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Variation in Soil Carbon Dioxide Efflux at Two Spatial Scales in a Topographically Complex Boreal Forest

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Abstract

Carbon dynamics of high-latitude regions are an important and highly uncertain component of global carbon budgets, and efforts to constrain estimates of soil-atmosphere carbon exchange in these regions are contingent on accurate representations of spatial and temporal variability in carbon fluxes. This study explores spatial and temporal variability in soil-atmosphere carbon dynamics at both fine and coarse spatial scales in a high-elevation, permafrost-dominated boreal black spruce forest. We evaluate the importance of landscape-level investigations of soil-atmosphere carbon dynamics by characterizing seasonal trends in soil-atmosphere carbon exchange, describing soil temperature-moisture-respiration relations, and quantifying temporal and spatial variability at two spatial scales: the plot scale (0–5 m) and the landscape scale (500–1000 m). Plot-scale spatial variability (average variation on a given measurement day) in soil CO_2 efflux ranged from a coefficient of variation (CV) of 0.25 to 0.69, and plot-scale temporal variability (average variation of plots across measurement days) in efflux ranged from a CV of 0.19 to 0.36. Landscape-scale spatial and temporal variability in efflux was represented by a CV of 0.40 and 0.31, respectively, indicating that plot-scale spatial variability in soil respiration is as great as landscape-scale spatial variability at this site. While soil respiration was related to soil temperature at both the plot- and landscape scale, landscape-level descriptions of soil moisture were necessary to define soil respiration–moisture relations. Soil moisture variability was also integral to explaining temporal variability in soil respiration. Our results have important implications for research efforts in high-latitude regions where remote study sites make landscape-scale field campaigns challenging.

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Introduction

Soil respiration, the sum of autotrophic and heterotrophic respiration, is a central component of the global carbon cycle (Raich and Potter, 1995), and its accurate quantification is particularly important in boreal regions where soils hold large stores of organic carbon (Schuur et al., 2008; Tarnocai et al., 2009). Soil conditions such as soil temperature and moisture are the primary factors responsible for determining rates of decomposition in soils (Raich and Potter, 1995; Davidson et al., 1998; Schlesinger and Andrews, 2000). While soil respiration frequently increases exponentially as a function of temperature (Raich and Potter, 1995; Schlesinger and Andrews, 2000), the effect of soil moisture on soil respiration is quite complex (Davidson et al., 1998; Raich and Potter, 1995). Soil moisture affects soil respiration by modifying the connectivity of soil pores and thereby influencing the diffusion of gas through the soil profile (Millington, 1959). Changes in soil diffusivity due to soil moisture can limit oxygen availability to soil organisms (Skopp et al., 1990) and retard the diffusion of CO_2 out of the soil by creating impermeable layers in the subsurface (Risk et al., 2002). Low soil moisture can also limit soil respiration through death or dormancy of organisms due to desiccation stress (Orchard and Cook, 1983). In addition to soil temperature and moisture controls, properties such as organic layer thickness, substrate quality, microbial activity, and photosynthesis also contribute to total efflux of CO_2 from soil (Hobbie et al., 2000; Hogberg et al., 2001; Bhupinderpal-Singh et al., 2003; Saiz et al., 2006).

Although rates of input, accumulation, and turnover of soil carbon are often highly variable, particularly in boreal regions (Harden et al., 1997; Trumbore and Harden, 1997; Hobbie et al., 2000; Grant, 2004; Vogel et al., 2005; McGuire et al., 2009; Wickland et al., 2010), some of the aforementioned soil factors that control soil CO_2 efflux are organized by landscape morphology. For example, soil moisture content and organic carbon accumulations are higher in areas of convergent topography, and aspects with greater sunlight exposure have higher soil temperatures (Bonan and Shugart, 1989). Several studies in temperate regions have identified landscape morphology as an important control in determining the spatial distribution of soil respiration drivers (Pacific et al., 2008; Martin and Bolstad, 2009; Riveros-Iregui and McGlynn, 2009). These studies suggest that detailed spatial descriptions of landscape morphology, including elevation and aspect, are useful for scaling up plot-level observations of soil CO_2 efflux to predict efflux at the landscape scale. In such landscape-scale estimates of soil CO_2 efflux, understanding of the extent, magnitude, and causes of spatial variability in soil respiration is integral to the success of these methods. An approach that allows plot-scale observations of CO_2 efflux to be scaled up to estimate efflux from a larger landscape is especially relevant in high-latitude regions where field sites are often remote and field campaigns are logistically complicated. However, implementation of such techniques requires a better understanding of variability in soil-atmosphere carbon exchange in high latitude regions, particularly in ecosystems where factors such as soil temperature, soil water distribution, and vegetation type and productivity are affected by the presence of permafrost.

Permafrost is defined as any subsurface Earth material remaining below 0 °C for at least two consecutive years, and it is frequently overlain by seasonal ice that persists above the permafrost table for much of the growing season. The presence of permafrost is mediated by many factors: soil texture can exert a control on permafrost presence by affecting soil moisture and thermal properties, surface and ground water can promote permafrost thaw through the movement of heat in the subsurface, vegetation insulates existing permafrost by intercepting incoming solar radiation, and, finally, topography influences presence and depth of permafrost by controlling solar radiation at the ground surface (Jorgenson et al., 2010). The influence of topography on solar radiation at the ground surface can result in the presence of permafrost on north-facing slopes and in valleys, but absence of permafrost, or deeper active layer depths, on south-facing slopes (Bonan and Shugart, 1989; Jorgenson et al., 2010). Because presence and depth of permafrost and seasonal ice is intricately connected to spatial and temporal variability in factors that control soil respiration, particularly soil temperature and moisture, further investigation into the spatial patterns of soil respiration in permafrost landscapes is highly necessary.

Our study aims to address the dearth of information regarding spatial variability of soil respiration in topographically complex permafrost-dominated ecosystems by exploring the variability in soil respiration at coarse and fine spatial scales. The objectives of this study are: (1) to characterize seasonal trends of soil-atmosphere carbon dynamics and describe soil temperature-moisture-CO_2 efflux relations at two spatial scales in a boreal forest ecosystem; and (2) to quantify spatial variability in CO_2 efflux at two spatial scales and evaluate the potential for up-scaling plot-level investigations in these ecosystems. Our study will help focus future research efforts and resource use in high-latitude field studies where study sites are frequently remote and landscape-scale investigations are logistically challenging to execute.

Methods and Analysis

SITE DESCRIPTION

The study site is the watershed of West Twin Creek (65°20′N, 146°54′W), a perennial headwater catchment in the Beaver Creek watershed in the White Mountains National Recreation Area of interior Alaska (Fig. 1). The West Twin Creek watershed ranges in elevation from 550 to 965 m and encompasses approximately 5 km^2. Annual mean temperature and total mean annual precipitation measured at the Upper Nome Creek Snotel Site (approximately 15 km west of the study site) during 2007 through 2010 is -2.6 °C and 0.51 m yr^{-1}, respectively (http://www.wcc.nrcs.usda.gov/nwcc/site?sitenum=1090&state=ak). The mean temperature for the duration of the study (May–September 2010) was 10.9 °C. Hillslope vegetation of the watershed is dominated by black spruce (*Picea mariana*) and scattered white spruce (*Picea glauca*), with an understory of forbs and herbaceous shrubs. Groundcover vegetation is dominated by peat moss (S*phagnum* spp.), feathermoss (*Pleurosium schreberi*, *Hylocomium splendens*), and lichens (*Cladina* spp.). The geology is characterized primarily by schist of the Yukon-Tanana terrane (Coney and Jones, 1985), overlain by loess deposits. Loess deposits exist in variable thickness throughout the watershed, with thicker deposits at lower elevations and thinner deposits at higher elevations (T. Jorgenson, personal communication). The site is underlain by continuous permafrost. Active layer depths are variable at this site and range from approximately 0.5 to 0.8 m; active layer depths are greater at the higher elevation plots, and shallower at the lower elevation plots (Table 1). Active layer depths are also most shallow under areas with thick organic soil horizons. The soils of this site, gelisol histels, have an organic horizon ranging in thickness from about 0.3 to 0.5 m (Table 1).

STUDY DESIGN

We established six study plots in May 2010 that were designed to capture variability in CO_2 exchange at two spatial scales: plot-scale variability and landscape-scale variability. Plot-scale variability describes the variability in CO_2 efflux on spatial scales of 0–5 m (the distance between measurement locations within one plot), and landscape-scale variability describes variability in CO_2 efflux on spatial scales of 500–1000 m (the distance between plots). All plots are located in an open canopy upland black spruce forest slightly below treeline, and range in elevation from about 580 to 690 m (Table 1; Fig. 1). All plots are located on an east-facing hillslope to minimize the soil and vegetation heterogeneity related to aspect, and to focus the study on quantifying spatial variability in CO_2 efflux related to the heterogeneity in soils systems existing across one hillslope of uniform aspect. Plots 1–3 are higher in elevation than Plots 4–6 (Table 1).

CO_2 FLUX MEASUREMENTS

Five polyvinyl chloride (PVC) flux chamber collars were installed at each of the six study plots, totaling 30 collars at the site. One collar was installed in the center of the plot, and four collars were arranged around the central collar at a distance of 5 m. The collars have a diameter of 0.37 m, are 0.1 or 0.2 m tall, and were inserted 0.05 to 0.1 m into the soil. No measurements were made within the first 72 h after collar installation to avoid disturbance effects. All groundcover vegetation within the collars was left intact, and the collars remained in place through the duration of the study.

Soil respiration and net CO_2 flux were measured one time at each collar during two consecutive days every one to two weeks from 21 May 2010 through 19 September 2010. Soil respiration was measured as the efflux of CO_2 from the ground surface and is hereafter referred to as soil CO_2 efflux. Soil CO_2 efflux measurements were made using an opaque PVC chamber 0.3 m tall and 0.37 m in diameter. Soil CO_2 efflux measurements include autotrophic respiration of above- and belowground vegetation plus heterotrophic respiration through the soil profile. Net CO_2 flux measurements were made using a transparent PVC-Lexan chamber and record heterotrophic and autotrophic respiration minus photosynthesis of mosses and vascular plants. We measured gas flux between 0900 and 1700 h and rotated the order in which the plots

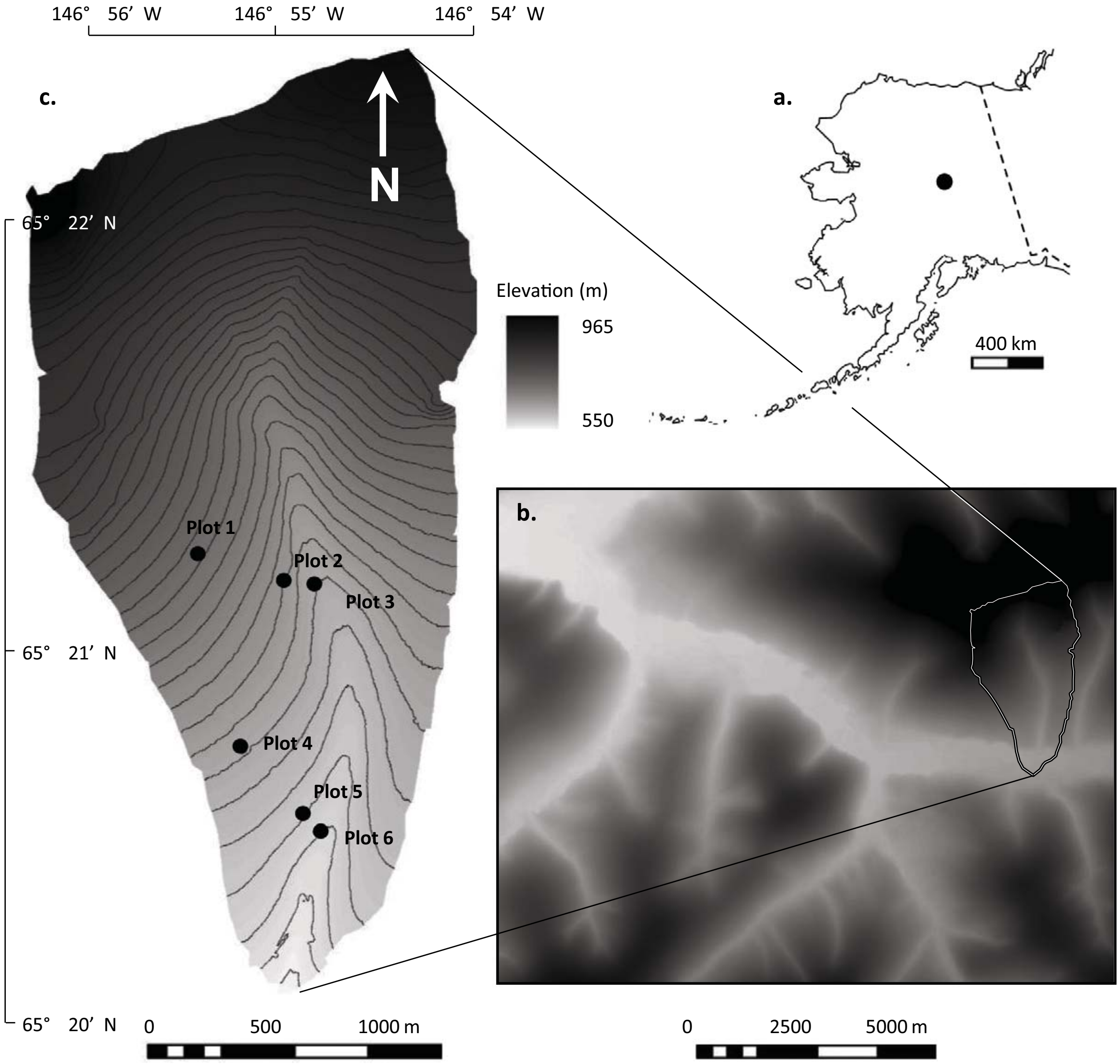

FIGURE 1. (a) Location of study site in Alaska; (b) digital elevation model (DEM) of the West Twin Creek Watershed in the White Mountains National Recreation area; (c) distribution of the 6 study plots across the West Twin Creek site (contour interval equals 10 m). Grayscale color bar indicates elevation on maps b and c; north arrow applies to all maps.

TABLE 1

Site Description

Plot	Elevation (m)	% C[a]	Tree diameter (cm)	Organic layer thickness (m)	Maximum active layer depth (m)	Average moss cover (%)[b]	Average lichen cover (%)[b]
1	692	46.78 (0.06) [c]	5.4 (3.0)	0.34 (0.09)	0.78 (0.07)	78	22
2	637	47.26 (0.11)	6.1 (3.5)	0.27 (0.03)	0.68 (0.01)	10	77
3	619	47.48 (0.45)	4.8 (3.4)	0.30 (0.12)	0.78 (0.02)	49	15
4	611	43.86 (0.89)	4.4 (2.3)	0.48 (0.02)	0.53 (0.04)	80	0
5	586	46.21 (0.29)	4.2 (1.2)	0.30 (0.05)	0.56 (0.09)	62	32
6	581	44.10 (0.17)	2.9 (1.5)	0.36 (0.11)	0.61 (0.08)	85	15

[a] % C determined from mean of three samples at one site collected within top 10 cm of soil.

[b] Moss and lichen cover is average % inside the collars at each plot.

[c] Standard deviation is shown in parentheses.

were visited to avoid time-of-day biases. Flux measurements were made by recording the change in concentration of CO_2 gas within the chamber for a period of time, in accordance with the closed chamber technique (Healy et al., 1996). During the measurement the chamber sits directly on the collar, and the interface is sealed with a rubber gasket. Chamber air was circulated through a portable infrared gas analyzer (IRGA; EGM-4 gas analyzer, PP Systems, Haverhill, Massachusetts). The IRGA pulls gas from a top port of the chamber, measures CO_2 concentration, and returns gas to a sidewall port at a rate of 0.3 L min^{-1}. An additional pump enhances circulation within the chamber at a rate of 3 L min^{-1}. We recorded the concentration of CO_2 within the chamber every 15 s for 5 min.

The flux of gas across the soil-atmosphere interface was calculated using:

$$J = (dC / dt)\, h \tag{1}$$

where J is the CO_2 flux (mol m^{-2} t^{-1}), C is the concentration of CO_2 gas in the chamber at ambient temperature and pressure (mol m^{-3}), t is time, and h is the chamber plus collar height (m) above the ground surface. The slope of the regression of gas concentration with time is represented by dC/dt. The slope was calculated between approximately 60 s and 180 s after chamber deployment using a non-linear, polynomial regression; all regressions have a $r^2 \geq 0.95$. Gross photosynthesis was calculated as the difference between CO_2 efflux and net flux. Positive fluxes represent transfer of CO_2 from the terrestrial system to the atmosphere, and negative fluxes represent transfer of CO_2 from the atmosphere to the terrestrial system.

ENVIRONMENTAL CONDITIONS

Air temperature one meter above the ground surface, and soil temperature at 0.05 m below the ground surface, were measured at every collar to coincide with gas flux measurements using a Fluke 51 Series II digital thermometer with a type K thermocouple (Fluke Corporation, Everett, Washington). Soil temperature was also measured and logged every 15 min with temperature sensors and dataloggers (Onset Hobo Micro Station H21-002 4 channel datalogger; S-TMB-M002 Temperature Smart Sensor, 2-m cable; Onset Computer Corporation, Bourne, Massachusetts) at one location per plot throughout the season. A temperature probe was installed in the organic horizon 0.07–0.1 m below the soil surface at each plot. This depth was chosen for measuring soil temperature because it is consistent with the depth of soil temperature measurements from other studies (O'Donnell et al., 2009; Webster et al., 2009; Wickland et al., 2010). All measurements are in the organic horizon because at many plots the mineral soil remained frozen throughout the summer.

Soil moisture, measured as the volumetric water content (VWC), was determined using two methods. Soil samples of known volume were collected weekly from a depth of 0.06–0.1 m below the soil surface at one location within each plot. Samples were sealed in soil tins, weighed, dried at 60 °C for 48 h, and then reweighed. Soil VWC is calculated by dividing the water volume (the difference in weight before and after oven drying) by the total soil sample volume. In addition, soil VWC was also measured using ECH_2O soil moisture probes (Decagon Devices Inc., Pullman, Washington). Soil VWC was logged every 15 min on a datalogger (Onset Hobo Micro Station H21-002 4 channel datalogger) at one location per plot throughout the season. Probes were inserted horizontally in the organic horizon 0.07–0.1 m below the soil surface. The VWC output from the probes installed in each study plot was corrected according to the methods of O'Donnell et al. (2009); calibration curves specific to the soils at each study plot were constructed using blocks of soil representative of the types of soil in which probes were installed.

SOIL CARBON, VEGETATION SURVEYS, AND ACTIVE LAYER DEPTH

Soil total carbon content was measured on samples collected from each plot within the top 0.1 m of soil near the central collar. Samples consisted primarily of partially to moderately decomposed plant litter and fine roots. Samples were oven dried at 60 °C for 48 h, ground, homogenized, and analyzed on an Exeter Analytical Incorporated CE 440 Elemental Analyzer (North Chelmsford, Massachusetts) to obtain values of percent carbon. One sample was collected at each plot and samples were analyzed in triplicate. Tree diameter at breast height (DBH) was measured on all trees over 2 m tall along three sub-transects of a 90-m transect established perpendicular to the hillslope through each study plot. Sub-transects were 14 m long and included trees within one meter on either side of the transect. Dead trees leaning >45° were not measured. Vegetation in the collars consisted of moss and lichen that covered 65–100% of the ground surface within every collar, and vascular plants whose canopy extended over the groundcover of moss and lichen. For the purposes of this study, groundcover vegetation within the collars was estimated as percent cover of lichen or moss, and does not include the percent cover of vascular plants. Active layer depth was measured at three locations in each plot in late August by inserting a probe into the soil until it met resistance.

DATA ANALYSES: SPATIAL AND TEMPORAL VARIABILITY OF CO_2 EFFLUX

Our study was designed to capture variability in CO_2 efflux at the plot scale (0–5 m; the distance between collars that comprise one plot) and at the landscape scale (500–1000 m; the distance between plots). Both spatial and temporal variability were quantified at the plot- and landscape scale by the coefficient of variation (CV): standard deviation divided by the mean. Plot-scale spatial variability is determined as the average variation among all collars within one plot on a given day. Landscape-scale spatial variability is determined as the average variation among all collars at all plots in a given week. Plot-scale temporal variability is the variation in efflux at one plot through the season (each plot measurement is the average of efflux from all five collars on one day), and landscape-scale temporal variability is the variation in efflux at all plots through the season.

DATA ANALYSES: SIGNIFICANCE OF SOIL TEMPERATURE AND MOISTURE

We determined regressions between soil CO_2 efflux and soil temperature and moisture to assess the relation between these parameters at the plot scale and at the landscape scale. In this analysis, 'plot-scale' regressions include soil CO_2 efflux, temperature or moisture measurements from one plot only, and 'landscape-scale' regressions include the average efflux and soil conditions from all 6 plots during one week of measurement.

To describe the interacting controls of soil moisture and soil temperature on soil CO_2 efflux, we used classification and regression tree analysis (CART). This method uses continuous predictor variables to explain a dependent response variable, CO_2 efflux, using an explanatory tree model to repeatedly split independent variables into dichotomous homogeneous groups. To avoid overfitting, regression tree growth limits were set at a maximum tree depth of two layers, minimum parent node size was set to 50, and minimum child node size was set to 25. CART analyses were done with SSPS Statistics 19 (IBM Corporation, Sommers, New York).

Results

ENVIRONMENTAL CONDITIONS

Seasonal mean soil temperature at 0.05 m depth ranged from 7.70 ± 3.75 °C at Plot 2, to 11.46 ± 3.12 °C at Plot 1 (Fig. 2). Soil temperature at all plots was greatest between Day 180 and 230, and decreased after Day 230 to temperatures lower than those at the beginning of the season (Fig. 3, part a). Seasonal mean soil VWC was lower at the higher elevation plots (Plots 1, 2, 3), and higher at the lower elevation plots (Plots 4, 5, 6; Fig. 2 and Fig. 3, part b). Soil carbon content is similar between all 6 plots (Table 1).

SOIL CO_2 EXCHANGE VARIABILITY

Soil CO_2 efflux, net CO_2 flux, and gross photosynthesis were variable through the season at all study plots (Fig. 4). The greatest seasonal mean efflux of CO_2 was measured at Plot 4, and the lowest at Plot 1 (mean ± standard deviation; 9.16 ± 2.89 and 6.35 ± 2.01 mmol CO_2 m^{-2} h^{-1}, respectively). None of the plots showed a pronounced seasonal peak in efflux; however, efflux was generally higher during the first half of the season than the end of the season. Minimum efflux was observed during the last 2 weeks of measurement at all plots.

Seasonal mean net CO_2 flux was negative during the day at 5 of the 6 plots measured. Of the 5 plots with a negative seasonal mean net CO_2 flux, net CO_2 exchange ranged from −3.46 ± 3.26 at Plot 4 to −1.01 ± 1.90 at Plot 1. Measurements at these 5 plots were positive during the first and last days of the season, but negative through the middle of the season. Plot 2 was the only plot at which the seasonal mean net flux was positive (3.40 ± 2.19 mmol CO_2 m^{-2} h^{-1}). There was very little seasonal trend in net flux at this plot; net CO_2 exchange was positive through the entire season.

Seasonal mean rates of gross photosynthesis were greatest (most negative) at Plot 4 and lowest (least negative) at Plot 2 (−12.69 ± 5.14 and −3.49 ± 1.99 mmol CO_2 m^{-2} h^{-1}, respectively). The greatest rates of gross photosynthesis occurred in the beginning and middle of the measurement season, and the lowest rates were observed during the last two weeks of measurement. Overall, gross photosynthesis varied in concert with peaks in efflux (Fig. 4). This observation is corroborated by a significant relationship between efflux and rates of gross photosynthesis across all

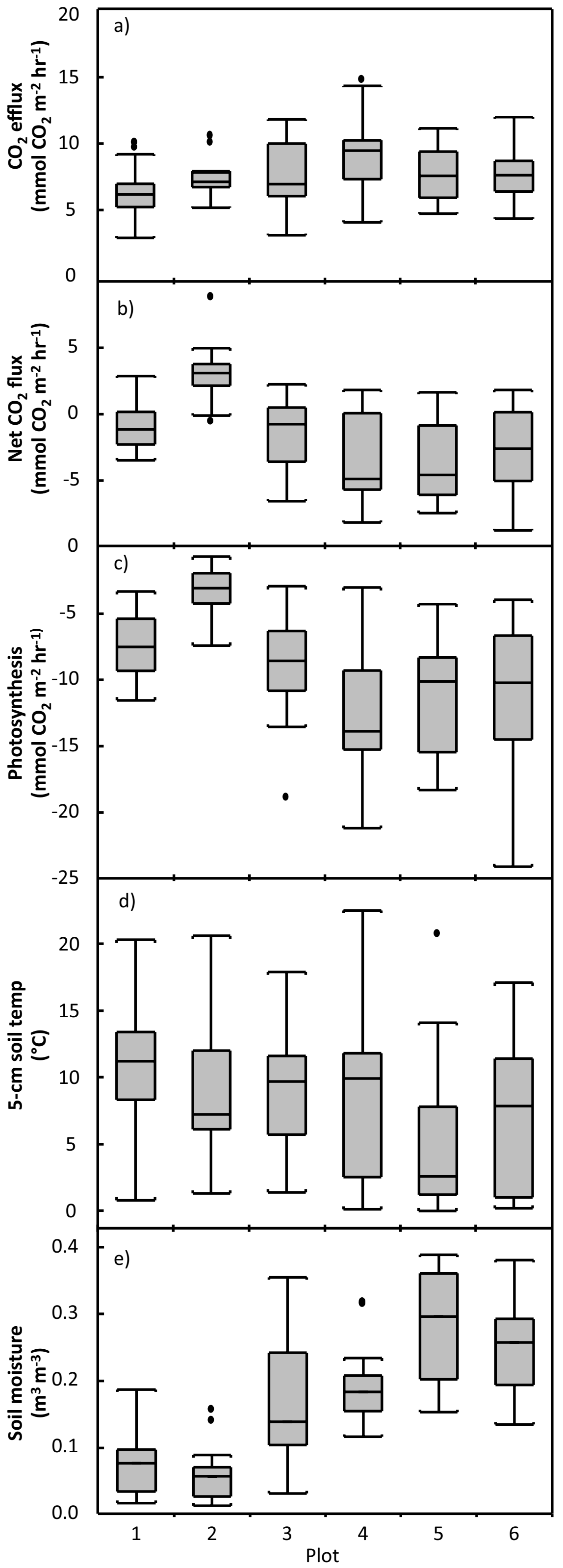

FIGURE 2. Box plots of seasonal mean (a) soil CO_2 efflux, (b) net CO_2 flux, (c) gross photosynthesis, (d) soil temperature 0.05 m below ground surface, and (e) soil moisture from 21 May 2010 through 19 September 2010. The horizontal lines represent the median, boxes represent the inter-quartile range, the whiskers the 10th and 90th percentiles, and solid circles represent outliers.

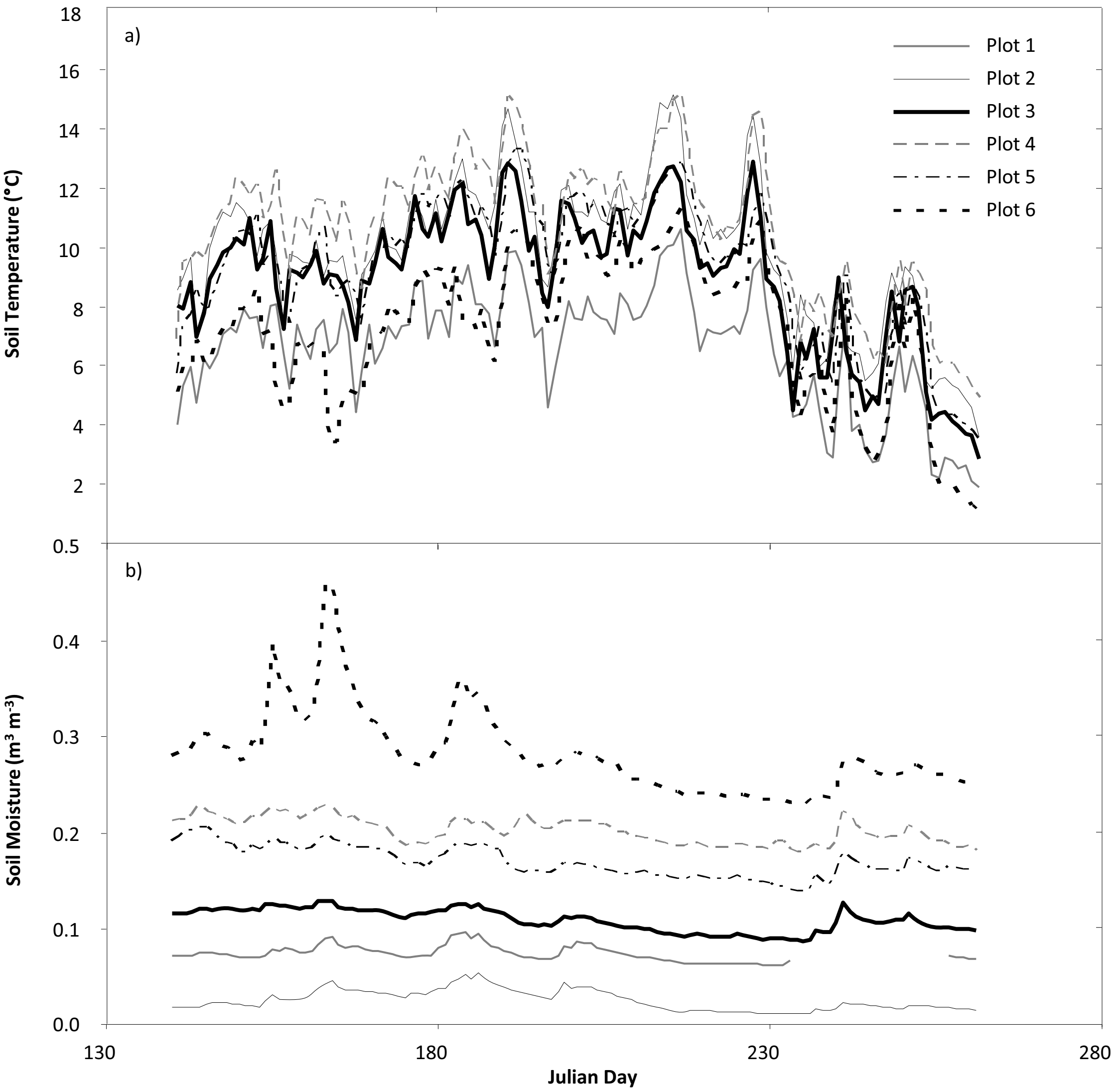

FIGURE 3. **(a) Mean daily soil temperature measured and logged with probes and dataloggers installed at the central collar within each study plot. Depth of probe installation from the ground surface at is as follows: Plot 1, 0.09 m; Plot 2, 0.1 m; Plot 3, 0.1 m; Plot 4, 0.09 m; Plot 5, 0.07 m; Plot 6, 0.09 m. (b) Mean daily soil moisture (m^3 m^{-3}) measured and logged with probes and dataloggers installed at the same depths at each plot as described above.**

plots ($y = 1.54x - 2.59$; $r^2 = 0.50$; $p < 0.0000$). The relationship between efflux and photosynthesis is further explained when vegetation type is taken into consideration. Measurements from lichen-dominated areas yield an efflux-photosynthesis relation with a slope of 0.44 ($p = 0.0002$), whereas measurements from moss-dominated areas yield a relation with a greater slope: 1.22 ($p <$ 0.0000).

In addition to investigating variability in carbon dynamics through seasonal trends, spatial and temporal variability were quantified through an analysis of the coefficient of variation. Plot-scale spatial variability (average variation on a given measurement day) in efflux ranged from a CV of 0.25 (Plots 1 and 4) to 0.69 (Plot 3), and plot-scale temporal variability (average variation of plots across measurement days) in efflux ranged from a CV of 0.19 (Plot 2) to 0.36 (Plot 3; Table 2). Landscape-scale spatial variability in efflux was represented by a CV of 0.40 and landscape-scale temporal variability was represented by a CV of 0.31 (Table 2).

SOIL CO_2 EFFLUX CONTROLS AND REGRESSION TREE ANALYSIS

Efflux increased exponentially with increasing soil temperature at all study plots except at Plot 2. Efflux is significantly related to soil temperature at Plots 1, 4, 5, and 6 ($p < 0.05$) and at Plot 3 ($p < 0.1$; Table 2). Efflux also increased exponentially with increasing soil temperature when the data were evaluated at the landscape scale ($p < 0.0005$; Fig. 5, Table 2). Soil CO_2 efflux was not correlated with soil VWC at the plot scale; however, soil CO_2 efflux was positively correlated with soil VWC at the landscape scale ($p = 0.0072$; Fig. 5, Table 2).

CART analysis, done using temperature and moisture as the continuous predictor variables, identified soil temperature as the independent variable with the greatest predictive power. Soil temperature was the only significant variable included in the left branch (Fig. 6) which described soil CO_2 efflux measurements at soil temperatures ≤9.65 °C with a mean efflux of 6.28 ± 2.98 mmol CO_2

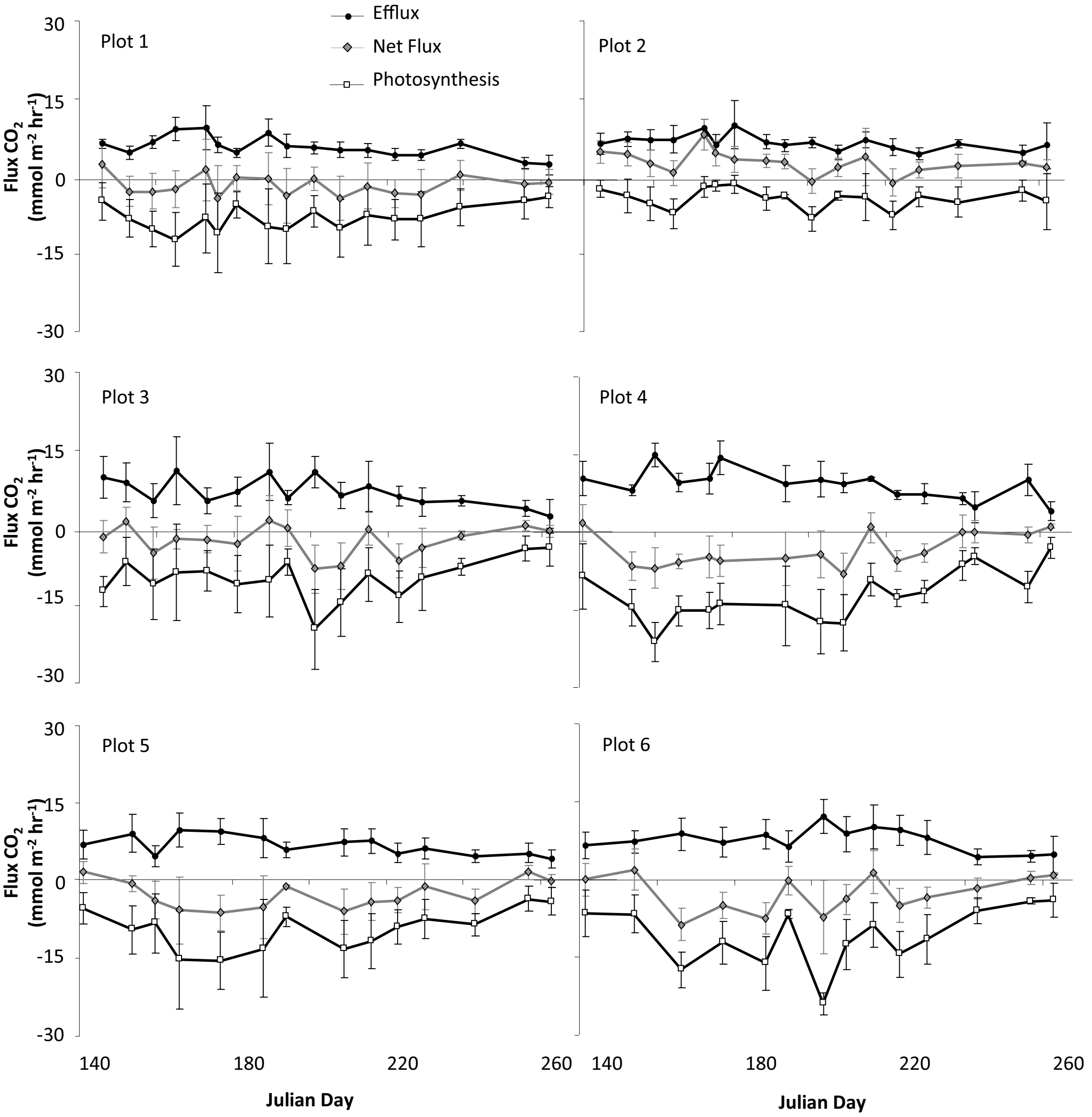

FIGURE 4. CO_2 **efflux (black circles), net** CO_2 **flux (gray diamonds), and gross photosynthesis (white squares) at Plots 1–6 from 21 May 2010 to 19 September 2010. Points represent mean of 5 measurements (one at each collar), and whiskers represent one standard deviation.**

m^{-2} h^{-1}. The left branch was further split along a temperature threshold of 4.90 °C; the mean efflux below and above this threshold was 5.30 ± 2.87 and 6.92 ± 2.94 mmol CO_2 m^{-2} h^{-1}, respectively.

The right branch included both temperature and soil VWC as significant variables; it includes soil CO_2 efflux measurements at soil temperatures >9.65 °C with a mean of 8.87 ± 3.28 mmol CO_2 m^{-2} h^{-1}. The right branch was further split along a VWC threshold of 0.15 m^3 m^{-3}. The left side of this split was characterized by VWC values ≤ 0.15 m^3 m^{-3} and a mean efflux of 7.32 ± 2.66 mmol CO_2 m^{-2} h^{-1}; the right side of the split incorporated measurements of soil VWC > 0.15 m^3 m^{-3} and mean efflux of 9.70 ± 3.28 mmol CO_2 m^{-2} h^{-1}.

Soil VWC was also an important factor in explaining temporal variability of efflux within this site. The seasonal range in soil moisture (maximum VWC minus minimum VWC) was significantly related to plot-scale temporal variability in CO_2 efflux (Fig. 7). The lowest variability in CO_2 efflux and smallest seasonal range in moisture was observed at the highest elevation and driest plots (Plots 1 and 2). The highest variability in CO_2 efflux was observed at a mid-elevation plot with intermediate moisture (Plot 3). Intermediate temporal variability in efflux was observed at the lowest elevation plots that had the highest moisture content.

Discussion

Our results demonstrate considerable spatial and temporal variability in the exchange of CO_2 with the atmosphere within a high elevation, permafrost-dominated black spruce forest. We find that although soil temperature and moisture are interacting, overarching controls over carbon dynamics at this site, plot-level measurements are not sufficient to demonstrate soil moisture as a control on soil CO_2 efflux; rather landscape-level measurements are necessary to detect the role of soil moisture as a control on soil CO_2 efflux. Additionally, landscape-level measurements of seasonal variability in soil moisture inform our understanding of plot-

TABLE 2

Spatial and temporal variability in CO_2 efflux, and relations between soil CO_2 efflux, soil temperature, and soil VWC

	Soil CO^2 efflux–soil temperature relation			Soil CO_2 efflux–soil VWC relation			Spatial and temporal variability in CO_2 efflux	
Plot	Regression	R Square	*P*-value	Regression	R Square	*P*-value	CV (temporal variability)	CV (spatial variability)
1	***y = 3.08exp(0.06x)***	***0.52***	***0.00***	y = 10.87x + 5.3	0.07	0.33	0.30	0.25
2	y = 8.36exp(−0.02x)	0.14	0.15	y = −4.80x + 7.4	0.02	0.33	0.19	0.28
3	y = 4.21exp(0.06x)	0.23	0.05	y = 5.09x + 6.4	0.03	0.60	0.36	0.69
4	***y = 3.76exp(0.08x)***	***0.83***	***0.00***	y = −7.36x + 10.1	0.03	0.56	0.31	0.25
5	***y = 4.51exp(0.06x)***	***0.45***	***0.01***	y = −6.58x + 9.2	0.07	0.39	0.33	0.38
6	***y = 4.57exp(0.06x)***	***0.59***	***0.00***	y = 9.12x + 5.4	0.09	0.32	0.31	0.41
All (Landscape-scale)	***y = 4.14exp(0.06x)***	***0.65***	***0.00***	***y = 21.19x + 4.3***	***0.46***	***0.00***	0.31	0.40

Bold italics indicate statistically significant regressions. Soil temperature is measured in °C and soil moisture is measured as soil volumetric water content (VWC) in $m^3\ m^{-3}$. For all regressions, x = independent variable (CO_2 efflux) and y = dependent variable (soil temperature in top half of table, soil VWC in bottom half of table.)

scale seasonal variability in efflux. Lastly, our plot- and landscape-scale investigations indicate that spatial variability of CO_2 efflux within this site is as great or greater at the plot scale than at the landscape scale.

ENVIRONMENTAL CONDITIONS AND CO_2 EFFLUX

Seasonal soil moisture and temperature conditions at this site are similar to those of other upland black spruce forests (Swanson and Flanagan, 2001; O'Connell et al., 2003; Vogel et al., 2005), although soil moisture is lower at this site than peatland and floodplain black spruce forest sites (O'Donnell et al., 2009; Wickland et al., 2010). Soil CO_2 efflux at this site is similar to other upland boreal black spruce forests (Nakane et al., 1997; Swanson and Flanagan, 2001; Wang et al., 2003; O'Donnell et al., 2009; Wickland et al., 2010) but lower than those from lower elevation, lower latitude, or wetter black spruce sites (Ruess et al., 2003; Vogel et al., 2005; O'Neill et al., 2006). The CO_2 efflux at this site is comparable to efflux from sites with a similar permafrost table depth (0.5 to 0.8 m depth) (Vogel et al., 2005; O'Donnell et al., 2009), but lower than other upland sites with a deeper or undetectable permafrost (Ruess et al., 2003; Vogel et al., 2005).

SOIL CO_2 EFFLUX-TEMPERATURE-MOISTURE RELATIONS

Soil temperature and moisture operate as interacting, overarching controls on CO_2 efflux at this site. Soil CO_2 efflux increases

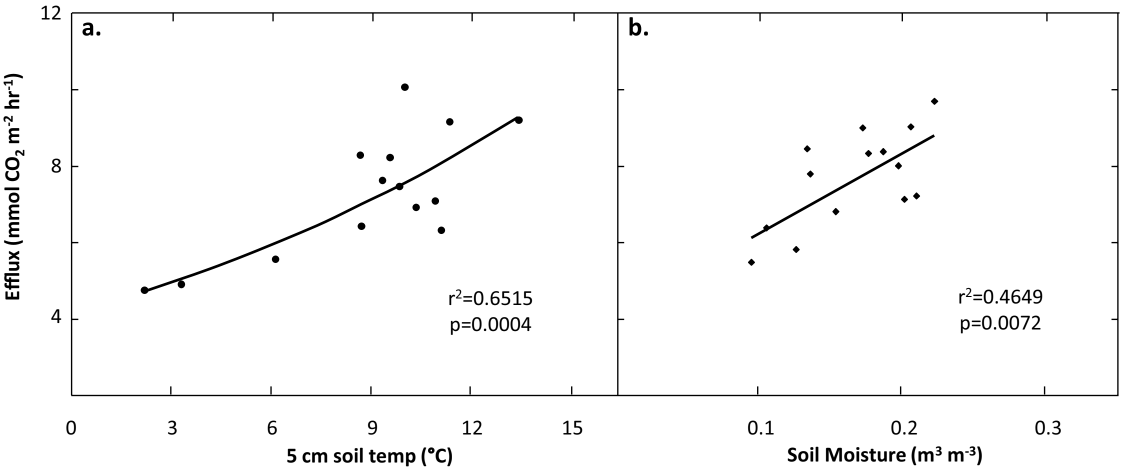

FIGURE 5. (a) Relation between soil temperature and soil CO_2 efflux evaluated at the landscape scale. One point represents the average soil temperature and average efflux of all study plots during one week of measurement. The equation for this fit is shown in Table 2 as the landscape-scale soil CO_2 efflux–soil temperature relation. (b) Relation between soil volumetric water content (VWC) and soil CO_2 efflux evaluated at the landscape scale. One point represents the average soil moisture and average efflux of all study plots during one week of measurement. The equation for this fit is shown in Table 2 as the landscape-scale soil CO_2 efflux–soil VWC relation.

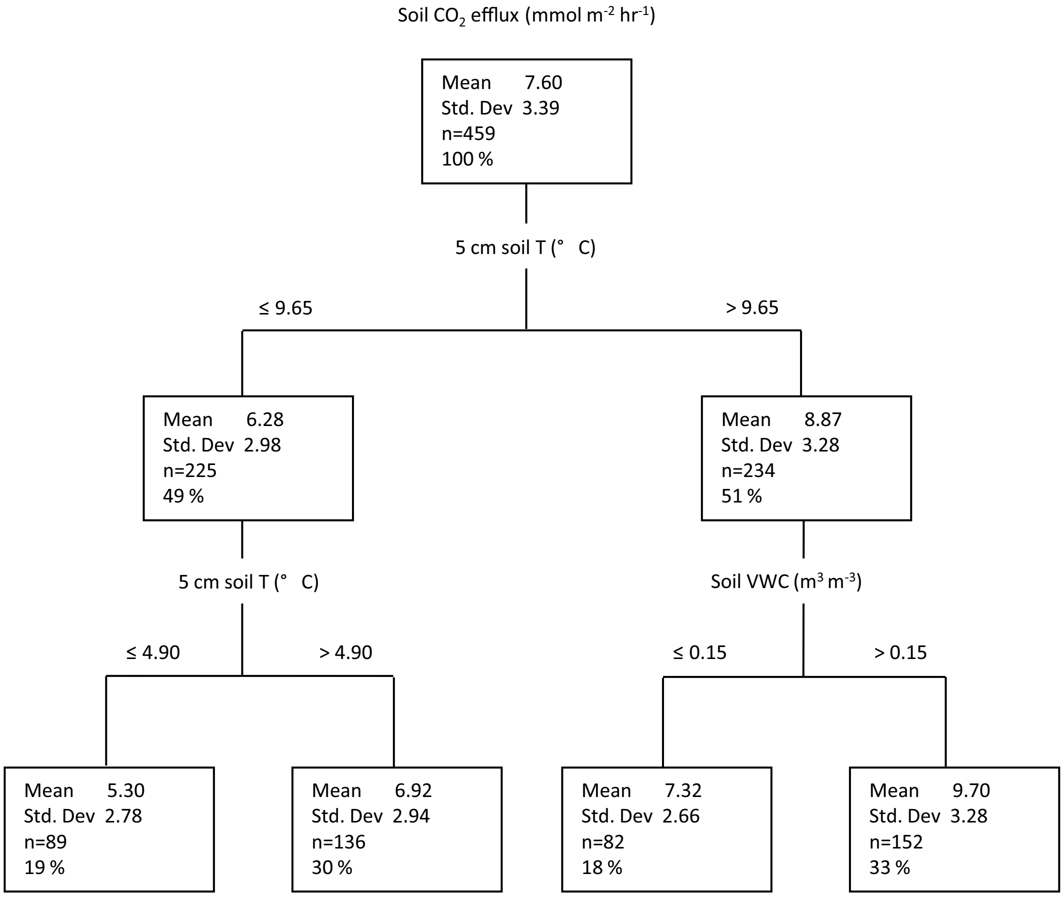

FIGURE 6. Regression tree prediction of CO_2 efflux based on soil temperature and moisture. Boxes display mean efflux (mmol CO_2 m^{-2} h^{-1}), standard deviation, number of total measurements in each node, and percent of total measurements in each node. Horizontal lines below each node indicate thresholds at which explanatory variables are significant. Soil temperature was measured at 0.05 m and soil moisture measured between 0.06 m and 0.1 m.

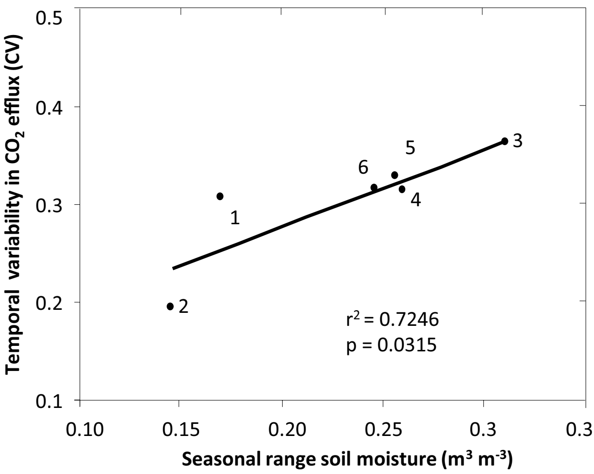

FIGURE 7. Relationship between seasonal range in soil moisture (maximum VWC − minimum VWC) and temporal variability in CO_2 efflux (CV). Each point represents the average range in moisture and average variability at one plot through the season. Numbers indicate the plot number of each data point.

exponentially with soil temperature at all study plots (except Plot 2), and efflux and soil temperature are also related when the data are integrated across the landscape scale. The absence of a positive relation between efflux and temperature at Plot 2 may be due to the vegetation composition at this plot. Higher tree density and larger diameter trees present at this plot suggest the potential for greater contribution of tree root respiration to total respiration, and a smaller contribution from heterotrophic respiration. Although heterotrophic respiration can contribute 47–63% of CO_2 emissions from black spruce forests (Schuur and Trumbore, 2006), site specific differences influence the partitioning of autotrophic and heterotrophic components of efflux in specific locations (Bond-Lamberty et al., 2004). The absence of a significant positive relation between respiration and temperature at Plot 2 may reflect the response of black spruce respiration to temperature and season that differs from temperature-induced changes in heterotrophic respiration (Grant et al., 2009; Bronson and Gower, 2010). The strength of temperature-efflux relations also varies between plots indicating that in addition to soil moisture and temperature, efflux at some plots may also be influenced by other factors such as heterogeneous vegetation within plots or variation in the abundance and composition of the soil microbial community (Davidson et al., 2006).

In addition to soil temperature, soil moisture is also an important control over CO_2 efflux (Davidson et al., 1998; Sommerkorn, 2008; Wickland and Neff, 2008; Webster et al., 2009). However, we find that in this boreal forest site, plot-scale moisture measurements are not sufficient to describe the role of moisture in determining CO_2 efflux, and a landscape-scale investigation of soil moisture is necessary to identify moisture as a control on CO_2 efflux. Soil VWC does not relate significantly with soil CO_2 efflux at the plot scale, potentially due to the relatively low spatial resolution of soil VWC measurements. However, the characterization of efflux-moisture relations is improved with a landscape-scale evaluation of moisture as soil CO_2 efflux is positively correlated with soil moisture when both efflux and moisture are evaluated at the landscape scale. Landscape-scale soil moisture data may yield significant relations with soil CO_2 efflux data because the landscape-scale moisture data represent broad trends in moisture transport (Martin and Bolstad, 2009; Riveros-Iregui and McGlynn, 2009). In this case, a landscape-scale evaluation may account for the complexity of soil water distribution across the landscape, and therefore efflux-moisture relations within this watershed are better characterized at the landscape scale. Additionally, because landscape-scale variations in soil moisture can affect plant species composition and plant productivity due to hydrologically driven differences in the soil nutrient regime (Giblin et al., 1991), landscape-scale descriptions of soil moisture may relate to soil respiration because they help account for inter-plot variation in plant productivity.

Landscape-scale soil efflux-temperature-moisture interactions were further explained by regression tree analysis, which was used to predict soil CO_2 efflux based on thresholds of soil temperature and moisture, independent of individual plot location. Regression tree analysis identified soil temperature as the dominant control over efflux at this site; however, at warmer soil temperatures the regression tree split the efflux data along a soil moisture threshold. Increasing importance of soil moisture as a control on efflux at warmer temperatures has been identified by both field and laboratory studies in a variety of ecosystems, including black spruce forests (Schlentner and Van Cleve, 1985; Kane et al., 2003; Conant et al., 2004; Jia et al., 2006; Wen et al., 2006; Wickland and Neff, 2008), and may be due in part to declining moisture content at higher soil temperatures. Additionally, this split may indicate a differential response between the heterotrophic response to warming (and drying) versus the autotrophic response, which could be less pronounced due to the ability of plants to move water vertical through the soil profile (Horton and Hart, 1998). Nevertheless, the moisture threshold present at higher temperatures within the CART model reinforces the importance of landscape-level understanding of moisture for predicting efflux.

PLOT- AND LANDSCAPE-SCALE VARIABILITY

The final goal of this research was to understand the importance of plot-level versus landscape-level variability in efflux, and to identify the sources of variability in CO_2 efflux at both coarse and fine spatial scales. To do this we quantified temporal and spatial variability in efflux at both the plot and landscape scale at the study site. We find large spatial variability at both the plot scale and the landscape scale. Because spatial patterns of CO_2 efflux can in some cases be significantly different between different landscape positions (Pacific et al., 2008), it seems intuitive that the variability between sites spanning different landscape positions would be large. However, we find that plot-scale variability is as great as landscape-scale variability, despite the location of the study plots at multiple elevations within the watershed. This surprising result indicates that variability may result from variable plot-scale soil conditions rather than soil factors that are organized by topography. One possible source of this fine-scale variability may be variable species composition of the forest floor and the resulting heterogeneity in rates of gross photosynthesis. Because live moss can be an additional source of autotrophic respiration in boreal systems, contributing up to 20% of total forest floor respiration (Swanson and Flanagan, 2001), greater CO_2 efflux from moss-dominated areas may contribute to the large plot-scale spatial variability in CO_2 efflux. Each plot investigated in this study had both moss and lichen present within the study site; 57% of measurement collars were dominated by moss ($>$75% cover), and 30% of the collars were dominated by lichen. Vegetation cover was also highly variable within each collar, and 13% of the collars were not dominated by a single vegetation cover type. The high variability in vegetation cover type may contribute to high variability in efflux on small spatial scales, especially considering the role of mosses in forest floor respiration.

Temporal variability is also high at both the plot scale and at the landscape scale (Table 2), but plot-scale temporal variability in efflux is explained by seasonal soil moisture conditions: plot-scale temporal variability (CV) of efflux is significantly related to the soil VWC range (maximum VWC – minimum VWC) at each plot through the season (Fig. 7). The lowest plot-scale temporal variability in efflux was observed at the two highest elevation plots (Plots 1 and 2) where soil moisture conditions are persistently dry. Mid-range temporal variability in efflux was observed at the lowest elevation plots (Plots 4, 5, and 6) where soil conditions are wet, and the highest temporal variability was observed Plot 3, a mid-elevation plot with intermediate moisture conditions. The dry, high-elevation plots may have low temporal variability in efflux because soil respiration is consistently limited by desiccation stress of organisms at low soil moisture conditions. The wet, low-elevation plots have intermediate variability, potentially due to intermittent periods of inundation where conditions are too wet for maximum efflux. High soil moisture conditions at these sites could limit CO_2 efflux both through limiting the diffusion of oxygen into the soil and thereby reducing production, or by hindering efflux of CO_2 out of the soil. The soils at this site are saturated at a VWC of approximately 0.4 to 0.5; seasonal trends of VWC at each plot (Fig. 3) indicate that the soils of the lower elevation plots may become saturated at the surface (5 cm depth) at times throughout the season, which could limit efflux of CO_2 out of the soil. Field observations established that the soils of the lower elevations sites were frequently saturated at depth, indicating that limited diffusion of oxygen into the soil may also be responsible for intermittent low efflux at the low-elevation plots. Finally, intermediate moisture conditions, such as those at Plot 3, may facilitate interactions between soil moisture and temperature that result in high temporal variability in efflux. This plot also displays the weakest relationship between soil temperature and efflux indicating that another factor in addition to temperature, potentially moisture, is influencing efflux at this site.

IMPLICATIONS FOR FUTURE RESEARCH

Soil carbon dynamics in high-latitude landscapes are difficult to investigate because soil conditions are highly heterogeneous, largely due to the presence of permafrost, and because field sites are generally remote. This study was designed to quantify spatial variability in CO_2 efflux at course and fine spatial scales to evaluate the potential for up-scaling plot-level investigations in these ecosystems and focus future research efforts. Our analysis of plot- and landscape-scale variability indicates that plot-scale spatial variability in efflux is as great as landscape-scale spatial variability. Therefore, higher spatial resolution of soil CO_2 efflux measurements is unlikely to constrain the spatial variability of efflux measurements from this watershed. However, several aspects of our study highlight the importance of landscape scale measurements, particularly of soil moisture, in understanding CO_2 efflux: (1) landscape-scale investigation of seasonal variability in soil moisture informs our understanding of plot-scale seasonal variability in efflux, (2) landscape-scale quantification of soil moisture is an important component of characterizing of moisture-efflux relations, and (3) landscape scale descriptions of soil moisture highlight moisture as an important predictor of efflux at warmer soil temperatures. Because soil moisture is strongly related to landscape morphology, we suggest that this type of landscape may be most effectively investigated by determining efflux-temperature relations over topographically driven gradients of soil moisture. Future studies that focus on accurate quantification of soil moisture at the plot- and landscape scale, including information from remote sensing or digital elevation models, will elucidate efflux-temperature relations over landscape-scale variation in soil moisture and improve our understanding of CO_2 dynamics from heterogeneous soils.

Conclusions

Quantification of spatial and temporal variability in soil atmosphere carbon exchange is integral to constraining carbon fluxes in high latitude regions, but highly variable soil conditions and soil characteristics, including soil temperature, soil moisture, and groundcover vegetation, result in highly spatially and temporally variable efflux of CO_2. Plot-scale spatial variability in soil respiration is as great as landscape-scale spatial variability at this site. Additionally, we find that landscape-scale descriptions of soil moisture are necessary to define soil respiration-moisture relations, and soil moisture variability was integral to explaining temporal variability in soil respiration. Further studies in boreal regions should focus on clarifying relations between soil CO_2 efflux and soil temperature under a range of soil moisture conditions, and quantifying the variability in soil moisture at multiple spatial scales with the use of landscape-scale investigative tools, including remote sensing, to further the understanding of the spatial variability in drivers of CO_2 efflux in boreal black spruce forests.

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