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High vapor pressure deficit constrains GPP and the light response of NEE at a Southern Hemisphere bog

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ABSTRACT

We used eddy covariance measurements of net ecosystem CO_2 exchange (NEE) in an undisturbed New Zealand bog to determine the major controls on gross primary production (GPP). In particular, we were interested in the relative importance of air temperature, saturation vapor pressure deficit (VPD), and diffuse fraction of incoming radiation (f_{diff}) in driving increases and restrictions to ecosystem photosynthesis. We found that NEE light response parameters for this peatland were remarkably similar year-round. We used four different light response functions to explore the influence of driving meteorological variables on daytime CO_2 uptake. This revealed that including VPD as a model input reduced the bias associated with estimates of NEE relative to the standard rectangular hyperbola. An apparent temperature restriction of light-saturated photosynthetic capacity was relieved when high VPD data were excluded from light response curve fits. We thus, utilized the model that incorporated VPD to fill gaps in daytime NEE data and to estimate GPP. Increases in mid-day GPP were associated with increasing total photosynthetic radiation and air temperature, especially during winter and spring/autumn seasons. However, in summer, mid-day GPP was capped by high VPD, likely due to a stomatal response triggered to reduce transpiration water losses. Although GPP did not directly respond to f_{diff}, both temperature and VPD were coupled to sky conditions. Furthermore, the highest mid-day mean GPP for high light levels always occurred during the periods of highest f_{diff}. These results have important implications for the future C sink strength of New Zealand peatlands given a trend toward drier summers with clearer skies.

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 CO_2 (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 among 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 among 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

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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 CO_2 exchange and, particularly, the controls on GPP.

Daytime NEE in terrestrial ecosystems is largely controlled by radiation, temperature, saturation vapor 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 with 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 CO_2 assimilation (Körner, 1995). High temperatures above an optimum can also lead to reduced photosynthetic rates (June et al., 2004) and contribute to reduced CO_2 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 CO_2 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 CO_2 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 CO_2 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 CO_2 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).

2. Methods

2.1. Site description

Kopuatai is a raised ombrotrophic peat bog that covers approximately 96 km^2 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 m^2) were destructively sampled for biomass and green area, resulting in an average (±standard deviation) of 0.39 (±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 m^2 m^{-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 (±standard deviation) total GAI of 1.32 ± 0.32 m^2 m^{-2} with range 0.90–2.0 m^2 m^{-2}.

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: 37.388S, longitude: 175.554E). 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 CO_2 and H_2O concentration, and three-dimensional wind data, respectively. The system was controlled with a CR3000 data log-