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Hydroclimatic influences on peatland CO₂ exchange following upland forest harvesting on the boreal plains

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Hydroclimatic Influences on Peatland CO2 Exchange Following Upland Forest Harvesting on the Boreal Plains

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1	Hydroclimatic Influences on Peatland CO ₂ Exchange Following Upland
2	Forest Harvesting on the Boreal Plains
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1 Abstract

A comparative study of forest clear-cut logging effects on daily growing season (May to October) net ecosystem CO₂ exchange (NEE) of adjacent peatlands was conducted in two neighbouring forest upland-peatland complexes over four-years (2005 to 2008) on the Boreal Plains (BP) of Alberta, Canada. Higher vapour pressure deficit at the harvested-upland (H-U) peatland, reflecting increased turbulent mixing after adjacent upland forest removal (2007 and 2008), resulted in increased peatland evapotranspiration rates that contributed to a seasonal decline in soil moisture (VMC) influencing NEE. Overall, a significant change in mid-season *NEE* occurred at the H-U peatland one-year post-harvesting, greater than *NEE* changes at the neighboring intact-upland peatland. However, two years post-harvesting, mid-season NEE returned to within range of pre-harvesting variability (-0.54 to 1.34 g CO₂-C m⁻² d⁻¹). Results of this study demonstrate that BP peatland NEE is largely regulated by site-specific water availability, which in turn, may be influenced in the short-term by shifting microclimate and soil moisture patterns due to clear-cut logging. As such, predicting long-term carbon storage function of BP peatlands will require careful consideration of changing hydroclimatic conditions due to rapid expansion of BP deforestation, given that these ecosystems already exist in a state of hydrologic risk in this moisture deficit eco-region.

19 Key Words: NEE, CO₂, peatland, forest harvesting, boreal forest, soil moisture, microclimate

1 Introduction

Peatlands and wetlands cover up to 50% of the land surface on the Boreal Plains (BP) and store a significant portion of carbon in Canada (Timoney, 2003; Kuhry et al., 1993). The BP of western Canada is experiencing extensive deforestation by timber harvesting (clear-cut) as well as road and corridor construction from industrial oil and gas expansion (Timoney, 2003). Forests regulate the microclimatic and hydrologic conditions (incoming solar radiation, wind velocity, turbulence, temperature and moisture of the air and soils) of edge and adjacent ecosystems (Chen et al., 1993; Flesch and Wilson, 1999; Petrone et al., 2007; Markfort et al., 2014). Rapid harvesting of upland forests may threaten the hydroclimatic stability of the already hydrologically tenuous adjacent peatland ecosystems on the BP (Solondz et al., 2008; Brown et al., 2010). While BP forest disturbance research has focused primarily on harvested areas and the associated water and carbon dynamics of the disturbed forest soils (e.g. Amiro et al., 2006; Petrone et al., 2015; Whitson et al., 2005; Carrera-Hernández et al., 2011), the potential impacts on the terrestrial-atmosphere exchange of water and carbon dioxide (CO_2) in adjacent peatlands remains unknown. Given the importance of peatlands for BP carbon storage and water supply (Ferone and Devito, 2004; Smerdon et al., 2005; Solondz et al., 2008;), understanding how these peatlands respond to upland clear-cut logging is fundamental to improving the design and implementation of landscape management and forestry practices across this eco-region (Johnson and Miyanishi, 2008).

Previous studies examining carbon exchange in peatlands show that soil temperature and
moisture conditions are well coupled to carbon losses (plant respiration and soil decomposition)
and carbon uptake (plant productivity) at both the plot-scale and ecosystem-level (Solondz *et al.*,
2008; Bubier *et al.*, 1998, 2003; McNeil and Waddington. 2003; Petrone *et al.*, 2011). The net

balance between CO₂ uptake and release (Net Ecosystem Exchange, NEE) is generally highest (i.e. increased net CO₂ release) under the most favourable conditions for microbial decomposition (i.e. warm, low moisture oxic peat) (Solondz et al., 2008; Bubier et al., 1998; Silvola et al., 1996). Although the impact of land use changes on peatland water cycling and NEE are widely investigated in peatlands on the Boreal shield of eastern Canada (e.g. Waddington and Price 2000; Tuittila et al., 1999), limited work on the response of peatland hydrology and/or trace gas exchange to anthropogenic disturbances exists on the BP of western Canada (Strack et al., 2014). Heterogeneous glacial deposits along with the sub-humid climate of the BP, whereby precipitation roughly equaling potential evapotranspiration, results in water table positions and soil moisture gradients that are not under topographic control (Devito *et al.*, 2005). As such, it is unknown if shifts in peatland moisture conditions, soil temperature and carbon dynamics in response to disturbance events observed in the runoff-dominated shield can be extrapolated to peatlands in the complex hydrology of the sub-humid climate of the BP.

Forest cutblocks experience higher wind speeds, short-wave radiation, air temperatures and lower atmospheric moisture relative to within forest canopy stands (Chen et al., 1993). Abrupt transitions between flat surfaces (e.g. cutblocks) and forest canopies or between vegetation types within a landscape can dynamically alter the atmospheric boundary layer and turbulent flow patterns across the transition zones (Markfort et al., 2014; Yang et al., 2006; Flesch and Wilson, 1999). As such, clear-cut logging has the potential to alter the microclimate conditions in adjacent peatlands to influence evapotranspiration (ET) and ecosystem water loss (Petrone et al., 2007; Helgason and Pomeroy, 2005; Helgason and Pomeroy, 2012; Wharton et al., 2010; Monteith, 1965). Given that subtle changes in ET can result in soil moisture deficits in this sub-humid climate (Devito et al., 2005), shifts in ET are likely to be important to the CO₂ sink or

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source status of BP peatlands. Due to the multitude of compounding hydrological interactions and feedbacks in northern peatlands (Waddington *et al.*, 2015), applying an integrated monitoring approach of hydrology, microclimate and CO_2 exchange is essential to evaluate the natural baseline ecohydrological conditions of BP peatlands (e.g. Solondz *et al.*, 2008) and to compare the potential impact of adjacent forest disturbance on the complex hydroclimatic and biogeochemical factors governing peatland *NEE*.

Long-term CO₂ exchange is coupled to atmospheric processes (Lafleur *et al.*, 1997). Increased summer warming in recent decades observed in western Canada (Gullet and Skinner, 1992) along with projections of rising global temperatures and greater drought frequency in Boreal regions suggests a future reduction in CO_2 sequestration by Boreal peatlands (Intergovernmental Panel on Climate Change (IPCC) 2014; Gorham, 1991). As such, understanding the short-term NEE response of BP peatlands to forest disturbances in the context of climate variability is essential to facilitate effective predictions of the long-term fate of these large carbon stores. Due to the large area of the BP covered by peatlands, establishing the relationships between clear-cut logging, peatland hydroclimate and NEE at the peatland-scale could provide the means to simplify and extrapolate the carbon functioning of these ecosystems to the landscape-scale and generalize peatland responses to disturbance by monitoring clear-cut areas across the eco-region. As such, the objectives of this study were to examine: (1) NEE of BP peatlands during the snow-free period; (2) the relative impact of upland clear-cut logging on adjacent peatland NEE, including the hydrologic and microclimatological controls on this exchange; and (3) estimate the sustainability of BP peatlands' functionality as a CO₂ source or sink in context of periodic land use disturbances and climate change.

23 Methods

Two adjacent forested-peatlands, one with an intact adjacent forested upland (I-U) and one with a harvested upland (H-U), were examined in this study located in the Utikuma Region Study Area (URSA) near Utikuma Lake, north-central Alberta, Canada (56° 20'N, 115° 30' W; Figure 1). The two complexes are located on a disintegration ice moraine landform (Paulen et al., 2004), within the Central Mixedwood Natural sub-region of the Boreal Forest in Alberta (Natural Regions Committee 2006) or Mid-Boreal Uplands Ecoregion of the Boreal Plains Ecozone Alberta, Canada (Ecological Stratification Working Group 1996). The climate in this region is characterized by short, warm summers and long, cold winters with a 30-year average annual temperature, precipitation and potential evapotranspiration (PET) for the region as 1.7 °C, 485 mm and 515 mm, respectively (Environment Canada, 2007). The mean annual temperature and precipitation at the study site for 2005, 2006, 2007 and 2008 were 2.5, 2.5, 1.5 and 0.9 °C and 491, 432, 530 and 504 mm, respectively making the study period slightly warmer and drier during pre-harvest and slightly cooler and wetter post-harvest than the 30-year normal. The prevailing wind direction across the study sites was from the South during the four-year study period (Supporting Information S1).

The two peatlands surround shallow ponds (< 1 m depth) and are adjacent to hillslopes with aspen-dominated uplands (up to 7 m above the pond surface) with a canopy height of approximately 17 m to 21 m on average (Brown *et al.*, 2013) and canopy coverage averaging 68% (Chasmer *et al.*, 2010). The peatlands and shallow ponds are located in a recharge zone, and water tables typically grade away from the peatlands into the hillslope (Ferone and Devito, 2004; Redding and Devito, 2008). Vegetation in the peatlands are comparable, composed of a shrub layer comprising mostly *Ledum groenlandicum*, *Vaccinium vitisidaea* and *Chamaedaphne*

calyculata as well as groundcover dominated by bryophyte and lichen species characteristic of
poor fen communities, mainly *Sphagnum* species and feather mosses (Solondz *et al.*, 2008;
Petrone *et al.*, 2011). A similar open canopy of black spruce (canopy coverage averaging 36 to
60% (Chasmer *et al.*, 2010)), approximately 2 m in height, occurs within these peatlands. Peat
physical characteristics (e.g. bulk density, hydraulic conductivity) do not differ between the
peatlands (Petrone *et al.*, 2008). Minimal peat subsidence occurs at these sites and does not
readily respond to water level changes in the peat or adjacent ponds (Petrone *et al.*, 2008).

8 CO₂ Field Measurements

Chamber CO₂ data was collected at ten sites within the harvested-upland (H-U) peatland and six in the intact-upland (I-U) peatland over the four snow-free seasons (Figure 1). At each site 20 cm (diameter) polyvinylchloride (PVC) collars were placed in adjacent lawns (classified as topographically high mounds) and depressions (low lying areas) to capture the range of microtopography in the peatlands and associated differences in CO₂ exchange (Petrone et al., 2011). CO₂ exchange was measured using a dynamic closed chamber system with an Infrared Gas Analyzer (IRGA) (EGM-4, PP Systems, Maryland, USA) (Solondz et al., 2008). Removable clear lexan chambers were fitted to the permanently installed collars, with coolant tubes and fans operating to mimic ambient air temperatures and gradients (Solondz et al., 2008; Welles et al., 2001). For each sample, concentrations of CO_2 ppm were measured at 30 second intervals for 2.5 minutes during 0900-1600 h approximately ten times per month each season. Sampling times at each location were randomly selected during each sampling day to ensure measurements were taken over a wide range of light and temperature regimes that may occur throughout the day. Chambers were covered with an opaque neoprene shroud when measuring the gross respiration $(R_{tot} = autotrophic and heterotrophic)$. Gross ecosystem productivity (*GEP*) was calculated as the

$$GEP = NEE - R_{\rm tot} \tag{1}$$

Negative values indicate a net CO₂ uptake by the peatland, and positive values indicate a net CO₂
release by respiration into the atmosphere.

5 Environmental parameters

Air (T_a) temperature and relative humidity (RH) (PP Systems, Maryland, USA), soil (T_{soil}) temperatures (Omega Engineering, Inc., Connecticut, USA) and photosynthetically active radiation (PAR) (Quantum Sensor; LiCor Inc., Nebraska, USA) were recorded at the same temporal and spatial scales as the CO₂ fluxes. T_a , RH and PAR were measured both inside and outside of the chamber at approximately 0.5 m above the surface during each 2.5-min chamber measurement. Soil (T_{soil}) temperatures were measured at 2, 5, and 10 cm depths and averaged for the values at the three depths. VMC was measured beside each collar using time domain reflectometry (TDR) (Hydrosense Probe, Campbell Scientific, Inc, Utah, USA) to give a bulk soil moisture value over the top 10 cm of the soil profile. The TDR was calibrated in the lab by drying representative undisturbed peat samples to different moisture contents (Solondz et al., 2008). The field point measurements were applied to the chamber CO_2 measurements to determine the modeling of GEP and R_{tot} . Water Table depth (WT), measured in meters below the surface, was recorded weekly using PVC pipe wells (5 cm O.D.) in the peatland and upland at each I-U and H-U site (Figure 1).

20 Meteorological towers (*MET*) located in each peatland (Figure 1) continuously measured 21 environmental parameters during the snow-free period (Day of Year (DOY)): 120 to 280) of

each year. Average *VMC* in the upper 30 cm of the peat was recorded using water content reflectrometry (CS616, Campbell Scientific Inc, Utah, USA) placed vertically in both a lawn and depression. Net radiation (Q^*) was measured at 1.5 m above the peat surface using a net radiometer (NRLite, Kipp and Zonen, The Netherlands). The T_a and *RH* (Vaisala, Finland) were measured at the same height. *RH* was not available at the H-U peatland mid season (DOY 201 to 243) in 2007 and therefore; vapour pressure deficit (*VPD*) was gap filled according to a regression (using all available *VPD* data from *MET* and manual chamber measurements during the post-harvesting period) as a function of T_{air} ,

$$VPD = 0.4748e(0.075T_{air}), r^2 = 0.87$$
 (2)

 T_{soil} was recorded at 2, 5 and 10 cm using thermocouples (Omega copper-constantin, Campbell Scientific Inc, Logan, Utah, USA) in a lawn and depression. Ground heat flux (Q_G) was measured according to the calorimetric method (Halliwell and Rouse, 1987; Petrone and Rouse, 2000; Petrone et al., 2007) using the soil temperature profile and heat capacity calculations for each soil layer (2 to 5 cm and 5 to 10 cm) accounting for changes in moisture content and state (Sutherland et al., 2014). Published values for heat capacities of peat soils under a range of moisture conditions were used in the calculation of ground heat flux (Q_g) (Brown *et al.*, 2010; Oke, 1987; Halliwell and Rouse, 1987; Petrone and Rouse, 2000; Petrone et al., 2007). Horizontal wind speed (u) measurements were collected using cup anemometers (014A, Met One. Oregon, USA) at 1.4 m at both the H-U and I-U sites (Figure 1).

Downstream from a surface discontinuity, such as that from a clear-cut forest to peatland, will create horizontal differences in roughness lengths (Helgason and Pomeroy, 2005). Such differences in momentum sinks will cause large horizontal wind variances in the peatland, which

1 means that mean average wind speeds may not increase but will become more variable in 2 intensity (Helgason and Pomeroy, 2012; Wharton *et al.*, 2010). Thus, horizontal turbulence 3 intensity (I_u) for the peatlands was calculated according to (Turnispeed *et al.*, 2003),

$$I_{\rm u} = \frac{\sigma_{\rm u}}{U} \tag{3}$$

6 where σ_u is the standard deviation of the mean daily horizontal wind speed (m s⁻¹) and U is the 7 mean of the mean daily horizontal wind speed (m s⁻¹) for the peatlands for each year of the study 8 period. Wharton *et al.*, (2010) suggest that this is a more reliable means of assessing changes in 9 turbulent regimes as a result of changing surface condition than more traditional approaches 10 based largely on the friction velocity (u*), which under these conditions may suggest weak 11 turbulent conditions while actual horizontal turbulent fluxes may be large.

12 Evapotranspiration

Surface conductance and aerodynamic measurements from the peatland *MET* and wind velocity
stations (see section above) were utilized to estimate *ET* by applying a standardized reference
Penman-Monteith equation (Chasmer *et al.*, 2011; Temesgen *et al.*, 2005; ASCE-EWRI, 2005),

$$ET = \frac{0.408\Delta(Q^{*}-QG) + \gamma \frac{900}{Ta+273}u (es-ea)}{\Delta + \gamma(1+0.34u)}$$
(4)

18 where *ET* is the daily evapotranspiration rate (mm d⁻¹), Q^* is the daily net radiation (MJ m⁻² d⁻¹), 19 Q_G soil heat flux (MJ m⁻² d⁻¹), T_a is the mean daily air temperature (°C), u is the mean daily wind 20 speed (m s⁻¹), e_s is the mean saturation vapor pressure (kPa), e_a is the actual vapor pressure (kPa),

 γ psychrometric constant (kPa °C⁻¹), 900 and 0.34 are constants for reference type and calculation time (mm d⁻¹) (Chasmer et al., 2011; Fournier et al., 2007; Temesgen et al., 2005; Banaszuk and Kamocki, 2008). Evaluating surface resistance (r_s) from individual chambers based on a Mann-Whitney Rank Sum Test showed no significant difference in r_s between the sites before or after harvesting (U = 34584, p < 0.05). Further, this ET model approach was validated by comparing the seasonal average evaporation rates calculated in this study with previously published ET values, from combined methods of eddy covariance and Priestley-Taylor model, at the H-U peatland in 2005 and 2006 (Brown et al., 2010; Petrone et al., 2007).

Peatland CO₂ modelling

At each peatland, growing season (DOY 120 to 280) CO₂ exchange was estimated using the field point flux measurements of *GEP* and R_{tot} (i.e. combined lawns and depressions). The relationship between GEP and PAR was fitted empirically using a rectangular hyperbola regression (Whiting, 1994; Waddington and Roulet, 1996),

$$GEP = \frac{PAR \cdot Q \cdot GP_{max}}{(PAR \cdot Q + GP_{max})}$$
(5)

where *PAR* is measured μ mol m² s⁻¹, Q is the quantum efficiency that describes the initial slope of the GEP versus PAR hyperbola, GP_{max} is the theoretical maximum rate of GEP, representing the asymptote of the hyperbola. Ecosystem R_{tot} was modeled using a linear regression with average T_{soil} (5 cm depth) according to,

$$R_{\rm tot} = a T_{\rm soil} + b \tag{6}$$

where a and b are parameters fitted by least squares regression. Peatland respiration is strongly

correlated with 5 cm soil temperatures at these sites (Solondz et al., 2008; Petrone et al., 2011) and frequently observed to correlate with soil temperature in other Boreal peatlands (e.g. Bubier et al., 1998). In this study, T_{soil} (5 cm depth) also showed the best overall correlation with R_{tot} of the measured environmental parameters across the four-year study and thus equation 6 was applied to each year for consistency in the model. The daily CO₂ exchange was estimated over the 160-day growing season by applying equations 5 and 6 to daily average PAR and T_{soil} measurements collected from the MET stations at each peatland (see Figure 1) in 2005 through 2008. Although variability in VMC within peatlands may influence T_{soil} , there was a general agreement between T_{soil} and VMC measured at the MET stations (i.e. T_{soil} used for R_{tot} modeling) with T_{soil} and VMC measurements at the chamber sites (Figure S2a and S2b). As such, MET station T_{soil} and VMC were used when analyzing temperature and moisture conditions between years and study sites. With the aim of highlighting differences between peatlands and the response to disturbance (rather than quantifying the exact carbon budgets), modeled GEP and $R_{\rm tot}$ parameters described the field point flux measurements fairly well for most sampling years (Table 1) and were comparable to scatter in GEP and R_{tot} models previously reported (e.g. Bubier et al., 1998; Lafleur, 1999; Petrone et al., 2011; Strack et al., 2014). Residuals from the regressions showed no systematic bias thus, the NEE models did not over- or under- estimate the effect of the harvesting treatment. Uncertainty estimates for NEE were assessed by assigning regression standard errors for the different models used each year.

20 Statistical analyses

21 Microclimatological and carbon exchange rate (*NEE*, *GEP* and R_{tot}) differences between the two 22 peatlands (i.e. I-U versus H-U) were analyzed using Kruskal-Wallis One-Way analysis of 23 variance (ANOVA) on Ranks and *post hoc* Tukey Test (TT), and within each peatland using

Freidman Repeated Measures on ANOVA on Ranks and TT over the four-year study between day of year (DOY) 201 to 243 (i.e. mid-season) due to missing microclimatological data outside this period in some years. Microclimatological parameters with unequal sample sizes within this time period were analyzed using Kruskal-Wallis One-Way ANOVA and *post hoc* test Dunn's Method (DM). Variations in *NEE*, *GEP* and R_{tot} (all available data for each year) were plotted against each environmental parameter to isolate relationships.

RESULTS

Climate and environmental variables

Minimum variability in the WT of the H-U peatland occurred between years, whereby median WT ranged from only 11 to 16 cm depth below surface (DBS) between the pre- and post-harvesting period (Figure 2). Despite relatively small WT fluctuations, large inter-annual variability in peatland volumetric moisture content (VMC) was measured. During pre-harvesting (2005 and 2006), median peatland VMC was high (0.69 and 0.52 $\text{m}^3 \text{m}^{-3}$, respectively) and responsive to precipitation events (i.e. increase VMC; Figure 2). However, post-harvesting (2007) and 2008) peatland VMC showed a consistent seasonal decline, despite greater and more evenly distributed precipitation. Median VMC in 2007 and 2008 was 0.43 and 0.47 m³ m⁻³, respectively and did not respond as strongly to precipitation events compared to the pre-harvesting years. In contrast to the H-U peatland, WT variability of the I-U peatland was much greater (Figure 2), where median WT ranged from 38 to 18 cm DBS across the four years. Although WT fluctuations were relatively large, variability in peatland VMC was minimal (0.24 to 0.26 $\text{m}^3 \text{m}^-$ ³). Overall, *VMC* at the I-U peatland was significantly different from the H-U peatland [H =

1 130.806, d.f. = 6, p < 0.001], with consistently lower [*post hoc* test (DM), p < 0.05] median VMC
2 in both the pre- and post-harvest periods.

 T_{soil} at the H-U peatland was most similar to T_a during the late growing season of the post-harvesting years only (2007 and 2008) when soil moisture declined to its lowest values (i.e. VMC $< 0.45 \text{ m}^3 \text{m}^{-3}$; Figure 3). In contrast, at the drier I-U peatland, a relatively stronger relationship between T_{soil} and T_a was observed across years (i.e. T_{soil} approximately equal to T_a). T_a was similar between sites, with differences in median T_a varying $< 3^{\circ}$ C during each year and showing minimal changes in each peatland between years (i.e. < 6 °C). Similarly, minimal differences in median photosynthetic active radiation (PAR) were observed between peatlands (i.e. $< 2 \text{ W m}^{-2}$) and within each peatlands (i.e. $< 40 \text{ W m}^{-2}$) across the four-year study period (Figure S3).

Significant differences in vapour pressure deficit (VPD) occurred at the H-U peatland [H = 94.520, d.f. = 3, p < 0.001] across years (Figure 4a). Pre-harvesting (2005 and 2006) median VPD was 0.37 and 0.82 kPa, respectively, and did not differ significantly [H = 151.730, d.f. = 7, d.f. = 7]p < 0.001, post hoc test (DM), p < 0.05 from VPD at the I-U peatland. However, post-harvesting (2007 and 2008), median VPD increased [post hoc test (DM), p < 0.05] to 1.53 and 1.62 kPa, respectively, and was significantly different [*post hoc* test (DM), p < 0.05] from the I-U peatland. The largest seasonal fluctuations in VPD and the highest recorded VPD (i.e. > 2 kPa) were measured at the H-U peatland in the post-harvesting years. In contrast, median VPD at the I-U peatland remained low (i.e. ≤ 0.79 kPa) during each year of the study. Wind speed at the H-U site significantly differed across years [$\chi^2(3) = 39.921$, p < 0.001] (Figure 4b); however, post hoc tests (TT) showed that wind speed (2007) did not significantly differ from pre-harvesting (2005). Median wind speed at the H-U site varied from 0.8 to 1.4 m s⁻¹ across years, and showed similar variability to wind speed at the I-U site (median 1.1 to 1.6 m s⁻¹). Despite minimal changes in

wind speed, turbulence intensity $(I_{\rm H})$ at the H-U site increased post-harvesting from 0.26 and 0.38 in 2005 and 2006 to 0.60 and 0.52 in 2007 and 2008, respectively (Figure 4b). In contrast, I_{μ} remained low at the I-U site across years, ranging from 0.24 to 0.34. Significant differences in ET [H = 79.355, d.f. = 3, p < 0.001] occurred at the H-U peatland across the four-years (Figure 4c). Similar to peatland VDP, post hoc tests (DM) showed ET was significantly different (p < p0.05) between pre- and post-harvesting years. Although ET also significantly increased [H =15.892, d.f. = 3, p < 0.001, post hoc tests (DM), p < 0.05] at the I-U peatland in 2008 compared to 2005, overall larger increases in ET occurred at the H-U peatland between the pre- and post-harvesting years, whereby median ET increased from 1.4 and 2.0 mm d⁻¹ in 2005 and 2006 to 3.4 and 4.3 mm d⁻¹ in 2007 and 2008, respectively.

11 Seasonal variation in peatland carbon exchange

During the pre-harvesting period (2005 and 2006), inter-annual variability of *NEE* between peatlands and within each peatland was low (Figure 5). NEE rates at the H-U peatland were consistently lower (i.e. greater carbon uptake) and significantly different [H = 285.517, d.f. = 7, d.f. = 7]*post hoc* test (TT), p < 0.05] from *NEE* at the I-U peatland. The H-U peatland fluctuated between a slight carbon source and carbon sink (median 0.52 and -0.03 g CO_2 -C m⁻² d⁻¹ in 2005 and 2006, respectively) while the I-U peatland functioned as a consistent slight carbon source (median 1.30 and 1.65 g CO₂-C m⁻² d⁻¹ in 2005 and 2006, respectively) (Figure 5). Pre-harvesting R_{tot} was lower at the H-U peatland (median 5.28 and 7.96 g CO₂ m⁻² d⁻¹ in 2005 and 2006, respectively) and significantly different [H = 282.365, d.f. = 7, post hoc test (TT), p < 0.05] from the I-U peatland (median 10.12 and 12.10 g CO_2 m⁻² d⁻¹ in 2005 and 2006, respectively; Figure 6a). In contrast, GEP was slightly higher at the H-U peatland in 2005 and 2006 (median 3.72 and 8.18 g $CO_2 m^{-2} d^{-1}$, respectively) from the I-U peatland (median 2.03 and 6.27 g $CO_2 m^{-2} d^{-1}$,

respectively) but did not significantly differ [H = 282.520, d.f. = 7, *post hoc* test (TT), p < 0.05]
between peatlands (Figure 6b).

One year post-harvesting (2007), both peatlands functioned as a net carbon sink from the atmosphere at the beginning of the season and showed a steady decline in carbon uptake (i.e. higher NEE) towards mid-season (Figure 5). NEE rates were lower (i.e. greater carbon uptake) and significantly different [H-U peatland, $\chi^2(3) = 91.660$, p < 0.001, post hoc test (TT), p < 0.05; I-U peatland, $\chi^2(3) = 99.865$, p < 0.001, post hoc test (TT), p < 0.05] from NEE in the pre-harvesting years at both peatlands. The H-U peatland functioned as a consistent net carbon sink from the atmosphere (median -1.34 g CO₂-C m⁻² d⁻¹) and significantly differed [H = 285.517, d.f. = 7, p <0.001, *post hoc* test (TT) p < 0.05] from *NEE* at the I-U peatland, which was a consistent net carbon source (median 0.62 g CO₂-C m⁻² d⁻¹). R_{tot} at the H-U peatland was lower (median 5.83 g CO₂-C m⁻² d⁻¹) and significantly different $[\chi^2(3) = 118.619, p < 0.001, post hoc test (TT),$ p < 0.05] from 2006, but did not significantly differ [*post hoc* test (TT), p < 0.05] from 2005 (Figure 6a). No significant change $[\chi^2(3) = 70.898, p < 0.001, post hoc test (TT), p < 0.05]$ in R_{tot} (median 10.89 g CO₂-C m⁻² d⁻¹) occurred at the I-U peatland relative to 2005 or 2006. Consistent with trends of the pre-harvesting period, R_{tot} at the H-U peatland was lower and significantly different [H = 282.365, d.f. = 7, post hoc test (TT), p < 0.05] from the I-U peatland. GEP increased within both peatlands and significantly differed [H-U peatland, $\chi^2(3) = 100.033$, p < 0.001, *post hoc* test (TT), p < 0.05; I-U peatland, $\chi^2(3) = 104.526$, p < 0.001, *post hoc* test (TT), p < 0.05] from 2005 and 2006 (Figure 6b). Similar to pre-harvesting, GEP at the H-U peatland remained slightly higher (median 10.63 g CO_2 m⁻² d⁻¹) but was not significantly different [H = 282.520, d.f. = 7, post hoc test (TT) p < 0.05] from the I-U peatland in 2007 (median 9.01 g CO₂) $m^{-2} d^{-1}$).

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Two years post-harvesting (2008), both peatlands showed a steady decline in net carbon uptake from the beginning to mid-season (Figure 5). NEE at the H-U peatland still remained lower (median 0.18 g CO₂ m⁻² d⁻¹) and significantly different [H-U peatland, $\chi^2(3) = 91.660$, p < 0.001, *post hoc* test (TT), p < 0.05] from *NEE* in 2005, however, was no longer significantly different [*post hoc* test (TT) p < 0.05] from 2006. In contrast, *NEE* at the I-U peatland was higher (median 2.67 g CO₂ m⁻² d⁻¹) and significantly different [$\chi^2(3)$ = 99.865, p < 0.001, post hoc test (TT), p < 0.05] from 2005 and 2006. *NEE* at the I-U peatland was significantly different [H = 285.517, d.f.]=7, post hoc test (TT), p < 0.05] from the H-U peatland in 2008, showing the greatest net carbon release from either site observed over the four-year study period. R_{tot} in both peatlands significantly differed [H-U peatland, $\chi^2(3) = 118.619$, p < 0.001, post hoc test (TT), p < 0.05; I-U peatland, $\chi^2(3) = 70.898$, p < 0.001, post hoc test (TT), p < 0.05] from the pre-harvesting years (2005 and 2006; Figure 6a). Although the highest R_{tot} was observed in both peatlands during 2008, R_{tot} at the H-U peatland (11.92 g CO₂ m⁻² d⁻¹) still remained lower and significantly different [H = 282.365, d.f. = 7, post hoc test (TT), p < 0.05] from the I-U peatland (15.98 g CO₂) m⁻² d⁻¹). GEP in both peatlands increased and were significantly different [H-U peatland, $\chi^2(3) =$ 100.033, p < 0.001, post hoc test (TT), p < 0.05; I-U peatland, $\chi^2(3) = 104.526$, p < 0.001, post *hoc* test (TT), p < 0.05] from 2005 and 2006 (Figure 6b). GEP was significantly higher [H = 282.520, d.f. = 7, post hoc test (TT), p < 0.05] at the H-U peatland relative to the I-U peatland (median GEP = 11.69 and 6.73 g CO₂ m⁻² d⁻¹, respectively; Figure 6b).

Despite large degree of uncertainty in the peatland *NEE* models, the scatter is typical of CO₂ flux models reported in other studies (e.g. Bubier *et al.*, 1998; Lafleur, 1999; Petrone *et al.*, 2011; Strack *et al.*, 2014). Mean standard errors for the *NEE* models ranged from \pm 0.73 to 1.6 g CO₂ m⁻² d⁻¹. Although the uncertainty for the models (i.e. maximum and minimum estimates) overlapped during the undisturbed period, the overall discrepancy in *NEE* between peatlands
 remained large after harvesting; therefore the interpretation of shifts in CO₂ exchange at the H-U
 peatland relative to the I-U peatland due to disturbance remains valid.

Hydroclimatic influence on peatland carbon exchange

NEE at the H-U peatland correlated well with changes in *VMC* during the post-harvesting period only (Figure 7a). Greater net carbon uptake (i.e. lower *NEE*) with increasing peatland soil moisture occurred in 2007 and 2008. In contrast, poor relationships between peatland *NEE* and *VMC* were observed during pre-harvesting (2005 or 2006). Minimal variability in *VMC* at the I-U peatland within growing seasons and across the study period resulted in no relationship between peatland *NEE* and *VMC* at the I-U site and as such, was not shown in Figure 7.

The distinct relationship between *NEE* and *VMC* at the H-U peatland in 2007 and 2008 reflected strong moisture linkages with GEP and R_{tot} (Figure 7b and 7c). For example, GEP in the H-U peatland increased with higher VMC (i.e. greater productivity with soil moisture) in 2006 to 2008 (Figure 7b). The strongest relationships between GEP and VMC occurred during the post-harvesting years (2007 and 2008). No correlation between GEP and VMC was observed in 2005. Similar to GEP, R_{tot} in the H-U peatland also correlated with VMC; however, the relationship only occurred during the post-harvesting years (2007 and 2008) and was seasonally dependent (Figure 7c). For example, during the early growing season of 2007 and 2008, R_{tot} showed a strong quadratic relationship with VMC peaking at 7.4 and 4.3 g CO_2 m⁻² d⁻¹, respectively, when the peatland soil was generally wet (Figure 2) and cool (Figure 3). By the end of the growing seasons, maximum R_{tot} peaked higher at 12.5 and 6.8 g CO₂ m⁻² d⁻¹ in 2007 and 2008, respectively when the peatland soil was generally dry and relatively warmer.

1 Discussion

2 Natural variability in BP peatland carbon dynamics

Throughout the study period, the H-U peatland functioned mainly as a net carbon sink while the I-U peatland was frequently a small net source. *NEE* rates in both peatlands ranged from -1.51 to 2.12 g CO₂-C m⁻² d⁻¹ during the undisturbed pre-harvest period (2005 and 2006) and were comparable to previous reports of natural *NEE* rates in Boreal peatlands (e.g. Bellisario *et al.*, 1998; Shurpali *et al.*, 1995; Humphreys *et al.*, 2006).

Differences in NEE between the H-U and I-U peatlands during the undisturbed period indicates the potential for large natural variability in carbon cycling of peatlands on the Boreal Plains (BP), even peatlands in relatively close proximity to each other as observed in this study (i.e. < 1Km distance). Higher inter-annual R_{tot} and frequently larger seasonal variability in R_{tot} at the I-U peatland relative to the H-U peatland likely reflected the consistently drier (i.e. lower water table and soil moisture) and warmer soils at that site. Greater CO₂ release has been observed under lower water table positions in both laboratory settings (Moore and Dalva, 1993; Van de Reit et al., 2013) and in situ studies (Silvola et al., 1996; Kim and Verma, 1992; Gažovič et al., 2013; Helfter *et al.*, 2015). Further, changes in peat temperature can alter decomposition rates and CO₂ emissions (Waddington *et al.*, 2001) whereby even minor soil temperature increases in high quality soils can provide optimal conditions for decomposition, thus increasing respiration (Solondz et al., 2008).

Soil moisture is also an important factor influencing peatland *Sphagnum* productivity (McNeil and Waddington. 2003), as was reflected by the slightly higher *GEP* at the wetter H-U peatland that contributed to the overall lower *NEE* (i.e. greater net carbon uptake) during the undistributed

period. However, despite WT and soil VMC being low and disconnected at the I-U peatland, maintenance of a sufficient water supply by dew or precipitation as well as moisture retention by the moss (Strack and Price, 2009) may have moderated the impact of low soil water availability on moss carbon uptake. This will maintain a relatively productive moss cover at the I-U peatland (i.e. median GEP at the I-U peatland was 54% to 76% of median GEP at H-U peatland). Together, differences in NEE linked to natural variations in site hydrology suggest the potential for spatially variable seasonal and inter-annual carbon exchange of peatlands on the BP, consistent with previous studies reporting soil moisture controls on CO₂ balances in peatlands (Lafleur et al., 2001; Strack et al., 2009; Trudeau et al., 2014). Therefore, assessing potential impacts of land use disturbances on NEE of BP peatlands requires careful consideration of site-specific natural variability in water availability influencing respiration and productivity across this eco-region.

Impact of forest harvesting on peatland hydroclimatic and carbon exchange

Shifts in peatland microclimate at the H-U site post-harvest may have reflected the loss of a protective sheltering effect created by the adjacent upland forest (Chen et al., 1993). Post-harvesting, higher vapour pressure deficit (VPD) measured in the newly exposed H-U peatland may have resulted from decreased stability of the surface boundary layer and increased mixing with the upper atmosphere due to an increase in fetch within the newly formed adjacent cutblock. Dynamic turbulent flow patterns occur across landscape transitions (e.g. Markfort et al., 2014; Yang et al., 2006; Flesch and Wilson, 1999). Although significant increases in wind speed were not observed in the H-U peatland after harvesting, wind speeds are expected to be more variable and turbulence increase with an increased momentum sink over the peatland relative to the clear-cut forested area (Helgason and Pomeroy, 2005; Helgason and Pomeroy, 2012; Turnispeed et al.,

2003), likely contributing towards higher peatland *VPD* and *ET* (Petrone *et al.*, 2007). Even
slight shifts in *ET* can alter the water balance of a peatland in this water deficit eco-region, given
that *ET* is the dominant component of peatland water budgets on the BP (Devito *et al.*, 2005;
Ferone and Devito, 2004; Smerdon *et al.*, 2005). As such, the greater evaporative water loss in
the H-U peatland post-harvesting may have contributed to the seasonal decline of peatland *VMC*at that site, despite a relatively consistent supply of precipitation and overall wetter conditions in
2007 and 2008.

Post-harvesting, VMC became a limiting control on NEE at the H-U peatland, as indicated by the strong relationship with peatland *NEE* occurring in 2007 and 2008 only. Moisture conditions are frequently well correlated with both carbon losses (plant respiration and soil decomposition) and carbon fixation (plant production) (Davidson et al., 2000; Bubier et al., 2003). Although the overall range of soil VMC was similar in each year of the four-year study period (~0.40 to 0.70 m³ m⁻³), the timing of moisture loss (i.e. consistent seasonal decline) appeared critical to influencing seasonal patterns of respiration and productivity during the post-harvesting period. For example, low VMC near the end of the 2007 and 2008 growing seasons corresponded with the warmest soil temperatures and thus, contributed to higher R_{tot} (i.e. greater carbon release to the atmosphere) relative to the wetter cool soils at the beginning of the season. In contrast, frequent re-wetting by precipitation events during the pre-harvesting period resulted in no seasonal trend between VMC, T_{soil} and R_{tot} in 2005 and 2006.

Strong correlations between increasing *GEP* and increasing *VMC* were observed at the H-U peatland from 2006 to 2008. The lack of a relationship between *GEP* and *VMC* in 2005 likely reflected the predominantly high moisture conditions that year. The strongest relationship between *GEP* and *VMC*, as well as higher *GEP* for a given *VMC* (i.e. more efficient carbon uptake), occurred during the post-harvesting years, likely reflecting the coinciding timing of high soil VMC and peak PAR during that period. For example, the highest GEP occurred during the beginning and mid-season, corresponding to the highest VMC and near maximum PAR, thus contributed toward the large net carbon accumulation. In contrast, lower GEP during pre-harvesting may reflect that the highest VMC occurred later in the growing season when PAR was generally lower. Consistent with our results, Griffis et al., (2000) found that large carbon accumulation in a subarctic fen was the result of wetter conditions and early snowmelt during the warm spring period, even when drier conditions persisted for the majority of the growing season.

9 Implications for land use management on the Boreal Plains

BP peatlands exist in a moisture deficit region, and are in a state of hydrologic risk. Results of this study indicate the importance of soil moisture influencing peatland productivity and respiration. Thus, any land-use disturbances impacting peatland water availability, such as changes to peatland microclimate observed in this study, are likely to have a direct influence on the CO₂ exchange of BP peatlands. Large inter-annual variability in CO₂ exchange is common in northern peatlands (e.g. Aurela et al., 2009), including shifts between a net CO₂ sink and source due to natural variations in hydrological and microclimatic conditions (Joiner et al., 1999; Shurpali et al., 1995; Lund et al., 2012). In this study, shifts in mid-season NEE one-year postharvesting were greater than the natural NEE variability of the pre-harvesting period at both peatlands. However, a larger relative change in NEE (i.e. greater net carbon uptake) occurred at the H-U site after forest removal. This suggests clear-cut logging may modify adjacent peatland microclimates and soil moisture conditions to influence GEP and R_{tot} in the short-term. However, given that mid-season NEE returned to within the range of the pre-harvest period two years post-harvesting suggests the relatively small-scale clear cutblock in this study may not sufficiently

alter NEE outside that of natural variation due to climate and/or site hydrology and/or microclimatic conditions. As such, the long-term carbon exchange function of BP peatlands may largely be influenced by changes in water availability resulting from drier conditions expected by future climate warming (IPCC, 2014). However, careful consideration of larger-scale logging due to rapid expansion of deforestation across this region (Timoney, 2003) may compound anticipated drought conditions induced by climate change. In particular, consideration of forest cutblock size (e.g. Flesch and Wilson, 1999) as well as orientation of cutblocks relative to the dominant wind direction may enhance alterations to adjacent peatland hydroclimatic conditions and CO₂ exchange dynamics and thus, impact stability of BP peatland water supply and carbon stores.

11 Conclusion

Peatland growing season ecosystem CO₂ exchange data suggest the potential for large variability in carbon cycling of undisturbed peatlands on the BP linked to natural hydrologic differences between sites (i.e. higher R_{tot} and NEE in the naturally drier peatland). The changes to peatland moisture soil conditions, linked to alterations in microclimate (i.e. increased turbulent mixing, vapour pressure deficit and evapotranspiration) by adjacent upland clear-cut logging, shifted peatland respiration and productivity patterns and thus, demonstrate that utilizing an integrated hydrometerological approach is fundamental to ecosystem monitoring as well as designing landscape management and forestry strategies for the protection of BP peatland ecosystem function. The results of short-term alterations to peatland hydroclimatic and carbon exchange dynamics by clear-cut logging indicates that in addition to climate change, the sustainability of BP peatlands ecosystem function may also depend on periodic forest disturbances expected with the rapid expansion of deforestation, while the particular peatland response is likely to be site-

specific due to natural variability in terrestrial-atmosphere exchange of water and CO_2 within these hydrologically tenuous ecosystems in this moisture deficit region.

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	GEP parameters			$R_{ m tc}$	$R_{\rm tot}$ parameters		
Site	GP_{max}	Q	R^2	а	b	R^2	
I-U Peatland							
2005	4.36	0.15	0.22	0.47	4.59	0.25	
2006	13.19	0.45	0.54	0.32	7.87	0.10	
2007	24.79	0.37	0.79	0.95	-0.74	0.64	
2008	33.93	0.10	0.55	1.08	1.33	0.74	
H-U Peatland							
2005	20.55	0.06	0.34	0.57	0.01	0.55	
2006	18.46	0.48	0.49	0.60	1.05	0.52	
2007	24.52	0.66	0.71	0.38	1.22	0.59	
2008	31.92	0.39	0.54	0.86	1.28	0.83	

Figure 1. Harvested-upland (H-U) and intact-upland (I-U) study complexes, located on the Boreal Plains Ecozone region of Northern Alberta. Shown are the ponds, surrounding peatlands and the adjacent uplands with locations of the meteorological stations (*MET*) and groundwater wells. Circles represent site locations of the point field measurements.

Figure 2. Water table (*WT*) position (dotted lines) from the peatland groundwater wells (see
Figure 1) and soil moisture content (*VMC*) of the peatland (solid lines) measured at the
meteorological stations (see Figure 1) and total daily precipitation (vertical bars) at the
harvested-upland (H-U) and intact-upland (I-U) complexes in 2005, 2006, 2007 and 2008,
Utikuma Region Study Area, Alberta, Canada.

Figure 3. Average daily air temperature (T_a) and soil temperature (T_{soil}) (averaged 2, 5 and 10 cm depths) measured at the meteorological stations (see Figure 1) at the harvested-upland (H-U) and intact-upland (I-U) complexes in 2005, 2006, 2007 and 2008, Utikuma Region Study Area, Alberta, Canada.

Figure 4. Mid-season (DOY 201 to 243) average daily (a) vapor pressure deficit (*VPD*), (c) wind speed and horizontal turbulence intensity (I_u), and (d) evapotranspiration (*ET*) measured at the meteorological stations (see Figure 1) at the harvested-upland (H-U) and intact-upland (I-U) complexes in 2005, 2006, 2007 and 2008, Utikuma Region Study Area, Alberta, Canada. N/A indicates data was not available.

Figure 5. Daily total net ecosystem CO₂ exchange (*NEE*) (error bars 95% confidence interval) in
the harvested-upland (H-U) peatland and intact-upland (I-U) peatland in 2005, 2006, 2007 and
2008, Utikuma Region Study Area, Alberta, Canada. Dotted lines represent the minimum and
maximum uncertainty estimates for the NEE models.

Figure 6. Daily average (a) total respiration (*R*tot) and (b) gross ecosystem productivity (*GEP*) in
the harvested-upland (H-U) peatland and intact-upland (I-U) peatland in 2005, 2006, 2007 and
2008, Utikuma Region Study Area, Alberta, Canada. For comparative purposed, seasonal *R*tot
were grouped into four different time periods (e.g. Solondz et al., 2008): early green (EG: DOY
120 to 160), green (G: DOY 161 to 218), late green (LG: DOY 219 to 250) and senescence (S:
DOY 251 to 278). N/A indicates data was not available.

Figure 7. Variations in (a) total net ecosystem exchange (*NEE*) with soil moisture content (*VMC*), (b) variation in gross ecosystem production (*GEP*) with *VMC*, and (c) variation in total respiration (R_{tot}) with *VMC* in the harvested-upland (H-U) peatland in 2005, 2006, 2007 and 2008, Utikuma Region Study Area, Alberta, Canada. Daily *NEE*, *GEP* and R_{tot} rates corresponding to daily *VMC* values were binned to improve data clarity, using an average value for each sample within 0.01 m³ m⁻³ interval. Seasonal R_{tot} were grouped into two different time periods: early season (DOY 140 to 179) and late season (DOY 180 to 278).





Figure 1

Fort McMurray Study Site **Boreal Plains** Edmonton Alberta, Canada ///////// Forested Harvested Upland Upland • Peatland Ν Pond H-U Peatland Peatland Site Pond I-U + Road Peatland Site Forested

⊗ MET ▼ Well Lawn ○ Depression Wind velocity

Harvested Upland

Figure 1. Harvested-upland (H-U) and intact-upland (I-U) study complexes, located on the Boreal Plains Ecozone region of Northern Alberta. Shown are the ponds, surrounding peatlands and the adjacent uplands with locations of the meteorological stations (MET) and groundwater wells. Circles represent site locations of the point field measurements.

Upland

100 m

 \otimes Peatland

190x142mm (300 x 300 DPI) P Figure 2





Figure 2. Water table (WT) position (dotted lines) from the peatland groundwater wells (see Figure 1) and soil moisture content (VMC) of the peatland (solid lines) measured at the meteorological stations (see Figure 1) and total daily precipitation (vertical bars) at the harvested-upland (H-U) and intact-upland (I-U) complexes in 2005, 2006, 2007 and 2008, Utikuma Region Study Area, Alberta, Canada. 190x142mm (300 x 300 DPI)

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Figure 3. Average daily air temperature (Ta) and soil temperature (Tsoil) (averaged 2, 5 and 10 cm depths) measured at the meteorological stations (see Figure 1) at the harvested-upland (H-U) and intact-upland (I-U) complexes in 2005, 2006, 2007 and 2008, Utikuma Region Study Area, Alberta, Canada. 190x142mm (300 x 300 DPI)





a) 2.5 : 2.0 (kta) 1.5 1.0 ŧ 0.5 0.0 b) . 6.0 Mind Speed (ms⁻¹) 4.0 3.0 5.0 Ŧ 1.0 I_u = 0.24 0.26 0.25 0.38 0.34 0.20 0.60 0.0 c) 6.0 (mm d⁻¹) Ē 2.0 : ŧ 0.0 Pre- Harvesting Post- Harvesting

Figure 4. Mid-season (DOY 201 to 243) average daily (a) vapor pressure deficit (VPD), (c) wind speed and horizontal turbulence intensity (Iu), and (d) evapotranspiration (ET) measured at the meteorological stations (see Figure 1) at the harvested-upland (H-U) and intact-upland (I-U) complexes in 2005, 2006, 2007 and 2008, Utikuma Region Study Area, Alberta, Canada. N/A indicates data was not available. 190x142mm (300 x 300 DPI)





Figure 5. Daily total net ecosystem CO2 exchange (NEE) (error bars 95% confidence interval) in the harvested-upland (H-U) peatland and intact-upland (I-U) peatland in 2005, 2006, 2007 and 2008, Utikuma Region Study Area, Alberta, Canada. Dotted lines represent the minimum and maximum uncertainty estimates for the NEE models. 190x254mm (300 x 300 DPI) Figure 6

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Figure 6. Daily average (a) total respiration (Rtot) and (b) gross ecosystem productivity (GEP) in the harvested-upland (H-U) peatland and intact-upland (I-U) peatland in 2005, 2006, 2007 and 2008, Utikuma Region Study Area, Alberta, Canada. For comparative purposed, seasonal Rtot were grouped into four different time periods (e.g. Solondz et al., 2008): early green (EG: DOY 120 to 160), green (G: DOY 161 to 218), late green (LG: DOY 219 to 250) and senescence (S: DOY 251 to 278). N/A indicates data was not available.

190x142mm (300 x 300 DPI)



Figure 7. Variations in (a) total net ecosystem exchange (NEE) with soil moisture content (VMC), (b) variation in gross ecosystem production (GEP) with VMC, and (c) variation in total respiration (Rtot) with VMC in the harvested-upland (H-U) peatland in 2005, 2006, 2007 and 2008, Utikuma Region Study Area, Alberta, Canada. Daily NEE, GEP and Rtot rates corresponding to daily VMC values were binned to improve data clarity, using an average value for each sample within 0.01 m3 m-3 interval. Seasonal Rtot were grouped into two different time periods: early season (DOY 140 to 179) and late season (DOY 180 to 278). 190x142mm (300 x 300 DPI)

Figure 7