic, raised bog, and the largest remaining unaltered

peatland ($\sim 90 \text{ km}^2$) in the country since the majority of New Zealand wetlands have been drained, primarily for agriculture (McGlone, 2009).

5.2.2. Eddy covariance CO_2 , H_2O and CH_4 flux measurements

We measured net ecosystem exchange of CO_2 (F_{CO_2}) and H_2O using the eddy covariance (EC) technique from 19 November 2011 to 31 August 2014, while methane flux (F_{CH_4}) measurements began 4 February 2012. Our EC instrumentation was mounted on a 4.5 m tall triangular lattice tower and included a sonic anemometer (CSAT3, Campbell Scientific Inc., Logan, Utah, USA), an open path $\text{H}_2\text{O}/\text{CO}_2$ analyzer (LI-7500, LI-COR Inc.) and an open-path CH_4 analyzer (LI-7700, LI-COR Inc., Lincoln, Nebraska, USA). Sensors were mounted on a horizontal boom approximately 1.5 m from the face of the tower with an uninterrupted fetch extending $>500 \text{ m}$ in all directions and relatively uniform canopy height and negligible slope over that distance. Data were collected at 10 Hz using a CR3000 datalogger (Campbell Scientific Inc.) and stored on a memory card.

Fluxes were processed with an averaging interval of 30 minutes using EddyPro software (v5.1.1, LI-COR Inc.). Time lags between the wind and scalar concentration time series were removed by covariance maximization. A fully analytic approach was chosen for correction of low-pass (Moncrieff et al., 1997) and high-pass filtering (Moncrieff et al., 2005) and the standard Webb et al. (1980) method was applied to compensate for air density fluctuations. A double-axis rotation was applied for sonic tilt correction and the concentration time series were de-trended by block averaging. Spikes in the high frequency data were removed according to Vickers and Mahrt (1997). During EddyPro flux

processing and computation, we implemented the Göckede et al. (2006) method to assign quality control (QC) flags to each 30-min flux, based on tests for well-developed turbulence and steady state conditions (flags 1 – 5, with 1 being best quality).

Ancillary measurements included incoming total and diffuse photosynthetic photon flux density (PPFD) (BF5 Sunshine Sensor, Delta-T Devices Ltd., Cambridge, United Kingdom) just above the canopy (~1.2 m above peat surface) and air temperature (T_{air}) and vapour pressure (fully aspirated HMP 155, Vaisala, Helsinki, Finland) at 4.25 m above the surface. Water table depth (WTD) was measured within a 1.5 m dipwell using a submersible pressure sensor (WL1000W, Hydrological Services, NSW, Australia).

5.2.3. Quality control, gap filling and flux partitioning

Fluxes assigned a quality control flag value > 1 were discarded from the analysis.

Data were then filtered for insufficient atmospheric turbulence using a threshold for friction velocity ($u_* < 0.15 \text{ m s}^{-1}$), below which all flux data were discarded. We chose this cut-off after calculating annual sums of F_{CO_2} and F_{CH_4} using a range of u_* thresholds and determining the value at which the annual sum stabilized (Loescher et al., 2006). For CO_2 fluxes, we removed remaining spikes in the CO_2 flux time series by calculating 30-day moving window statistics and testing each half-hourly flux against the median for the corresponding time period. Fluxes exceeding the median ± 2 (daytime) or ± 3 (night time) standard deviations were flagged and any half hours with more than 1 (daytime) or 4 (night time) flags were rejected (Campbell et al., 2014; Goodrich et al., 2015). In

addition, fluxes were discarded when associated wind direction fell within a 55° sector including the tower and site infrastructure.

The artificial neural network (ANN) used to fill gaps in F_{CH_4} was described in Goodrich et al. (accepted). The F_{CH_4} measurements began 4 February 2012, therefore we used the ANN developed for F_{CH_4} gap filling to estimate January 2012 fluxes and to obtain a full two year dataset. Gaps in the F_{CO_2} time series were also filled using an ANN approach (Papale and Valentini, 2003), separately for daytime ($\text{PPFD} > 5 \mu\text{mol m}^{-2} \text{s}^{-1}$) and night time ($\text{PPFD} \leq 5 \mu\text{mol m}^{-2} \text{s}^{-1}$). The night time ANN consisted of nine input nodes including air temperature (T_{air}), peat temperature at 50 mm below the surface (T_{peat}), water table depth, four fuzzy datasets representing season, one fuzzy dataset representing the year of study period, and an offset node. The night time ANN included four hidden nodes and sigmoid transfer functions were applied to the weighted sums from the hidden and output layers (Dengel et al., 2013; Papale and Valentini, 2003). The daytime ANN had inputs of PPFD, T_{air} , canopy surface temperature (T_{surf}), atmospheric vapour pressure deficit (VPD), VPD calculated using T_{surf} (VPD_{surf}), WTD, and the same fuzzy datasets described for the night time ANN. Since each neural network run gives a unique result, both day time and night time ANN models were trained and fitted 20 times and the median value was used to fill gaps (Knox et al., 2014). Similarly, the ANN used to fill gaps in daytime H_2O fluxes consisted of six input variables (horizontal wind speed, air temperature, saturation vapour pressure deficit (VPD) measured at 4 m height, vegetation surface temperature, net radiation, and within-canopy VPD), and eight fuzzy variables describing season of year and time of day (Campbell et al., in

preparation). Night time gaps in H₂O fluxes were filled with ANN output driven by air temperature, saturation vapour pressure deficit (VPD) measured at 4 m height, canopy wetness, net radiation, and horizontal wind speed), and three fuzzy variables describing season of year (Campbell et al., in preparation).

For this chapter net ecosystem production (NEP) is used to refer to the difference between GPP and ER, such that $NECB = NEP - F_{CH_4} - F_{DOC}$, and positive NECB indicates C uptake by the ecosystem. To partition F_{CO_2} into GPP and ER, we estimated daytime ER by applying the night time ANN to daytime driver data. Night time GPP was assumed to be zero and day time GPP was estimated by subtracting modelled daytime ER from gap-filled F_{CO_2} .

5.2.4. DOC export

A detailed description of the methods used for estimating C loss via dissolved organic C (DOC) export in subsurface water (F_{DOC}) was given by Sturgeon (2013) and is the subject of Campbell et al., (in preparation). Briefly, during 2012, DOC was sampled monthly at nine sites across the EC footprint, at three peat depths, by extracting water from PVC wells inserted to 30 cm, 60 cm, and 100 cm. The concentration of DOC in water samples was determined with a TOC-VCSH analyser (Shimadzu, Kyoto, Japan). Monthly water seepage from the EC footprint was estimated with a water balance approach: $Q = P - E - \Delta S$, where P is rainfall, E is evaporation calculated from the eddy covariance latent heat flux, and ΔS is change in water storage (all with units mm). F_{DOC} for 2012 was then estimated as the product of depth-weighted mean monthly DOC concentration and monthly Q . For remaining years, F_{DOC} was estimated using a relationship between $P - E$ and F_{DOC} (Campbell et al., in preparation).

5.2.5. Uncertainty estimates

Random uncertainty for each half-hourly value of F_{CH_4} was estimated based on whether the value was measured or gap-filled (Dragoni et al., 2007). For measured values we applied the ‘paired-days’ approach of Hollinger and Richardson (2005) for which the difference between matching half-hourly fluxes (either ΔF_{CO_2} or ΔF_{CH_4}) on adjacent days were examined if environmental data were similar (PPFD within $75 \mu\text{mol m}^{-2} \text{s}^{-1}$, T_{air} within 3°C , wind speed within 1 m s^{-1}). To apply this approach to F_{CH_4} , additional constraints were added for WTD (within 5 mm) and T_{peat} (within 2°C) given their potential influence on CH_4 production and flux in peatlands. Double exponential distributions were fitted to ΔF_{CO_2} and ΔF_{CH_4} binned by flux magnitude and the uncertainty of each measured half-hourly flux value ($\sigma_m = (\sqrt{2})\beta$) was determined as a function of the mean flux between the measurement pairs (Dragoni et al., 2007; Hollinger and Richardson, 2005). We also utilized the residuals from the 20 ANN simulations to estimate uncertainty based on the gap-filling approach. These residuals were normally distributed so the standard deviations (σ_{gf}) were determined as functions of the gap-filled flux magnitudes (Dragoni et al., 2007). We also assessed the impact of several post-processing choices on the annual flux estimates for both NEP and F_{CH_4} with an approach similar to Elbers et al. (2011). Annual EC-based flux estimates at our site were affected by the choice of u_* threshold, QC flag filter, and the size of the excluded wind sector downwind of the tower and site infrastructure. Therefore, we explored the impact of these choices by slightly varying each filter and recalculating annual sums. Uncertainty in annual F_{DOC} is described in Campbell et al. (in preparation).

5.3. Results

5.3.1. Meteorological conditions

Meteorological conditions for the study period covered in this analysis (Figure 5.1) were described in Chapters 3.3.1 and 4.3.1. In addition, the difference between monthly precipitation (P) and eddy covariance-derived evaporation (E), further highlights the water deficits during summers 2013 and 2014 (Figure 5.2). January – March exhibited negative $P - E$ in those years, whereas all months in 2013 had positive water balance, with the exception of May and November, which exhibited only slight deficits. Interestingly, later months in 2013 and 2014 had higher precipitation inputs than 2012, which led to relatively similar annual totals for the two full measurement years (1153 mm and 1105 mm in 2012 and 2013, respectively) and annual total E was slightly higher in 2012 (571 mm) than 2013 (564 mm).

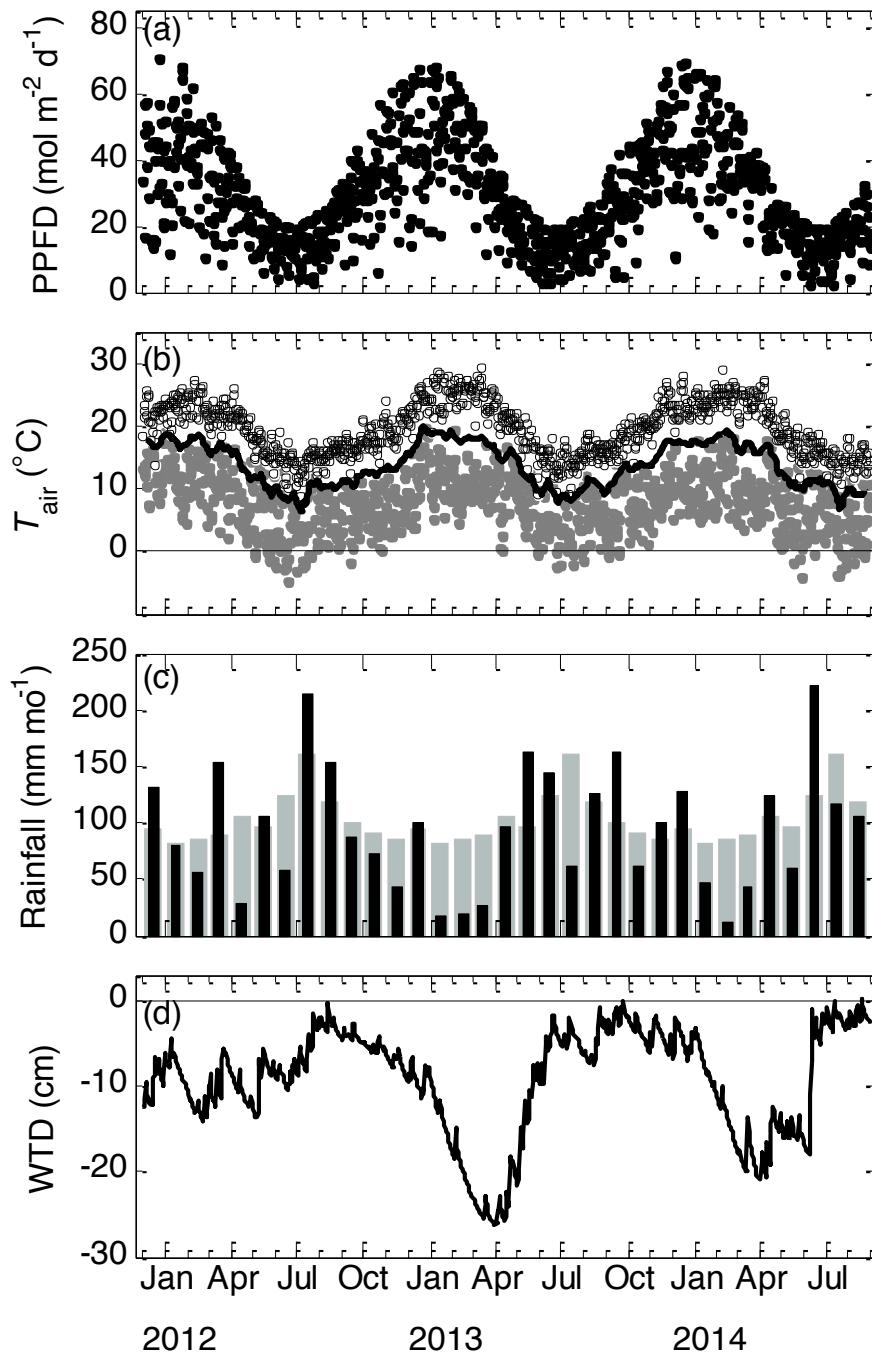


Figure 5.1. Meteorological and hydrological variables at Kopuatai bog, 1 December 2011 – 31 Aug 2014: (a) daily total PPFD, (b) daily minimum (grey points) and maximum (open points) air temperatures (T_{air}), and the 15-day running mean of T_{air} (line); (c) monthly total rainfall (black bars) and monthly normals (1980-2010) taken from a nearby climate station (grey bars), (d) daily mean water table depth (WTD) (zero line is the peat surface).

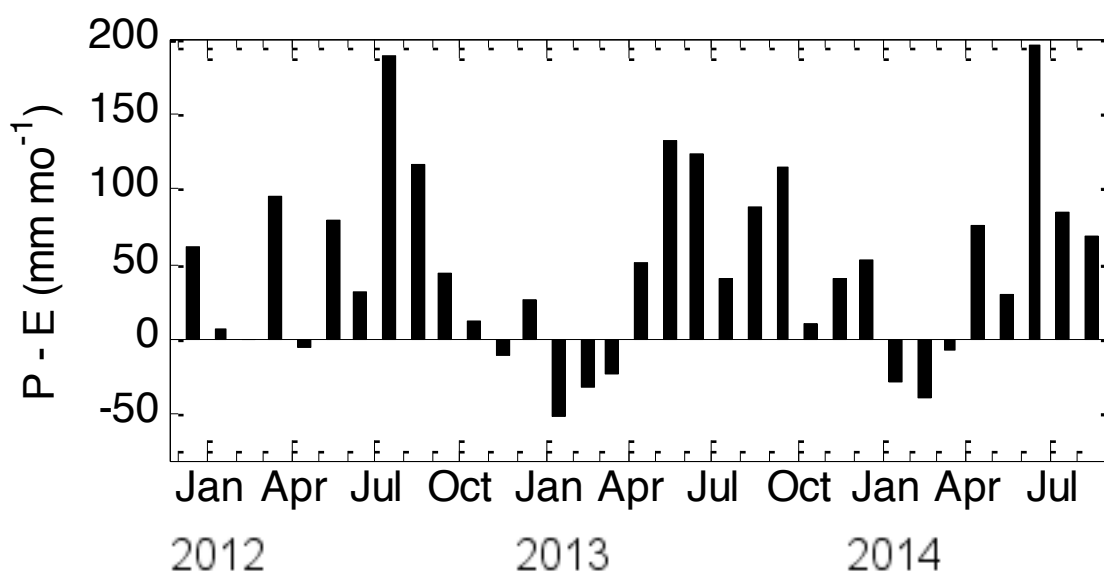


Figure 5.2. Monthly total precipitation (P) minus evaporation (E) at Kopuatai bog from December 2011 to August 2014.

5.3.2. NECB components

Annual NECB at Kopuatai bog was 152.6 and $74.5 \text{ gC m}^{-2} \text{ yr}^{-1}$ in 2012 and 2013, respectively (Table 5.1). GPP and ER were the largest terms in the budget for both years. Annual GPP in 2012 ($776.4 \text{ gC m}^{-2} \text{ yr}^{-1}$) was similar to the 2013 estimate ($745.6 \text{ gC m}^{-2} \text{ yr}^{-1}$), and monthly GPP was $>20 \text{ gC m}^{-2}$ for every month of the study period (Figure 5.3a). Ecosystem respiration was 10% greater in 2013 ($635.4 \text{ gC m}^{-2} \text{ yr}^{-1}$) than in 2012 ($580.2 \text{ gC m}^{-2} \text{ yr}^{-1}$), primarily as a result of enhanced respiration during drought months (Figure 5.3b). The resulting annual NEP was $199.0 \text{ gC m}^{-2} \text{ yr}^{-1}$ in 2012 and $110.0 \text{ gC m}^{-2} \text{ yr}^{-1}$ in 2013 (Table 5.1). The bog switched from $\text{CO}_2\text{-C}$ sink to $\text{CO}_2\text{-C}$ neutral or source one month earlier in 2013 and 2014 than in 2012 owing to the drier conditions and elevated ER in the former. However, the bog was a $\text{CO}_2\text{-C}$ source for only three months during each of the two dry summers and neutral for a fourth month.

Table 5.1. Annual carbon balance and component fluxes from Kopuatai bog (all units are $\text{gC m}^{-2} \text{yr}^{-1}$).

Year	$\text{CO}_2\text{-C}$			Non- $\text{CO}_2\text{-C}$		NECB
	GPP	ER	NEP	$F\text{CH}_4$	FDOC	
2012	776.4	580.2	199.0	21.5	16.7	152.5
2013	745.6	635.4	110.0	14.5	15.7	74.5

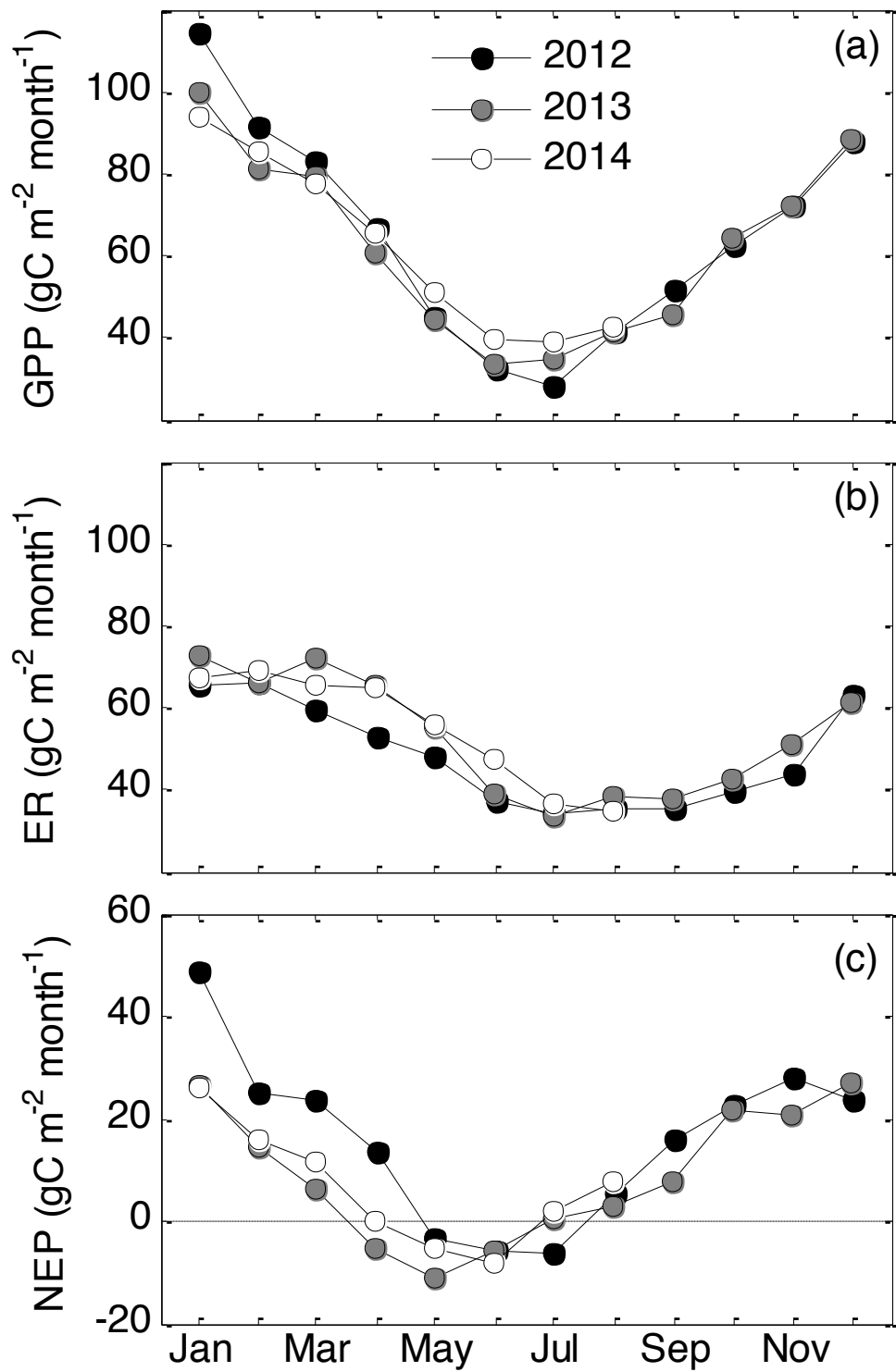


Figure 5.3. Monthly total CO₂-C flux components at Kopuatai bog from January 2012 to August 2014. (a) gross primary production (GPP), (b) ecosystem respiration, (c) net ecosystem production (NEP).

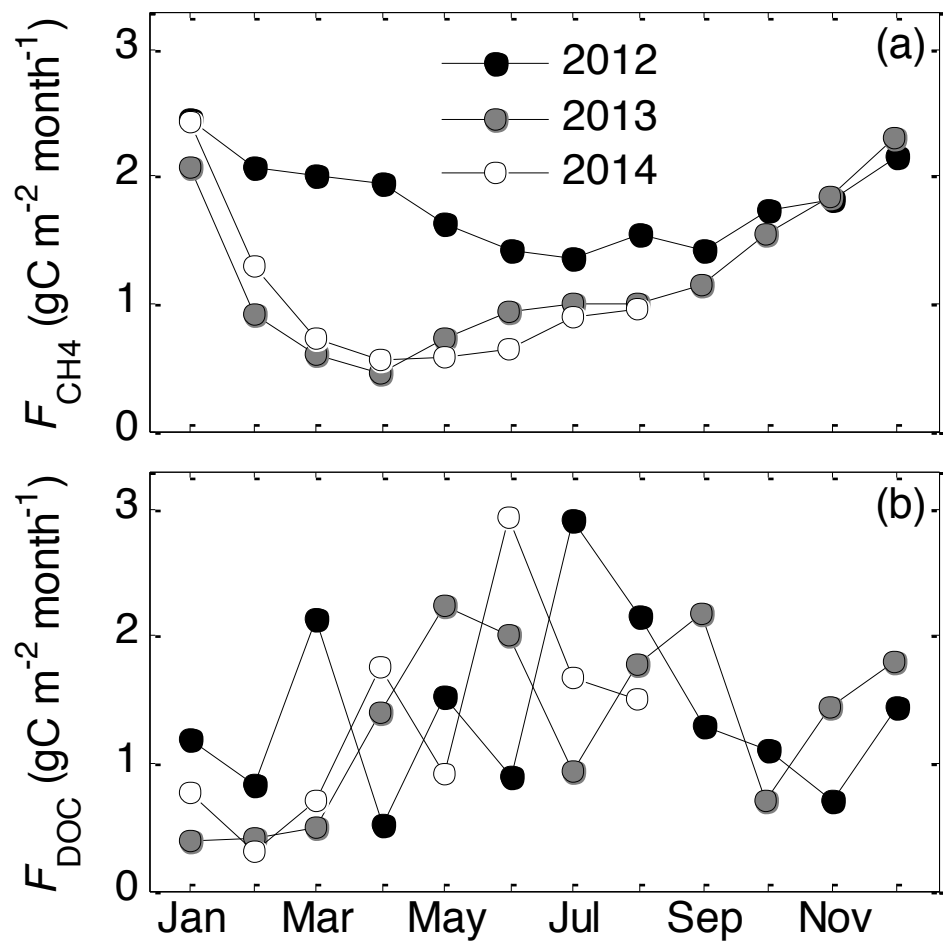


Figure 5.4. Monthly total non- CO_2 -C flux components at Kopuatai bog from January 2012 to August 2014. (a) methane flux (F_{CH_4}), (b) dissolved organic carbon export (F_{DOC}).

Annual F_{CH_4} was a much smaller component of the NECB than NEP, contributing 21.5 (14%) and 14.5 $\text{gC m}^{-2} \text{ yr}^{-1}$ (19%) in 2012 and 2013, respectively (Table 5.1) with much lower monthly fluxes during the drought months and subsequent slow recovery after water table recharge (Figure 5.4a). Annual F_{DOC} contributed a similarly small proportion but consistent flux of 16.7 (11%) and 15.7 $\text{gC m}^{-2} \text{ yr}^{-1}$ (21%) in 2012 and 2013, respectively (Table 5.1). F_{DOC} was the most variable flux from month to month (Figure 5.4b) being driven primarily by $P - E$.

5.3.3. Seasonal variation in F_{CO_2}

Mean diurnal variation in F_{CO_2} during 2012 showed relatively small differences in night-time fluxes among seasons, with summer and autumn F_{CO_2} approximately $0.7 \mu\text{mol m}^{-2} \text{s}^{-1}$ greater than winter and spring (Figure 5.5a). Mean daytime F_{CO_2} in 2012 followed the expected seasonal pattern with maximum uptake in summer and minimum in winter months, with a difference in peak uptake of approximately $3 \mu\text{mol m}^{-2} \text{s}^{-1}$ from winter to summer. In contrast, the daytime uptake in 2013 was more tightly constrained among seasons with a difference from winter to summer $< 2 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Figure 5.5b). In addition, the mean

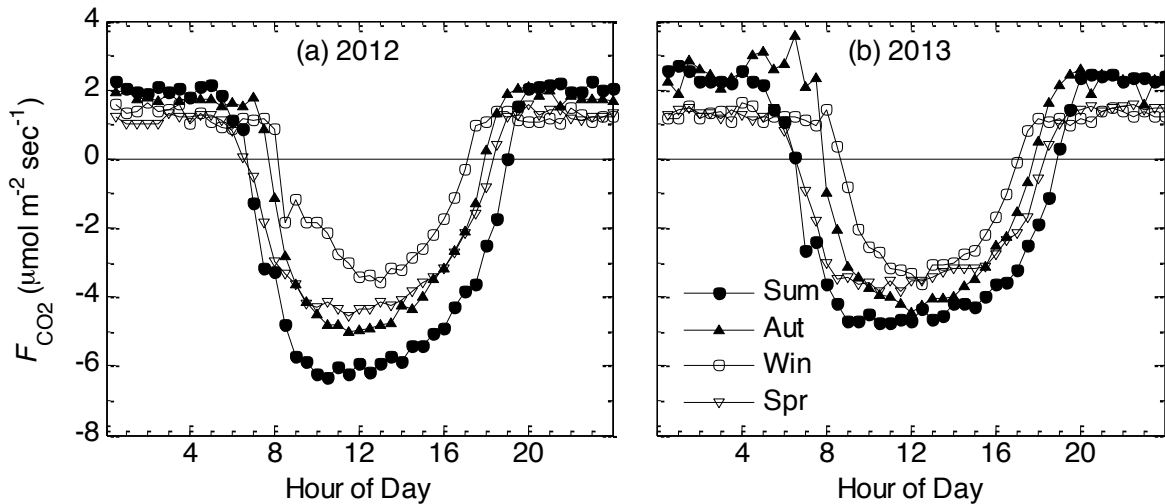


Figure 5.5. Seasonal ensemble average F_{CO_2} for (a) 2012 and (b) 2013. Summer 2012 includes data from December 2011 – February 2012, while summer 2013 included data from December 2012 – February 2013. Autumn was March – May, winter was June – August, and spring was September – November.

night time F_{CO_2} during the 2013 summer and autumn were higher by approximately $0.7 \mu\text{mol m}^{-2} \text{s}^{-1}$ than those in 2012, whereas winter and spring night time fluxes were similar between years (Figure 5.5b).

5.3.4. Flux uncertainties

Random uncertainties in NEP and F_{CH_4} associated with measurements and gap filling were $< 1 \text{ gC m}^{-2} \text{ yr}^{-1}$ for both 2012 and 2013. We found that $\sigma_m (\text{CO}_2)$ scaled linearly ($p < 0.01$) with mean flux according to $\sigma_m = 0.37 - 0.09F_{\text{CO}_2}$ for negative fluxes and $\sigma_m = 0.15 + 0.21F_{\text{CO}_2}$ for positive fluxes, similar to a grassland system reported in Richardson et al. (2006). The regression between $\sigma_m (\text{CH}_4)$ and mean F_{CH_4} also yielded a significant linear relationship: $\sigma_m = 0.36 + 0.21F_{\text{CH}_4}$. Varying u^* threshold from $0.11 - 0.17 \text{ m s}^{-1}$ resulted in 0.84 and $1.81 \text{ gC m}^{-2} \text{ yr}^{-1}$ difference in annual NEP for 2012 and 2013, respectively. The same range in u^* threshold resulted in annual differences in F_{CH_4} of 0.16 and $0.09 \text{ gC m}^{-2} \text{ yr}^{-1}$. With respect to QC flag filter, NEP was reduced by 13.4 and $14.4 \text{ gC m}^{-2} \text{ yr}^{-1}$ if all fluxes assigned QC flags ≤ 4 were accepted (relative to only accepting QC flag = 1), whereas annual F_{CH_4} was increased by 0.91 and $0.76 \text{ gC m}^{-2} \text{ yr}^{-1}$ for 2012 and 2013 data, respectively. Finally, we found that expanding the excluded wind sector downwind of the tower and infrastructure from 0° to 55° resulted in annual differences in NEP of 1.6 and $3.1 \text{ gC m}^{-2} \text{ yr}^{-1}$ for 2012 and 2013, respectively, and in differences of 0.51 and $0.17 \text{ gC m}^{-2} \text{ yr}^{-1}$ for 2012 and 2013, respectively for annual F_{CH_4} .

5.3.5. Controls on ecosystem C fluxes

In 2012, NECB remained positive until May and the bog was a small source of C from May to July (Figure 5.6). In contrast, the bog switched from C sink to source earlier in 2013 and 2014 (Figure 5.6). Variation in monthly NECB with monthly total PPFD was described by a simple linear regression, whereby the ecosystem was a significantly stronger C sink during summer months than during winter months (Figure 5.7). As GPP was the largest gross term in the budget, the

seasonal progression of NECB was generally similar to that of GPP (Figure 5.3a) and NEP (Figure 5.3c), effectively resulting in light limitation of overall NECB at monthly timescales (Figure 5.7). However differences among months of different years were driven by changes to both ER and GPP (Figures 8 and 9).

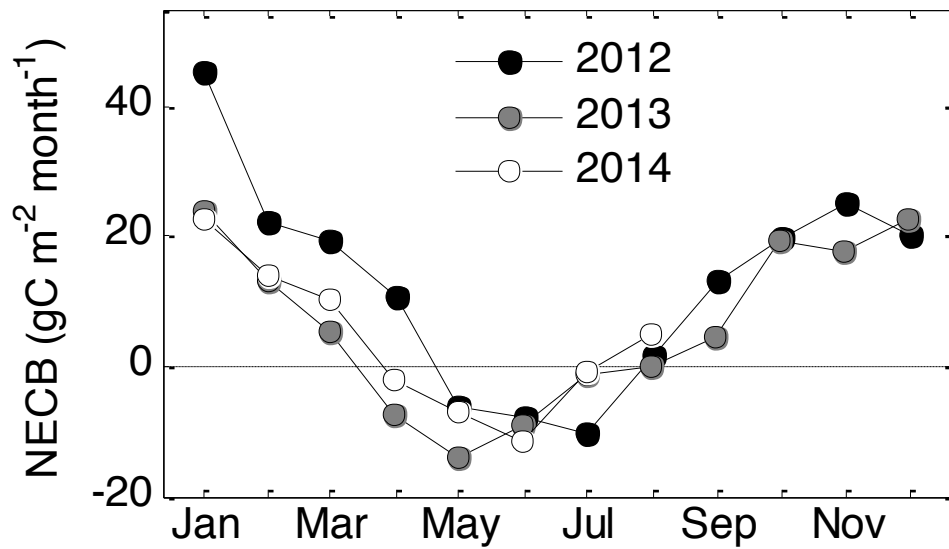


Figure 5.6. Monthly total net ecosystem C balance at Kopuatai bog from January 2012 to August 2014.

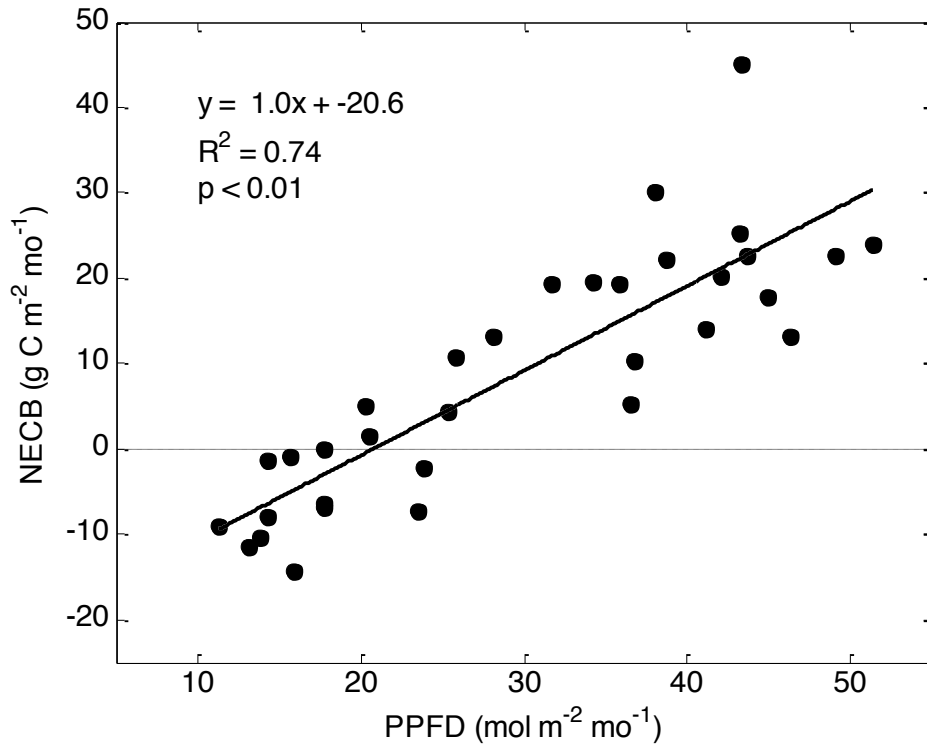


Figure 5.7. Monthly total NECB vs. integrated PPFD at Kopuatai bog from January 2012 to August 2014.

To assess inter-annual deviations in ER and GPP, we isolated summer and autumn months since differences in mean fluxes between dry and wet years were largest during these seasons (Figure 5.5). For January – April (summer/autumn) we had three years of data for comparison. We calculated the mean of each month across those three years and subtracted that from each individual monthly sum (for ER and GPP) or mean (for driver variables). Inter-annual deviations from mean monthly ER were driven by differences in WTD and peat temperature, whereby lowered water tables led to higher respiration (Figure 5.8). The enhancement in ER may also be exacerbated by higher T_{peat} (vertical stratification of colors in Figure 5.8), however more data is needed to confirm this possible trend. The corresponding deviations from mean monthly

GPP among years were largely driven by differences in total PPFD, whereby higher PPFD lead to lower GPP (Figure 5.9). The months with higher PPFD generally also exhibited higher mean VPD (Figure 5.9), whereas lowered water table *per se*, did not seem to impact GPP significantly (not shown). Although drier, warmer conditions had a larger proportional impact on summer ER (increasing with lowered water tables) than GPP (decreasing with higher VPD and PPFD), the contribution of lowered GPP to the overall NECB during those months was similar (Figures 8 & 9) because of the larger relative magnitude of GPP (Figure 5.3).

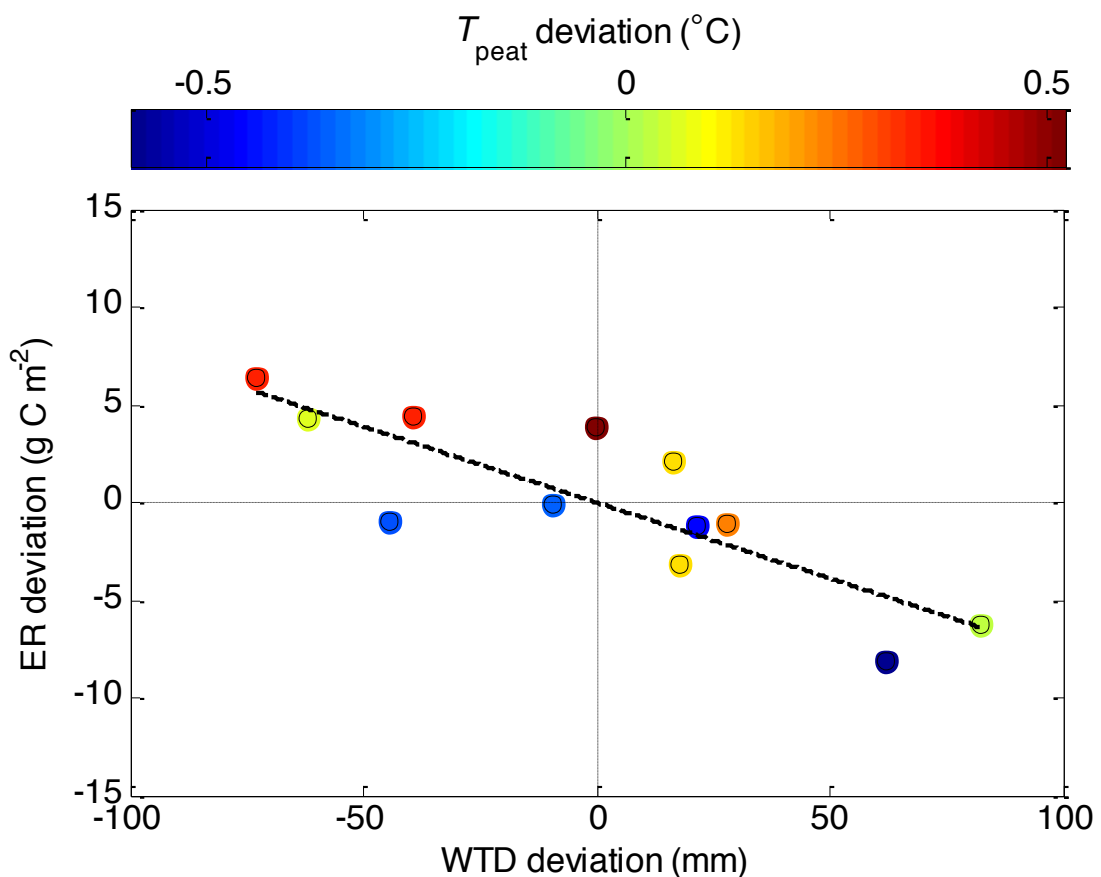


Figure 5.8. Deviations from mean monthly ER, WTD, and peat temperature for summer and autumn months (January – April) 2012 – 2014 at Kopuatai bog. A positive deviation in ER indicates that individual month had higher ER than the three-year mean for that month. Regression results: $y = -0.1x + 0$; $R^2 = 0.70$; $p < 0.01$.

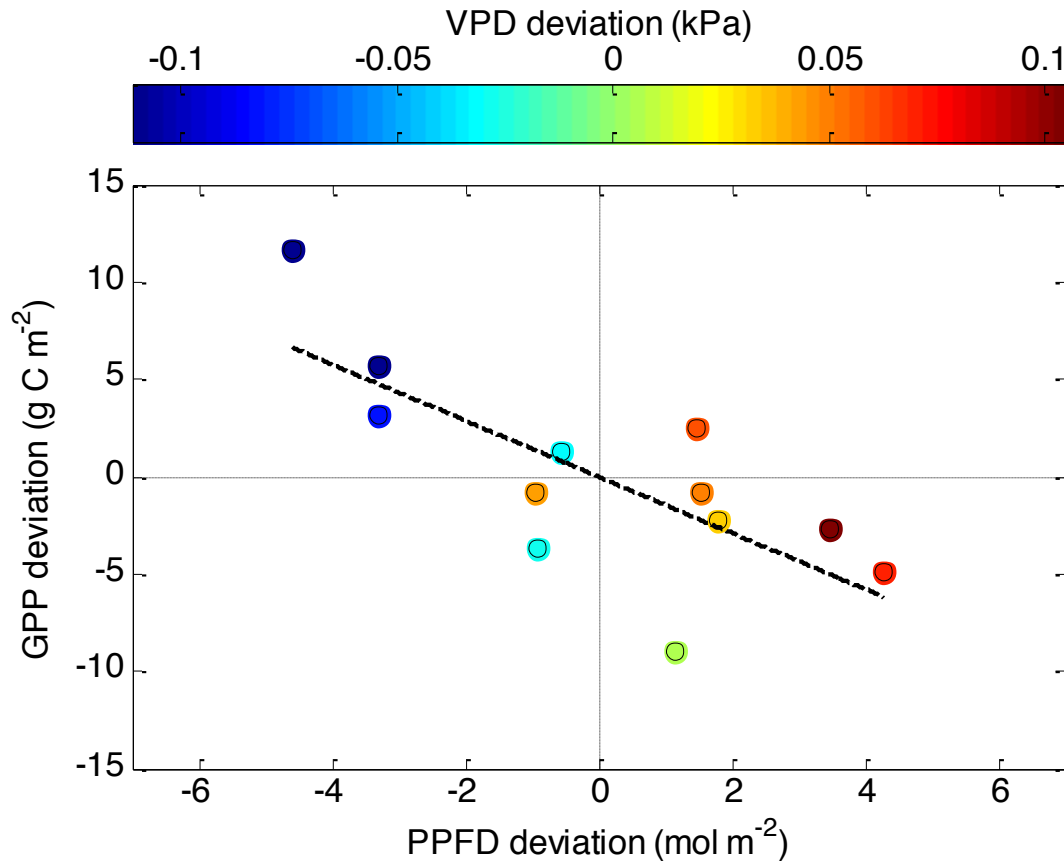


Figure 5.9. Deviations from mean monthly GPP, PPFD, and VPD for summer and autumn months (January – April) 2012 – 2014 at Kopuatai bog. A positive deviation in GPP indicates that individual month had higher GPP than the three-year mean for that month. Regression results: $y = -1.4x + 0$; $R^2 = 0.55$; $p < 0.01$.

5.4. Discussion

5.4.1 Peatland net ecosystem C balance

Kopuatai bog was a strong C sink during two years with contrasting

environmental conditions that included a drought in summer 2013. For both full

measurement years, Kopuatai NECB was at the higher end of Northern

Hemisphere peatland annual NECB estimates, which range from losses of 14 g C

$\text{m}^{-2} \text{yr}^{-1}$ to gains of 101 $\text{g C m}^{-2} \text{yr}^{-1}$ (Dinsmore et al., 2010; Gažovič et al., 2013;

Koehler et al., 2011; Nilsson et al., 2008; Olefeldt et al., 2012; Roulet et al., 2007).

The CO₂ flux components were the largest terms in the Kopuatai NECB for both full years, whereas losses from F_{CH_4} and F_{DOC} constituted 11 – 13% and 9 – 14% of NEP, respectively (Table 5.2). These are comparable to percentages estimated in other peatland NECB studies (Koehler et al., 2011; Nilsson et al., 2008; Roulet et al., 2007). However, the relatively short season of C loss at Kopuatai was largely due to the mild climate that results in year-round growing conditions and relatively large annual NEP (Table 5.2). This result is in agreement with Campbell et al. (2014), who found large annual NEP for a drainage impacted New Zealand bog despite having similar peak summertime CO₂ uptake to Northern Hemisphere peatlands. The Campbell et al. (2014) study was conducted at Moanatuatua, a remnant bog site with prevalence of the taller, late successional species (Clarkson et al., 2004), *Sporadanthus ferrugineus* (giant cane-rush) in addition to *E. robustum*, resulting in greater mid-day CO₂ uptake and annual GPP than we measured at Kopuatai. However, mean night time F_{CO_2} (Figure 5.5b) and total ER during summer drought months at Kopuatai (Figure 5.3b) were similar to those during summer at Moanatuatua bog, despite water tables reaching 80 cm below the surface there (Campbell et al., 2014) compared to < 30 cm below the surface at Kopuatai (Figure 5.1). Similarly, Lafleur et al. (2005) showed that ER at the relatively dry Mer Bleue bog, in Ontario, Canada was only weakly correlated to water table depth. The lack of increase in ER at Mer Bleue with dropping water tables may have been related to compensating factors of decreased respiration from dessicated surface *Sphagnum* and increased respiration of deeper heterotrophic microbial communities (Dimitrov et al., 2010). Our results suggest that lowered water tables increase ER at Kopuatai but

there may be a limit to this increase with drier conditions and more work is needed to explore this factor.

Northern Hemisphere peatland growing seasons are generally bounded by frozen or snow-covered winters but year-round GPP > 0 has been reported at an Atlantic blanket bog, Glencar, subject to a relatively mild, maritime climate (McVeigh et al., 2014; Sottocornola and Kiely, 2010). However, peak summer GPP and ER at Kopuatai ($114.4 \text{ gC m}^{-2} \text{ mo}^{-1}$ and $73.0 \text{ gC m}^{-2} \text{ mo}^{-1}$, respectively) were substantially higher than reported for Glencar ($63.7 \text{ gC m}^{-2} \text{ mo}^{-1}$ and $38 \text{ gC m}^{-2} \text{ mo}^{-1}$, respectively) (McVeigh et al., 2014), which may be due to the lower peak LAI at Glencar ($\sim 0.6 \text{ m}^2 \text{ m}^{-2}$) compared to Kopuatai ($1.3 \text{ m}^2 \text{ m}^{-2}$) (Goodrich et al., 2015), as well as less available solar radiation at the higher latitude Irish site. In contrast, a moderately rich treed fen in Western Canada with higher LAI ($2.61 \text{ m}^2 \text{ m}^{-2}$) had larger peak GPP and ER than we found at Kopuatai, leading to similar annual values ($713 \text{ gC m}^{-2} \text{ yr}^{-1}$ and $596 \text{ gC m}^{-2} \text{ yr}^{-1}$, respectively) despite a shorter growing season (6 months) (Syed et al., 2006). Lund et al. (2010) showed that LAI and growing season length explained a large proportion of the variance in NEP and its components across a range of northern peatlands. Our results from Kopuatai bog are consistent with the relationship between summertime NEP and LAI established by Lund et al. (2010).

5.4.2. Drought effects on peatland CO₂ exchange

During one of the most severe and widespread meteorological droughts in New Zealand in the past 70 years (MPI, 2013), NECB at Kopuatai bog was reduced by roughly 50% compared to the previous, relatively wet year. However, the bog was still a strong C sink during early drought months (Figure 5.6) and overall during the drought year (Table 5.1). The reduction in NEP during dry summer

and autumn conditions was driven by the combination of up to 20% increase in monthly ER as a result of lowered water tables and 5 – 18% decrease in monthly GPP due to high light and VPD, although GPP appeared not to be directly impacted by changes in WTD. GPP in January 2012 was higher than any other month during the study period (Figure 5.3). This month was relatively cool and cloudy with more precipitation than January 2013 and 2014 (Figure 5.1). The high GPP in January 2012 was likely caused by the low, but still saturating, PPFD and the associated low VPD conditions (Goodrich et al., 2015). This also fits within a general pattern whereby positive deviations in monthly GPP from year to year were related to reduced VPD and light, while negative deviations were driven by the opposite (Figure 5.9). We have previously demonstrated the sensitivity of GPP at Kopuatai to clear-sky, high VPD conditions (Goodrich et al., 2015) and this effect seems to have constrained CO₂ uptake during the clearest summer months in 2013 and 2014 (Figure 5.9). Similarly, Aurela et al. (2007) showed that GPP was relatively unchanged at a sedge fen in Finland during a drought summer, although rates of uptake during clear-sky afternoons within drought months were suppressed due to high VPD, contributing a small percentage of the overall drought-induced reduction in NEP.

Some Northern Hemisphere peatlands shift from annual (or growing season) sinks to sources of CO₂ in response to dry conditions (Alm et al., 1999; Joiner et al., 1999; Shurpali et al., 1995). Reduction in peatland NEP during dry conditions can result from reduced GPP, increased ER, or a combination of both. F_{CH_4} tends to be reduced during dry years (Brown et al., 2014; Moore et al., 2011), while observations of F_{DOC} during dry years in different peatland types are less

conclusive (Koehler et al., 2011; Roulet et al., 2007). Nonetheless the contribution of non-CO₂-C loss during drought generally does not lead to reduced annual NECB. The relative response of GPP and ER to dry conditions has important implications for the future role of peatlands under changing climate (Wu and Roulet, 2014). However there is no consensus on whether GPP or ER is more important to the peatland NEP drought response (Lafleur, 2009).

Most studies reporting peatland CO₂ fluxes during relatively dry conditions attribute some portion of the NEP reduction to an increase in ER and therefore, the ER response at Kopuatai was expected. However, the reported effects of a lowered water table *per se*, on GPP are more varied. Bubier et al. (2003) found that an increase in ER dominated the effect on NEP across sites measured with chambers within Mer Bleue bog in Ontario, Canada, but the GPP effect was dependent on vegetation community. Bog sites dominated by ericaceous shrubs were not impacted until the tail-end of the most severe dry conditions, indicating a better adaptation of evergreen shrubs to stress than the sedge fen sites (Bubier et al., 2003). However, eddy covariance fluxes from the same peatland suggested ER was relatively unchanged during an extended dry period, whereas daytime NEP was reduced due to decreased photosynthesis of the surface mosses (Lafleur et al., 2003). Similarly, GPP at a *Sphagnum* bog in Finland was severely reduced during a summer drought due to irreversible desiccation of the mosses, while respiration was enhanced leading to a large annual net loss of CO₂ to the atmosphere (Alm et al., 1999). Arneeth et al. (2002) found that a warm, dry summer reduced growing season NEP at two bog sites in Russia and Siberia, while the bog with fewer trees and shrubs became an annual

source of CO₂. They found smaller inter-annual differences in ER and attributed the reduction in NEP mainly to reduced GPP (Arneeth et al., 2002). Finally, Shurpali et al. (1995) found that Bog Lake fen in Minnesota, USA, became a source of CO₂ over the course of a warm, dry growing season due to moisture and VPD stress on surface mosses that usually contributed ~50% of GPP at that site.

The studies discussed above all suggest that sites where *Sphagnum* mosses contribute significantly to ecosystem GPP are particularly sensitive to dry conditions, which is likely due to the inability of *Sphagnum* to control capitulum moisture content when water tables drop (Laitinen et al., 2008). Sulman et al. (2010) observed opposite responses of fens and bogs to inter-annual differences in water tables, conjecturing on the importance of relative *Sphagnum* cover in the observed differences. However, sites dominated by vascular vegetation can also exhibit reduced GPP with lowered water tables, and the magnitude of the response may depend on timing of dry conditions. Joiner et al. (1999) found that a late summer drought led to early autumn senescence of the vascular vegetation at a fen site in Manitoba, Canada, while ER remained steady until temperatures dropped. In contrast, Griffis et al. (2000) showed that dry periods during the early growing season in a sub-arctic fen, while plants were developing, led to substantially reduced GPP relative to wetter years and impacted the whole growing season CO₂ uptake such that the ecosystem was a source of CO₂. Lund et al. (2012) showed a very similar effect of a springtime-initiated drought on GPP at a Swedish raised bog, where plant development and moss biomass accumulation were suppressed, impacting NEP over the course of

the year and causing the ecosystem to act as a source of CO₂. However, at the same site, a mid-summer drought did not have the same effect on the vegetation and only ER was enhanced (Lund et al., 2012).

A synthesis of data from across 11 biomes within the FLUXNET database suggested that GPP was more sensitive to drought stress than ER (Schwalm et al., 2010). While recognizing the under-representation of 'wetland' ecosystems (including peatlands) in their analysis (three such sites were included), the authors suggested that drought events drive water tables farther below the surface, which may enhance both gross CO₂ fluxes (Schwalm et al., 2010). While there were not large differences in GPP among years due to WTD changes at our site, indicating relative insensitivity to the observed summer water table drawdown, it is clear that extended sunny and dry summer periods do not enhance photosynthetic uptake in *E. robustum*-dominated peatlands. Some researchers have reported relatively low sensitivity of annual GPP to lowered water tables, often due to compensating factors that allowed NEP to recover despite either temporary reductions in GPP or increases in ER. For example, Aurela et al. (2007) showed that ER at a boreal sedge fen increased during a dry summer but the reduced NEP during drought months was partially offset by an increased growing season length, which led to an extended period of plant uptake before autumn senescence. The only peatland in which GPP has been reported to increase in response to drought conditions was a treed, moderately rich fen in Western Canada (Cai et al., 2010; Flanagan and Syed, 2011). However, that site may have been within a successional phase toward increased tree growth and more above ground C allocation (Flanagan and Syed, 2011). As

mentioned above, the first multi-year NEP data from a New Zealand peatland revealed very high annual CO₂ uptake despite lowered water tables due to surrounding farm drainage (Campbell et al., 2014). Vegetation at that site contained the later successional species *Sporadanthus ferrugineous* (giant cane-rush), which have deeper roots (Clarkson et al., 2009b) and higher above-ground biomass than the mid-successional *E. robustum* (Thompson et al., 1999), dominant at our study site. This highlights the need for future work in New Zealand peatlands to investigate the potential shift in C allocation from below ground (accumulating peat) to above ground (vegetation biomass) resulting from succession or disturbance, such as long-term lowering of the water table. Dominant vegetation type is clearly a critical component in determining the peatland NEP response to dry conditions. Timing of drought is also critical but the impact of timing seems dependent on vegetation and few examples of early spring droughts are available in published peatland NEP records. However, Kupier et al. (2014) used mesocosms from a raised bog to demonstrate that peatland plant functional types determined when the peatland shifted from CO₂ sink to CO₂ source in response to drying.

5.5. Conclusions

We have shown that a warm temperate bog in New Zealand dominated by the vascular plant, *E. robustum* was a strong C sink even during drought years. Our results from Kopuatai bog extend the coverage of ecosystem-scale C response with a globally unique peatland plant functional type and provide insight into the role of plants in the drought response of peatlands in general. Vascular plants are better adapted to functioning during dry conditions, given their ability

to control water loss through stomata (Körner, 1995). Furthermore, evergreen species (e.g., ericaceous shrubs and restiads) seem to be particularly resilient to drought stress. *E. robustum* peatlands may be especially well-equipped for drought given the mulch-like layer of dead stem material that accumulates above the surface, partially contributing to reduced evaporation rates during dry conditions (Campbell and Williamson, 1997). Although peak GPP was reduced on dry summer days, the overall effect was not large enough to shift the ecosystem to a CO₂ source over the course of a dry summer. Furthermore, the importance of summer NEP to annual totals was minimized due to the year-round growing conditions. The drought resilience of Kopuatai bog in terms of reduced, but still relatively large, annual carbon uptake, also provides insight into the existence of these peatlands in a climatic setting that would not generally be considered conducive to peatland development and persistence given the often negative summer water balance and warm annual temperatures (McGlone, 2009). The negative feedback between the dry conditions and lower evaporation rates (Campbell and Williamson, 1997), while reducing GPP, helps maintain high water tables, which may limit respiration losses of C and maintain plant functioning.

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Chapter 6. Summary and conclusions

6.1. Introduction and review of thesis objectives

Peatlands store roughly one third of global soil carbon resulting from these ecosystems' slight imbalance between net CO₂ uptake and ecosystem respiration throughout the Holocene (Yu et al., 2010). Saturated conditions also restrict decomposition rates and result in methane (CH₄) production, making peatlands globally important sources of atmospheric CH₄ (Bousquet et al., 2006). Therefore, efforts to understand peatland carbon (C) exchange dynamics are important toward constraining estimates of the current and future climate feedbacks with these ecosystems (Frolking et al., 2011; Limpens et al., 2008; Wu and Roulet, 2014). The majority of the world's peatlands are located in the high-latitude Northern Hemisphere zones (Roulet, 2000) and consequently, most research has been conducted in these regions (Frolking et al., 2011). Studies from Southern Hemisphere systems, therefore provide valuable contributions to the international peatland literature and improve understanding of an understudied ecosystem type.

Typically, Northern Hemisphere bogs are thought to be constrained to regions with high summer precipitation (> 250 mm) and low mean annual temperatures (< 2 °C) (Charman, 2002; Glaser and Janssens, 1986; McGlone, 2009; Vitt, 1994). However, mean annual temperatures in northern New Zealand are much higher (e.g., 14 °C at Kopuatai), suggesting the above descriptors are insufficient to explain the distribution of restiad peatlands. A more important factor may be the degree to which peatland vegetation restricts evaporation rates below potential evaporation (Admiral et al., 2006). For example, Mer Bleue bog in

Ontario, Canada, exhibits substantially deeper summer water tables than restiad bogs of northern New Zealand during average climatic years but growing season precipitation was similar to or greater than evaporation for that site (Lafleur et al., 2005b). The *E. robustum* – dominated peatlands of the North Island of NZ developed under often large potential summer water deficits and warm mean annual temperatures (~14 °C) (McGlone, 2009). Therefore, the conservative evaporation rates exhibited during dry conditions in northern NZ peatlands (Campbell and Williamson, 1997), may be critical in keeping water tables high (Hodges and Rapson, 2010) and consequently in sustaining C (i.e. peat) accumulation (this study). The globally distinctive peat-forming vegetation dominating northern NZ peatland systems makes them ideal for expanding our understanding of peatland processes that has largely been informed by studying Northern Hemisphere systems.

In addition, NZ peatlands are a potentially important component of regional and national carbon budgets (Tate et al., 2005). However, there is very little information on which to assess the current status of carbon and greenhouse gas exchanges or future responses to changing climate. Furthermore, the majority of all New Zealand's wetland areas have been drained and converted to agricultural land (McGlone, 2009; Pronger et al., 2014). Pasture-converted peatlands in northern NZ are CO₂ neutral or annual CO₂ sources (Campbell et al., 2015; Nieveen et al., 2005) but little is known about the C balance and associated controls in unaltered NZ peatland remnants.

My aim in this research was to quantify the net carbon balance and to understand the sensitivity of the gaseous component fluxes to climatic drivers in

a Southern Hemisphere restiad peatland. I achieved this using continuous measurements of ecosystem-scale CO₂ and CH₄ fluxes at Kopuatai bog in the Hauraki Lowlands of the North Island, New Zealand from late 2011 to mid 2014. To understand NECB dynamics of this peatland site, I began with analysis of GPP. This is the largest term and sole C input to the carbon balance of Kopuatai. In addition to its direct influence on annual peatland NECB, the C fixed by surface vegetation influences both CO₂ respiration rates and CH₄ production via substrate supply as root exudation of labile carbon compounds in the peat profile on short time scales (Ström et al., 2003; Whiting and Chanton, 1992) and by decaying litter in surface peat on longer time scales (Frolking et al., 2010). The main C loss pathway was via ER, which is largely controlled by water table depth and temperature in peatlands (Campbell et al., 2014; Dimitrov et al., 2010; Lafleur et al., 2005a) and as such, the consideration of ER at Kopuatai was crucial for understanding the overall NECB response to drought. Methane fluxes were analysed in detail separately as well as in relation to the overall NECB. The data I have presented are the first ecosystem-scale methane flux data from a New Zealand peatland and expand the range of climatic, biotic, and hydrologic settings covered in published peatland methane flux literature. The methane flux data are not only important to understanding C and greenhouse gas budgets of New Zealand peatlands, but also provide some insights relevant to the international peatland community.

My main objectives at the outset of this research were to:

1) determine magnitudes and drivers of gross primary production (GPP) , which is the sole C input at Kopuatai (and usually the largest peatland C input), from half-hourly to weekly timescales;

2) quantify annual methane fluxes and determine the relative importance of temperature and water table depth in driving daily to annual temporal variability;

3) couple CO₂ and CH₄ fluxes to develop a full carbon balance for Kopuatai and explore the effects of drought on each carbon balance component at monthly to annual timescales, with a particular focus on CO₂-C components (ER and GPP).

6.2. Net ecosystem C balance of Kopuatai bog

Although each of the three objectives outlined above are specifically addressed in the main results chapters, for coherence here, I have presented the summary of CO₂ component fluxes separately from CH₄ fluxes. Furthermore, as the CO₂ components (gross primary production (GPP) and ecosystem respiration (ER)) dominated the net ecosystem carbon balance (NECB) at Kopuatai in both years, I have included the primary summary of NECB in line with these components.

6.2.1. CO₂-C components

Using eddy covariance measurements of CO₂ and CH₄ fluxes and a water balance approach to estimating dissolved organic C export via sub-surface water flow (Sturgeon, 2013), I found that the NECB of Kopuatai bog is exceptionally large (annual gains of 74.5 – 152.5 gC m⁻² yr⁻¹) when compared to Northern Hemisphere bogs and fens, which typically range from gains of 90 gC m⁻² yr⁻¹ to losses of 15 gC m⁻² yr⁻¹ (Koehler et al., 2011; Nilsson et al., 2008; Roulet et al.,

2007). The main reason for this was large annual net CO₂ uptake resulting from very long growing seasons relative to Northern Hemisphere peatlands where plant growth is restricted by freezing winters (Adkinson et al., 2011; Griffis et al., 2000; Humphreys et al., 2014; Lafleur et al., 2003) or kept low due to winter light limitation (Sottocornola and Kiely, 2010).

The largest component of Kopuatai bog's C balance was GPP, which ranged between 30 and 110 gC m⁻² mo⁻¹ throughout the study period. Furthermore, the maximum photosynthetic potential was essentially constant among seasons. GPP was limited by light and temperature, which drove seasonality, whereas maximum plant uptake was constrained by high vapour pressure deficit during clear-sky periods, primarily in summer months. This plant response to elevated VPD is generally enacted to reduce transpiration water losses by stomatal closure, which restricts CO₂ assimilation (Körner, 1995). Although the lowered water tables during drought months did not seem to control GPP directly, the increased frequency and duration of high VPD during drought months did reduce the overall carbon budget during two summers with less than average precipitation.

ER was the second largest component of the NECB and was strongly driven by temperature and water table depth. Respiration was low during 2012 when the water table remained within 15 cm of the peat surface. However, when the water table lowered during the summer and autumn drought conditions of 2013 and 2014 monthly ER increased by 23% compared to 2012 with a consequent reduction in the overall C balance. Mean diurnal net ecosystem exchange (NEE) from Kopuatai revealed that night time NEE (i.e. ER) during drought months was

similar to that measured at Moanatuatua bog, where water tables were much lower (~80 cm below the surface) (Campbell et al., 2014). This simple comparison may offer insights into peatland restoration. The water table at Moanatuatua may have been impacted by surrounding land drainage but may also be naturally lower due to the hydrological setting (Campbell et al., 2014; Kuder et al., 1998) and, although long-term drainage effects are not directly equivalent to a summer drought, any similarities in C fluxes between the two peatlands are worth considering. Differences in vegetation must also be taken into account since higher green plant area index (GAI) at Moanatuatua may contribute to higher autotrophic respiration (i.e. more respiring plant surface area) (Lund et al., 2010). Nonetheless, this comparison suggests that ER may be constrained by low moisture at Moanatuatua, whereas any potential moisture constraint at Kopuatai remains undetermined. Future research at Kopuatai should address whether continued lowering of the water table below 30 cm from the surface (the deepest water table observed in this study) results in continued increase in ER or determine the water table depth at which ER becomes moisture limited. This will determine whether continued water table drawdown would temper the effects of drought on future carbon storage capacity by limiting ER or would enhance the effects by further increasing it.

Droughts are recognized as the most important driver of inter-annual variation in both peatland CO₂ and CH₄ exchange (Lafleur, 2009). In New Zealand, a long-term trend of increasing summer atmospheric pressure has been identified, suggesting greater persistence of blocking high-pressure weather systems (MPI, 2013). Such synoptic behaviour is generally a good indicator of clear-skies that

lead to high radiation and VPD as well as lowered water tables, although difficult to predict with models (Parsons et al., 2014). Nonetheless, any such trend in synoptic-scale climate variability will determine how often New Zealand bogs are subjected to extended clear-sky periods when high VPD reduces plant CO₂ uptake. Furthermore, greater frequency of droughts is also projected (Clark et al., 2011) and the reduced precipitation that causes lowered water tables will likely increase peat respiration based on the results I have presented.

Despite the reduced C sink strength of Kopuatai bog during drought, the relatively large drought-year NECB (74.5 gC m⁻² yr⁻¹) suggests some degree of drought resilience. This is perhaps the major aspect that sets restiad peatlands apart from Northern Hemisphere bogs and fens. Peat accumulation remains substantial, albeit reduced, even during drought years with the most extreme summer water deficits. Therefore, *E. robustum*-dominated peatlands may be placed at one end-point of the peatland drought response continuum, discussed in Chapter 5, from a C balance perspective in order of increasing vegetative drought resilience: *Sphagnum* < sedge/grass < shrub/tree < *E. robustum*.

6.2.2. CH₄ fluxes

Ecosystem methane fluxes were severely reduced during drought months from ~100 mg m⁻² day⁻¹ to ~20 mg m⁻² day⁻¹, when the water table was lowered.

Although the contribution of methane flux to the NECB was small, it is critical to understand the drivers of methane flux variability from the perspective of peatland biogeochemistry and greenhouse gas exchange. There are very few data sets of continuous ecosystem-scale CH₄ fluxes from peatlands that cover drought periods (Brown et al., 2014). However, many studies utilizing

incubations, mesocosms, and chamber work have investigated drought effects on peatland methane production and flux, providing a basis for interpreting results at the ecosystem scale (Blodau and Moore, 2003; Estop-Aragonés and Blodau, 2012; Knorr and Blodau, 2009; Moore and Roulet, 1993; Tian et al., 2012; Yavitt, 2013). At Kopuatai, there was not only a reduction in methane flux with lowered water tables but also a delayed recovery of fluxes after water table recharge in autumn. The drought effects on CH₄ flux therefore extended several months after water table recovery. There are a number of potential mechanisms for this delayed response (discussed more fully in Chapter 4) but the cause and length of recovery time-scale need to be investigated with controlled experimentation.

A key finding with regard to methane flux at this peatland was the sensitivity to very small variations in water table depth. For example, drought conditions that led to water table reductions of less than 15 cm resulted in up to 80% reductions in methane flux. This is a very small water table depth range when considering reported methane flux datasets from Northern Hemisphere peatlands and their response to water table fluctuations (Turetsky et al., 2014). For example, Brown et al. (2014) observed that the water table dropping from 30 cm to 50 cm below the surface led to increases in methane fluxes and these fluxes were not reduced until the water table dropped below 50 cm from the surface.

Furthermore, there was a strong influence of water table variations over synoptic-scale time periods at Kopuatai. As the water table rose and fell within the top 10 cm of peat after rain events in spring and early summer, there were consistent increases in flux, which peaked roughly 10 days following rain. This

behaviour is consistent with a highly constrained zone at that depth where methane production potential is highest (see Chapter 5). The location and bounds of this zone have important implications for ecosystem-scale CH₄ fluxes given that water table depth determines access to substrate of both aerobic and anaerobic decomposers. Furthermore, the extended exposure of this zone to oxygen, such as during drought conditions observed here, led to severe and extended reductions in flux magnitudes, potentially illustrating the sensitivity of the methanogenic community at this site. However, to identify the primary limitation of methanogenesis during drought recovery we need to better understand the CH₄ production potential with depth, and the response of the methanogenic community to changing redox conditions and presence of alternative electron acceptors.

6.3. Broader implications

6.3.1. Peatland radiative forcing

The peatland-atmosphere exchanges of CO₂ and CH₄ are important from both a C and greenhouse gas source/sink perspective. Both CO₂ and CH₄ play a role in radiative forcing but determining the relative importance of emission or storage of each gas ultimately depends on timescale and relative emission magnitudes of both gases. The climate effect of greenhouse gas emissions is often assessed using the global warming potential (GWP) approach developed by the IPCC (1990). The change in radiative forcing resulting from a pulse emission of a greenhouse gas is estimated based on the direct effects (potential for direct radiation absorption and atmospheric lifetime) and indirect effects (relevant atmospheric interactions) considered over a particular time-span (Forster et al., 2007; Ramaswamy et al., 2001). The standard used in most emissions

considerations is a 100-year time horizon. Thus atmospheric CH₄ is generally considered to be 28.5 times more potent as a greenhouse gas than CO₂, because over a 100-year time span, a molecule of CH₄ emitted from the surface will result in 28.5 times the radiative forcing of a molecule of CO₂ (IPCC, 2013).

Using GWP factors (associated with a 100-yr time horizon), peatland researchers have estimated that annual fluxes of CH₄ from peatlands can often offset the carbon gains from net CO₂ uptake depending on latitude and environmental conditions in a given year (Friborg et al., 2003; Roulet, 2000; Whiting and Chanton, 2001). However, Frolking et al. (2006) compared the radiative forcing impact of sustained peatland CH₄ flux and carbon sequestration over the 'lifetime' of a peatland with a simple atmospheric box model. They showed that from the time of peatland formation, the sustained CH₄ emissions dominate the radiative forcing signal for about 50-100 years before the methane effect stabilizes due to a relatively short atmospheric lifetime (~12 years) and the CO₂ uptake effect continues to accumulate leading to net atmospheric cooling. The switchover time, from net warming to cooling, depends on the ratio of annual CH₄ flux to CO₂ uptake. Expanding on this methodology, Frolking and Roulet (2007) showed that the radiative forcing of northern peatlands throughout the Holocene was likely somewhere between -0.2 to -0.5 W m⁻², a substantial cooling effect given that total estimated radiative forcing of human activities since the industrial revolution was 2.3 W m⁻² (IPCC, 2013).

If the standard 100-year GWP factor is applied to the annual CH₄ fluxes from Kopuatai bog, the result suggests that this peatland had a net warming effect on the atmosphere in both full measurement years. This is a surprising conclusion

considering the large annual NEP compared to Northern Hemisphere bogs (Roulet et al., 2007) and the very deep peat deposits that have accumulated over Kopuatai bog's 14,000-year development (Newnham et al., 1995), both of which would normally be associated with cooling effects through removal of atmospheric carbon. For example, the CH₄ emission to CO₂ uptake ratio was ≈ 0.1 for both full measurement years in this study. A constant emission ratio of 0.1 from peatland formation throughout the Holocene would result in a switch from positive to negative radiative forcing after roughly 300 years, and that the peatland would then have a continued cooling effect on the atmosphere (Frolking et al., 2006). However, this ratio would not likely remain constant over the lifetime of a peatland due to fen-bog transition (Hodges and Rapson, 2010) and vegetation succession (Clarkson et al., 2004). Nonetheless, while short-term changes to CH₄ emissions can lead to abrupt changes in peatland radiative forcing, changes in CO₂ dynamics, while dampened in the short-term, are cumulative and much longer-lasting (Frolking and Roulet, 2007).

Radiative forcing considerations have important implications for peatland restoration efforts because the carbon balance – and thus the ratio of CH₄ emission to CO₂ uptake – should be considered a key aspect of a functioning peatland. The loss of carbon due to peatland drainage for agriculture in New Zealand (Campbell et al., 2015; Nieveen et al., 2005; Pronger et al., 2014; Schipper and McLeod, 2002) likely has a profound impact on the relationship between that peatland and the climate system (Frolking and Roulet, 2007; Frolking et al., 2006). Thus the transient warming impact of CH₄ emissions upon re-wetting/re-establishing a peatland is trivial compared to the need to restore

the peatland's ability to accumulate carbon. Furthermore, Shoemaker and Shrag (2013) illustrated the dangers of over-valuing the climate impact of CH₄ compared to CO₂ if the ultimate goal is to slow the warming effects of anthropogenic activities. Similar to Frolking et al. (2006), Shoemaker and Shrag (2013) point out that the climate impact of CO₂ emissions is cumulative whereas methane emission effects on climate are short-lived and diminish after ~50 years. They acknowledge that short-lived greenhouse gases have an important role in climate but stress that focusing on CO₂ reduction would have a greater long-term impact. Reductions in CH₄ emissions may delay further climate warming for the next 50 years, but if the atmospheric burden of CO₂ is allowed to increase, the cumulative warming due to CO₂ will become dominant and non-reversible. Furthermore, the inherent timescale dependence may preclude any effective comparison between CO₂ and CH₄ impacts on climate and Shoemaker and Shrag (2013) suggest it will always be better in the long run to focus on reducing atmospheric CO₂ concentration or slowing its rate of increase.

6.3.2. Relevance to long-term peatland carbon accumulation rates

The long-term carbon accumulation rates in peatlands are estimated using cores to obtain the age of peat stored at various depths down to the basal peat, combined with estimates of peat carbon content and bulk density (Gorham, 1991; Turunen et al., 2002; Yu et al., 2010). Measurements of contemporary carbon fluxes above the peat surface have been compared to long-term carbon accumulation rates (e.g., Flanagan and Syed, 2011; Roulet et al., 2007). In making this comparison, one assumes that the contemporary mass-balance approach at the surface is analogous to determining how much carbon will be

deposited permanently at that stage in the peatland's development. For instance at Mer bleue bog in Ontario, Canada, Roulet et al. (2007) found reasonably good agreement between their NECB measurements and the long-term carbon accumulation rates estimated from peat cores at that site. At Kopuatai, the long-term rate of carbon accumulation (LORCA) can be estimated from peat core data collected by Newnham et al. (Newnham et al., 1995) as approximately $46 \text{ gC m}^{-2} \text{ yr}^{-1}$ over the past 700 years, with longer-term rates of $7 - 20 \text{ gC m}^{-2} \text{ year}^{-1}$. Schipper and McLeod (2002) also used tephra deposits of well-known age within Moanatuatua bog (60 km from Kopuatai) to estimate a carbon accumulation rate of $34 \text{ gC m}^{-2} \text{ yr}^{-1}$ over the past 1800 years. In contrast, measurements of NECB for 2012 and 2013 at Kopuatai were much larger (152.6 and $74.5 \text{ gC m}^{-2} \text{ yr}^{-1}$, respectively). If we assume the contemporary NECB should be similar to longer-term rates of accumulation, then there are a number of hypotheses that can be raised to reconcile the differences between these estimates at Kopuatai including fire recovery stage, volcanic tephra deposition, and fen-bog transition with subsequent succession.

Fire recovery stage of peatland vegetation has a strong influence on the annual carbon balance (Turetsky et al., 2002) and, in New Zealand peatlands, the frequency of fire has been estimated from charcoal deposits throughout the profile to be once every 100 to 700 yrs (Newnham et al., 1995). Fires in New Zealand peatlands can burn off standing biomass and shallow surface peat layers, although the depth of burned peat is restricted by high water tables (Clarkson, 1997). Consequently, measured NECB during non-burn years will always be greater than estimates of long-term C accumulation from peat cores.

The discrepancy between the measured contemporary NECB using eddy covariance and the long-term accumulation from cores may further depend on the current position along the fire recovery curve due to succession and subsequent resumption of peat accumulation (Clarkson, 1997).

Similarly, volcanic tephra deposition is well-documented in New Zealand peatlands (17 widespread tephra layers deposited within 15,000 BP) (Lowe et al., 2013; Newnham et al., 1995). Sufficiently thick volcanic ash deposits can suppress plant growth or even cause substantial die back (Burnham, 1993; Whittaker et al., 1992). If peatlands are similarly impacted, the recovery from tephra deposition events may be analogous to fire-recovery, making comparisons between contemporary NECB and long-term accumulation rates very time-dependent. Peat accumulation rates may also be strongly dependent on the natural successional phase of the peatland (Holmquist and MacDonald, 2014; Packalen and Finkelstein, 2014). As Kopuatai bog developed through fen-bog transitions (Hodges and Rapson, 2010) and vegetation succession with age (Clarkson et al., 2004), it is unlikely that peat accumulation rates were constant. Comparisons of contemporary NECB between mid-successional *E. robustum*-dominated Kopuatai bog and late-successional *S. ferrugineus*-dominated Moanatuatua may provide some insight into the carbon allocation of these two successional phases of New Zealand bog development. For instance, both peatlands exhibit relatively large annual net CO₂ uptake (Campbell et al., 2014; this study) when compared to Northern Hemisphere bogs (e.g., Humphreys et al., 2014) but C allocation to growing biomass relative to accumulating peat may be different. Understanding successional transitions is crucial in determining the

efficacy of comparing contemporary NECB to long-term carbon accumulation and more work is clearly needed toward this goal.

In fact, some suggest we should reject the assumption that contemporary NECB should match the long-term carbon accumulation rates estimated from peat cores. Frohking et al. (2014) argue that contemporary measurement records of peatland NECB are not yet long enough to relate to actual peat accumulation rates estimated from cores. Furthermore, NECB measurements include fluxes resulting from the decomposition of the entire peat column and production by the canopy, which precludes isolating only the contribution of peat accumulating at the surface (i.e. over the period being measured) (Frohking et al., 2014). To address these issues, models of peat accumulation parameterized by peat core data and informed by contemporary information about carbon exchange processes can be used to investigate changes in peat accumulation rates over the lifetime of a peatland with respect to available climate records and/or under various disturbance scenarios (Frohking et al., 2010). However, such models have yet to be tested in New Zealand peatlands, presenting an important future research opportunity.

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Appendix A Research site images



Figure A2. Aerial photograph of Kopuatai oriented approximately southeast. Eddy covariance flux tower site location is highlighted by the red circle. Photo by J.P. Goodrich.

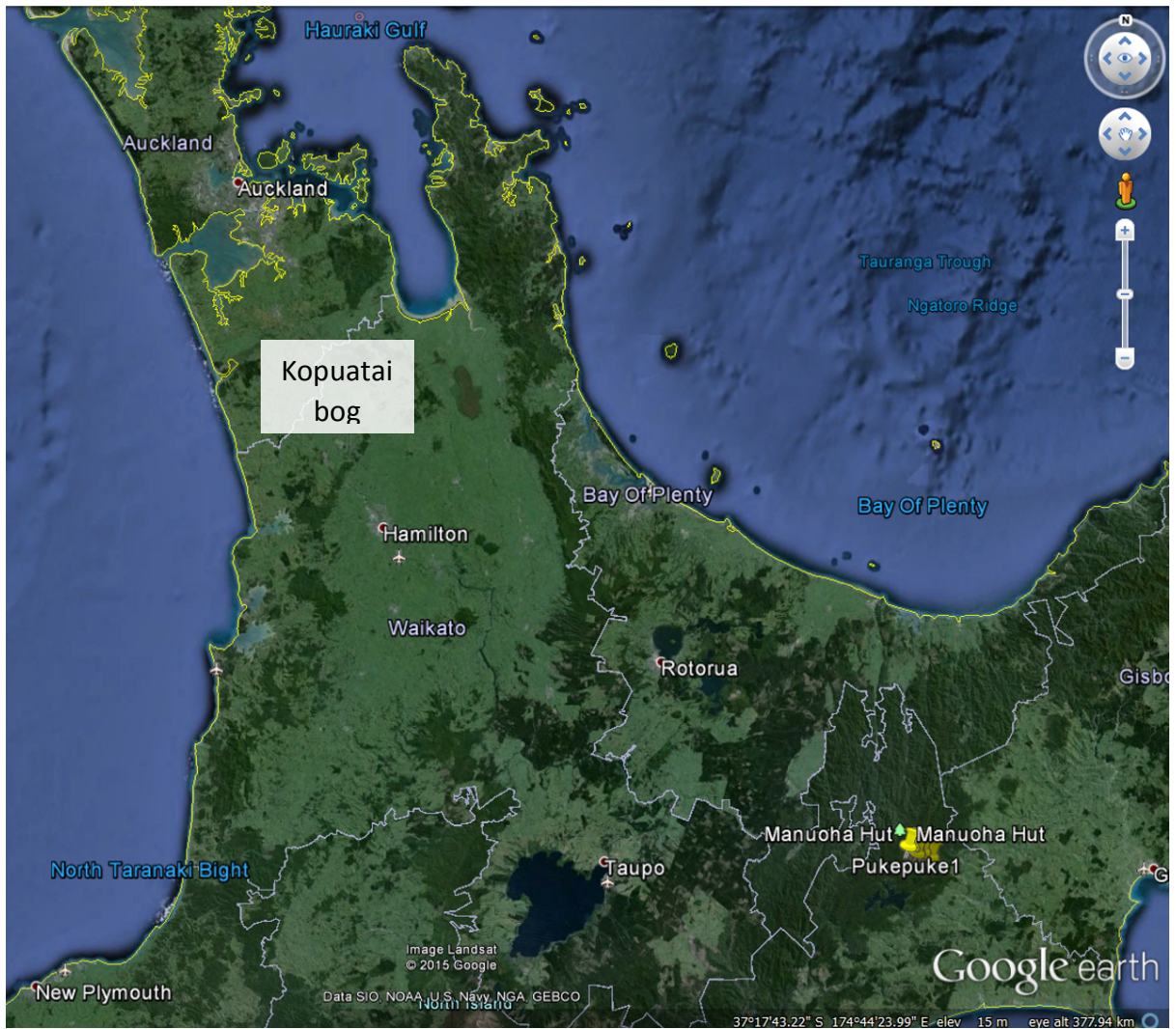


Figure A1. Google Earth screenshot of North Island, New Zealand showing location of Kopuatai bog.



Figure A3. Photograph of the Kopuatai eddy covariance tower set-up. Photo by J.P. Goodrich.

Co-Authorship Form

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Please indicate the chapter/section/pages of this thesis that are extracted from a co-authored work and give the title and publication details or details of submission of the co-authored work.

As it stands in the submitted thesis, Chapter 3 has been published by the Journal Agricultural and Forest Meteorology. The title of the published article is the same as the title of the thesis chapter: High vapor pressure deficit constrains GPP and the light response of NEE at a Southern Hemisphere peatland.

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by PhD candidate

Collected, processed, and analyzed data, including creation of figures used for this work.
Wrote the manuscript/thesis chapter.

Extent of contribution
by PhD candidate (%)

90%

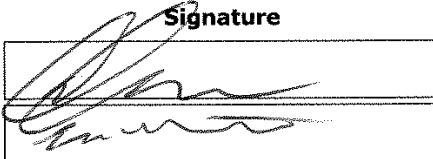
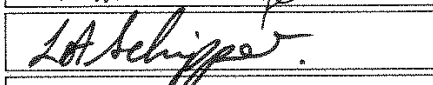
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Dave Campbell	Project conception; collaboration on data interpretation and visualization; provided substantial comments and editing of numerous versions of the manuscript/thesis chapter.
Mike Clearwater	Collaboration on data interpretation and visualization; provided substantial comments and editing of versions of the manuscript/thesis chapter.
Susanna Rutledge	Collaboration on data interpretation and visualization; provided substantial comments and editing of versions of the manuscript/thesis chapter.
Louis Schipper	Collaboration on data interpretation and visualization; provided substantial comments and editing of versions of the manuscript/thesis chapter.

Certification by Co-Authors

The undersigned hereby certify that:

- ❖ the above statement correctly reflects the nature and extent of the PhD candidate's contribution to this work, and the nature of the contribution of each of the co-authors; and
- ❖ in cases where the PhD candidate was the lead author of the work that the candidate wrote the text.

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Please indicate the chapter/section/pages of this thesis that are extracted from a co-authored work and give the title and publication details or details of submission of the co-authored work.

As it stands in the submitted thesis, Chapter 4 has been accepted for publication in the *Journal of Geophysical Research – Biogeosciences* pending minor revisions. The title of the accepted article is the same as the title of the thesis chapter: **Regulation and magnitude of daily to annual methane fluxes from a Southern Hemisphere raised bog**, although this may change upon revision.

Nature of contribution by PhD candidate	Collected, processed, and analyzed data, including creation of figures used for this work. Wrote the manuscript/thesis chapter.
Extent of contribution by PhD candidate (%)	90%

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Please indicate the chapter/section/pages of this thesis that are extracted from a co-authored work and give the title and publication details or details of submission of the co-authored work.

As it stands in the submitted thesis, Chapter 5 is being prepared for submission to the Journal Ecosystems. The title of the manuscript in preparation is the same as the title of the thesis chapter: Drought resistance allows a Southern Hemisphere raised bog to persist as a strong carbon sink. Although the title may change in subsequent revisions.

Nature of contribution
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Wrote the manuscript/thesis chapter.

Extent of contribution
by PhD candidate (%)

90%

CO-AUTHORS

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Louis Schipper	Collaboration on data interpretation and visualization; provided substantial comments and editing of versions of the manuscript/thesis chapter.

Certification by Co-Authors

The undersigned hereby certify that:

- ❖ the above statement correctly reflects the nature and extent of the PhD candidate's contribution to this work, and the nature of the contribution of each of the co-authors; and
- ❖ in cases where the PhD candidate was the lead author of the work that the candidate wrote the text.

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