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Examining moisture and temperature sensitivity of soil organic matter decomposition in a temperate coniferous forest soil

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Abstract

Temperature and moisture are primary environmental drivers of soil organic matter (SOM) decomposition, and the development of a better understanding fo their roles in this process through depth in soils is needed. The objective of this research is to independently assess the roles of temperature and moisture in driving heterotrophic soil respiration for shallow and deep soils in a temperate red spruce forest. Minimally disturbed soil cores from shallow (0–25 cm) and deep (25–50 cm) layers were extracted from a 20 yr old red spruce stand and were then transferred to a climate chamber where they were incubated for 3 months under constant and diurnal temperature regimes. Soils were subjected to different watering treatments representing a full range of water contents. Temperature, moisture, and CO_2 surface flux were assessed daily for all soils and continuously on a subset of the microcosms. The results from this study indicate that shallow soils dominate the contribution to surface flux (90%) and respond more predictably to moisture than deep soils. An optimum moisture range of 0.15 to 0.60 water-filled pore space was observed for microbial SOM decomposition in shallow cores across which a relatively invariant temperature sensitivity was observed. For soil moisture conditions experienced by most field sites in this region, flux-temperature relationships alone can be used to reasonably estimate heterotrophic respiration, as in this range moisture does not alter flux, with the exception of rewetting events along the lower part of this optimal range. Outside this range, however, soil moisture determines SOM decomposition rates.

1 Introduction

Soil is the largest terrestrial store of carbon (C), with more than two thirds of terrestrial C stored in soils (Hibbard et al., 2005). The terrestrial surface flux of carbon dioxide (CO_2) is a significant contributor to global carbon cycling, generating emissions of 50–75 Pg of C per year (Raich and Schlesinger, 1992). Surface CO_2 flux is a measure of the rate of soil respiration and represents the integration of a number of complex subsurface interactions, including the production and transport of CO_2 through the profile. At any time, heterotrophic respiration comprises a fraction of this flux, while the other component is derived from autotrophic respiration, where CO_2 is respired from living roots, by microbes fed by root exudates, and by ectomycorrhizal fungi (Lavigne et al., 2004).

In terrestrial ecosystems, soil organisms decompose organic molecules from soil organic matter (SOM) and produce CO_2, among other greenhouse gases, in the process of their metabolism. Most of the respired CO_2 from SOM decomposition is derived from a small fast cycling labile carbon (C) pool (Trumbore, 2000), with the production of CO_2 highest at the surface organic layers and declining with depth (Fang and Moncrieff, 2005; Risk et al., 2008b). Although the concentration of organic C is generally lower in subsurface horizons than in organic surface horizons, the total contribution from subsurface soil layers can be 50% of the total organic C in a 1 m profile (Batjes, 1996). Subsurface soils are composed of SOM that is generally considered unavailable for decomposition through physical separation (Xiang et al., 2008), inaccessibility within aggregate structures (Denef et al., 2001), or due to inherent chemical recalcitrance (Agren and Bosatta, 2002; Giardina and Ryan, 2000).

CO_2 flux from SOM decomposition is typically related to soil temperature as it provides the best overall predictive tool of SOM decomposition. Heterotrophic soil respiration typically increases exponentially with an increase in temperature and may be inhibited at low or high moisture levels (Luo and Zhou, 2006). The temperature sensitivity of SOM decomposition is important in determining soil C balance with shifts in climate as it provides an indication of the sensitivity of SOM decomposition to temperature changes (Kirschbaum, 2000; Davidson et al., 2006a). The temperature sensitivity itself is altered by factors that constrain access to substrate, such as low or high water content, oxygen availability, and accessibility (sorption and aggregate status), which can result in an observed “apparent” temperature sensitivity that may be higher or lower than the actual intrinsic sensitivity (Davidson et al., 2006a). Furthermore, experimental conditions can introduce changes to soil structure and substrate availability, so care must be taken to interpret estimates of temperature sensitivity within the defined methodology (Wixon and Balser, 2009).

The impact of moisture on SOM decomposition is more complex than temperature because microbial activity is affected by several physical processes that vary with water content (Rodrigo et al., 1997), including water movement, gas and solute diffusion to sites of microbial activity, and the survival and motility of microorganisms (Luo and Zhou, 2006). By altering solute and oxygen diffusion, this indirectly affects substrate supply and decomposition rates (Davidson et al., 2006a), although the temporal and spatial scale may determine which environmental factor is most important (Savage et al., 2009). The relationship between soil moisture and respiration also depends on physical characteristics of each soil that affect its moisture content, including texture, porosity, and organic matter content. Nutrient cycling is also subject to non-linear shifts in dynamics as changing hydroclimatic conditions can force the soil-water system through a number of bifurcation points (Manzoni et al., 2004). Soil respiration can also be affected by sudden changes in moisture availability. Over very short time scales (minutes to hours), infiltrating water is known to result in a large pulse of CO_2 immediately after the event, and it is suggested that this rapid pulse is transport-related, with a displacement of CO_2 from subsurface pore space (Xu et al., 2004; Smart and Penuelas, 2005; Luo and Zhou, 2006; McCulley et al., 2007; Liu et al., 2009). Over longer time scales (days), rewetting stimulates microbial growth and activity (Iovieno and Baath, 2008), resulting in a large sustained release of soil CO_2: the so-called “Birch effect” (Jarvis et al., 2007). Respiration rates can be as high as 500% faster than the rates before the rewetting and the pulse can last for 2–6 days after the rewetting event depending on the pulse size, among other factors (Fierer et al., 2003a).

A major challenge in studying the effects of temperature or moisture on heterotrophic soil respiration is that a change in one factor is usually accompanied by a change in the other. Since temperature and water content co-vary in situ, they are thus confounding factors for soil respiration (Davidson et al., 1998; Fang and Moncrieff, 2001), making it difficult to separate the effect of temperature on respiration from the effect of moisture in a natural setting. Establishing relationships between controlling variables and CO_2 flux from SOM decomposition is also challenging due to the high spatial and temporal variability in bulk density, SOM content and quality within a field site and through depth. Observed in situ soil CO_2 fluxes are thus highly variable, and this presents difficulty for the identification of a land use or climate driven change (Kellman et al., 2007). One potential reason for the observed variability is that many studies do not attempt to isolate CO_2 flux from decomposition from other CO_2 generating processes in situ such as the autotrophic component of soil respiration from roots. Field measurements of CO_2 surface flux and subsurface production must consider the contribution of both sources in their assessment of temperature sensitivity across growing seasons. This can be accomplished through root exclusion, including trenching (Lavigne et al., 2004; Risk et al., 2008b), using spatial gradients in the landscape (Baldocchi et al., 2006), or girdling (Hogberg et al., 2009).

In an effort to minimize potential confounding influences, standard laboratory incubations are often employed with a particular set of sample preparation procedures. These incubations are then typically carried out on sieved and homogenized soil under fixed temperature and/or moisture conditions, with optima of 20–25 °C and 50–60% of water holding capacity (Hopkins, 2008). Standard laboratory incubations are subject to criticism, however, because they do not not adequately reflect field conditions. Optimal temperatures and moistures for microbial activity have been experimentally determined from incubations of processed soils, but it is likely that microbes in natural field conditions rarely experience these optimal conditions (Fang and Moncrieff, 2001). Furthermore, in situ mineralization rates may contrast highly with those determined from standard laboratory incubations (Oburger and Jones, 2009). Due to the complex and highly variable nature of soil (Young and Crawford, 2004), most standard laboratory incubations require highly processed treatments that disrupt natural soil structure. This represents another abstraction from field conditions that has implications for water dynamics due to altered aggregate and pore structure (Beare et al., 2009), and to microbial community dynamics. Standard laboratory incubations also rely on incubations of shallow soil, where it is thought most microbial activity occurs. Although lower soil organic carbon (SOC) mineralization rates are observed in situ for deep soils (Risk et al., 2008b), potential SOC decomposition rates derived from laboratory incubations with sieved and homogenized soil can be similar to those for native surface soils (Salome et al., 2009). This certainly indicates that physical controls at depth in the field setting can play an important role in dictating decomposition rates, and that the potential for unrealistic estimates based upon measured soil temperature are greater in the deeper zones of the soil profile.

Here we present results of a study whose research objective is to independently assess the role of temperature and moisture in driving heterotrophic soil respiration for shallow and deep soils in a temperate red spruce forest. The physical environment in soils exerts a primary control upon rates of soil organic matter (SOM) decomposition, however quantifying the relationships amongst temperature, moisture and SOM decomposition is methodologically challenging in situ, especially for deep soil. Ideally, it is important to consider the role of each while the other is held constant. In this study, the incubation of intact soil cores represents an intermediate between field measurements and laboratory incubations, employed in order to more realistically simulate field conditions and to allow shallow and deep soil responses to changes in environmental conditions to be documented. In using this approach, the original soil structure is maintained in intact cores in order to minimize confounding factors on substrate supply, especially through disturbance, which then allows environmental factors to be manipulated independently in a climate-controlled facility in a manner that addresses problems inherent in standard incubation approaches.

2 Materials and methods

This study was conducted within a temperate red spruce (*Picea rubens* Sarg.) forest in the Abraham's Lake area of the Liscomb Game Sanctuary in central Nova Scotia, Canada (45.1° N 62.83° W). A chronosequence representing forests in various stages post-harvest, along with an old growth stand with no record of harvesting (Neily et al., 2003) has been studied since 2005 for soil C stores (Diochon and Kellman, 2008, 2009; Diochon et al., 2009) and biogenic gas emissions. As part of this study, a set of root exclusion plots were installed in order to isolate heterotrophic respiration in these forest soils. This 20 yr old forest site (plantation) is in close proximity to the studied chronosequence, providing an ideal opportunity to examine in situ microbial respiration processes and to carry out parallel studies using extracted soil cores and controlled climate manipulations.

The stand is situated on well-drained, sandy loam soil within the Governor Lake Ecodistrict in the Eastern Ecoregion of Nova Scotia, Canada. The soil is from the Halifax Series, derived mainly from quartzite, and is an Orthic Humo-Ferric Podzol. The B_{fh} horizons of the Halifax series are known to be high in organic matter (MacDougall, 1963). Soil properties from this site are summarized in Table 1. Soil bulk density was determined using the method of Huntington et al. (1988) due to the rocky nature of these soils. The organic layer was generally quite shallow (less than 5 cm), with a ground cover of mosses and needle litter. The mineral soil depth interval of 0–5 cm was generally coincident with the E horizon, while the remaining soil represented the B horizon. The A horizon was typically <1 cm or absent. This site was previously whole tree harvested. Additional information about sampling methods can be found in Diochon et al. (2009).

The climate of the site is temperate, characterized by warmer winters and cooler summers with a mean annual temperature of 5.8 °C, a mean summer temperature of 16.3 °C, and a mean winter temperature of –5 °C. This site receives 1440 mm of precipitation and has 1522 growing degree-days and 196 growing season days (Neily et al., 2003). The red spruce stands of this forest are typical of the Acadian Forest Region (Mosseler et al., 2003).

2.1 Experimental approach

This study employed both a field and laboratory approach. The presence of in situ root exclusion plots allowed for field measurements of SOM decomposition while a coupled incubation of intact cores was carried out in order to isolate specific environmental responses. The incubation of intact soil cores represents an intermediate between field measurements and highly processed standard laboratory incubations. The original soil structure is maintained in intact cores in order to minimize confounding factors on substrate supply, especially through disturbance. Environmental factors can then be manipulated in isolation in a climate-controlled facility. Eight shallow and four deep samples were extracted from each of three soil plots, for a total of 24 shallow cores and 12 deep cores, allowing for 3 replicates for each experimental treatment.

2.2 In situ gas sampling

Field sampling took place at a series of six root exclusion plots that were established in 2005. The root exclusion plots are 4 m^2 and 1 m deep, with temperature probes (Campbell Scientific 107) inserted at three depths in the subsurface (7.5, 22.5 and 37.5 cm). Time domain reflectometry (TDR) moisture probes (CS 615 and CS 616) were inserted vertically into the soil at each root exclusion plot and data was collected continuously with a datalogger (Campbell Scientific 23X). One PVC collar (10 cm) was pressed into the surface layers of each plot to a depth of approximately 5 cm for placement of a LI-8100 (LI-COR Biosciences, Ltd.) chamber used to measure soil surface CO_2 flux. CO_2 flux was calculated by the LI-COR software from the rate of increase in CO_2 concentration measured by the instrument's infrared gas analyzer (IRGA). The observation length was 2 min with a 20 s deadband. Field sampling occurred biweekly during the growing season (May to November) of 2007 and 2008. Collar offsets were recorded on each sampling day.

2.3 Sample extraction and experimental set-up

Minimally disturbed shallow (0–25 cm) and deep (25–50 cm) soil cores were extracted on 9 and 10 June 2008 from 3 randomly located plots within a 400 m radius of the root exclusion plots. After extraction, they were immediately placed in insulated containers, constructed from 30 cm diameter PVC pipe with a wall thickness of 2 cm cut in lengths of 30 cm. A PVC base (1 cm thick) with a small hole for drainage was fitted to the bottom of each microcosm. Insulation was wrapped around the exterior of the cylinder to minimize radial temperature influences (Reichstein et al., 2005). Immediately following collection, all microcosms were covered with plastic to maintain soil at field moisture until incubation. These microcosms were then transported to the Phytotron, a climate-controlled facility, at the K.C. Irving Environmental Science Centre at Acadia University, Wolfville, NS. Samples were placed on top of large metal trolleys at a height of 1.5 m in triplicate groups (Fig. 1).

Instrumentation

Soil gas exchanges were monitored on 10 cm PVC collars inserted at the soil surface into the centre of each core using one of two portable LiCor CO_2 infrared gas analyzers (LI-COR 8100, LI-COR Biosciences Ltd.). Flux rates were monitored daily for all treatments and a subset were monitored continuously (every 15 min) for up to 24 h. The LI-COR 8100 gas analyzers were calibrated independently two months before use, but linear offsets were applied to the data to calibrate results between the two instruments.

Environmental variables within the room were collected continuously (room temperature and relative humidity). Temperature probes (CS107, Campbell Scientific) were inserted in one set of the triplicate cores at two depths: 5 and 15 cm. Probe data was collected every 15 min with Campbell Scientific 10X dataloggers. Profile soil moisture was measured for each soil microcosm using 30 cm TDR probes inserted vertically or at a slight angle (<10 degrees) (CS616, Campbell Scientific) and installed for the duration of the incubation. Soil moisture was also measured daily on all samples and on a subset of the samples at the surface of the soil core using a 5 cm TDR soil moisture probe (ECHO – Decagon Devices), installed as a peripheral device to one of the LiCor 8100 units.

2.4 Climate-controlled facility experiments

We employed parallel incubations of soil microcosms with constant and diurnal temperature cycling. Half of the shallow samples were placed in one constant temperature treatment (18.5 °C), while the others were placed in a chamber that cycled around a mean temperature of 18.5 °C with an amplitude of 10 °C. This mean and amplitude are the same as the typical July mean air temperature in the region (Halifax Airport, NS). Shallow soils were exposed to both the constant and a diurnal temperature regime. Deep soils were only subjected to a constant temperature regime as this more accurately reflected the dampened temperature signals deep soils would experience in the field setting (Beltrami and Kellman, 2003). The constant temperature chamber shifted by approximately 1 °C d^{-1} and this temperature shift was considered during data analysis. We omitted data from days where high external air temperatures imposed technical constraints on temperature control that compromised the treatment. After 90 days, the mean air temperature of both chambers was raised by 10 °C (from 18.5 °C to 28.5 °C) for 4 days to allow for stabilization at this higher temperature.

Shallow microcosms were incubated the day following extraction for a 95 day period. Deep samples were stored at 4 °C for 39 days. The deep soils replaced the shallow constant microcosms on room trolleys and were then outfitted with temperature and moisture probes and incubated for a 56 day period. After an equilibration period of 2 weeks, the temperature was regulated in both chambers, and microcosm sample moistures were adjusted. The first two weeks of incubation were considered to be an equilibration period, consistent with observations from other soil core incubation studies which have documented a rapid decline in fluxes post-disturbance followed by a leveling off of fluxes (Reichstein et al., 2005).

At fixed moisture contents, high frequency flux measurements (every 15 min) of shallow soil microcosms in the diurnal chamber were used to investigate the flux-temperature relationship. These continuous CO_2 fluxes were observed on a subset of samples that represented a range of moisture contents.

2.4.1 Moisture adjustment

Triplicate soil microcosms were adjusted to four target moistures in both the constant and diurnal temperature environments. The replicate cores (from the three soil plots) were divided into one of four soil treatments that represented target maximum moisture content ranges: (i) <0.1, (ii) 0.1–0.2, (iii) 0.2–0.3 and (iv) >0.3 volumetric water content. Soil was wetted in groups (ii), (iii), and (iv). Soils in wetting treatments were wetted incrementally over a period of two weeks from dry (approx. 0.1 vol/vol) until they reached the targeted water content with measured amounts of deionized water applied with a misting sprayer. Soils in group (i) were never wetted. The slow wetting was performed to minimize the trapping of air within the soil matrix and to allow observation of soil respiration responses to gradual shifts in soil moisture.

Constant shallow soils were wet first, followed by the diurnal shallow and then the deep samples in order to assess the response of CO_2 flux after each incremental wetting event. During the moisture adjustment period, soils from moisture groups (ii), (iii) and (iv) were wet almost every day receiving approximately four or more wettings per day. Total daily water additions were generally less than 20 mm; however, group (iv) microcosms were wet in greater increments (up to 50 mm) once the target moistures of the other samples had been achieved. At this point, the drainage hole was sealed to allow the sample to be wet beyond field capacity. The seal was removed 24 h after observing standing water.

2.4.2 Soil water characteristics

Soil water characteristics (volumetric water content at field capacity and saturation) were determined using the intact cores. The maximum volumetric water content achieved when the soil was saturated was designated as the total porosity (refer to Table 1). The field capacity was taken as the volumetric water content 2 days after drainage (removal of tape). These measurements allowed for an estimation of water-filled pore space (WFPS), a measure of water content allowing better comparisons among sites of similar soil texture. The intact soil pore network of these cores allow for little alteration of natural aggregate dynamics and therefore it is reasonable to use porosity estimates derived from saturation water content to normalize volumetric water content (Reichstein et al., 2005). Volumetric water contents from the TDR probes were converted into WFPS using experimentally determined porosity, such that:

$$\mathrm{WFPS} = \frac{\theta}{\rho} \tag{1}$$

where θ is the volumetric water content and ρ is the soil porosity.

For the purpose of data analysis, moisture conditions were considered to fall under a rewetting (RW) or steady-state (SS) classification, depending on their recent wetting history. Samples that were wet within 5 days were classified as RW, whereas any samples that had not been wet within 5 days were classified as SS.

2.4.3 Monitoring of CO_2 flux

Measurements of CO_2 flux were taken daily when the air temperatures were equivalent in the constant and diurnal treatments. CO_2 flux was measured immediately following each wetting on a subset of the samples. High frequency CO_2 flux measurements were taken overnight on a subset of samples, focusing on the driest and the wettest microcosms to assess changes in respiration with wetting.

2.5 Data analysis

In order to facilitate comparisons amongst soil core replicates, flux data was normalized by dividing by the initial rates after temperature equilibration, allowing for detection of changes in relative fluxes. When considering the effect of soil moisture on SOM decomposition, CO_2 flux data was binned according to soil moisture ranges, where mean fluxes were calculated for bin widths of 0.1 WFPS. This approach was used instead of calculating mean flux on each sampling day because soil moisture was not always the same among the microcosms, despite efforts to ensure that the sample moisture levels increased at the same rate.

All CO_2 flux data was fitted to a two-parameter exponential model with temperature, such that SOM decomposition as CO_2 flux, or soil respiration, R_h:

$$R_h = ae^{bT} \tag{2}$$

where a and b are constants (van't Hoff, 1884). The temperature sensitivity, Q_{10}, could then be generated from the b parameter, such that:

$$Q_{10} = e^{10b} \tag{3}$$

Q_{10} was also calculated from all daily flux data when the chamber air temperature was raised by 10 °C near the end of the experiment (after 90 days). Since the soil temperature did not differ by exactly 10 °C, a modified van't Hoff relationship (Davidson et al., 2006a) was used to generate Q_{10} values at two temperatures, T_1 and T_2, where:

$$Q_{10} = \frac{R_{hT_2}}{R_{hT_1}}^{\frac{T_2-T_1}{10}} \tag{4}$$

Statistical analyses (curve fitting and significance (ANOVA)) were carried out using Sigmaplot 8.0 and SPSS 15.0, respectively. Error measurements are expressed as the standard error (SE) of the mean.

3 Results

3.1 Soil temperature and moisture

During the bulk of the experimental temperature period in the constant room, soil temperature at 5 cm remained relatively constant with a mean of 18.5 °C, fluctuating systematically over the day between 18 °C and 19 °C. In the diurnal chamber air temperature cycled with an amplitude of 10 °C, from 13.5 to 23.5 °C which typically resulted in a soil temperature shift at 5 cm of 5 °C and at 15 cm of 3 °C diurnally.

Surface soil moisture, as measured by 5 cm probes, responded quickly to moisture additions, but recorded profile soil moistures rose only after 2–3 days of consecutive wettings. Soil moisture decreased gradually over time in microcosms without moisture adjustments.

3.2 Soil CO_2 flux – general patterns

Shallow soil fluxes ranged from 0.8 to 4.5 µmol m^{-2} s^{-1} once the climate chambers' temperatures were regulated to a mean of 18.5 °C. CO_2 flux adjusted quickly to the temperature cycles, with stable fluxes in both constant and diurnal samples. Deep soil fluxes were in the range of 0.05 to 0.3 µmol m^{-2} s^{-1}, about an order of magnitude smaller than shallow soils.

The mean cumulative mass of C respired over a 48 day period for all samples in the shallow constant temperature treatment was 41.5 g C (SE = 3.53, $n = 12$) with shallow diurnal samples respiring 31.3 g C (SE = 3.80, $n = 12$). The deep soils respired much less (mean 5.1 g C, SE = 0.38, $n = 12$). Thus the shallow constant temperature incubation was 714% greater and shallow diurnal was 514% greater than the deep soils over a similar time period. Adjusted for C content (Table 1), the contribution from the shallow constant and shallow diurnal would become only 210% and 134% higher, or three times and two times as high as the deep, respectively.

3.3 CO_2 flux across a range of soil moisture conditions

CO_2 fluxes under steady-state conditions (no wetting events within 5 days) were differentiated from rewetting fluxes. Figure 2a and b demonstrate the relationship between CO_2 flux and WFPS for rewetting (RW) and steady-state (SS) conditions from shallow and deep soil under constant temperature conditions. In shallow soils, a temporary elevated flux response is seen after wetting until 0.4 WFPS. After this point up until 0.6 WFPS, normalized fluxes are variable but similar for both RW and SS conditions. Above a WFPS of 0.60, the flux rates for both RW and SS conditions drop. Except for the initial rewetting, enhanced respiration with rewetting as measured by flux was not observed in the deep samples (Fig. 2b). Deep samples showed no discernable pattern with WFPS, with a range of normalized flux values across the moisture range. Deep microcosm contributions to total profile flux were less variable than shallow, representing generally less than 10% of the combined total flux from both soil layers across the moisture range (Fig. 2c).

Segments of the data where changes in the moisture flux relationship were evident occurred for <0.20 WFPS, 0.20 to 0.60 WFPS and >0.60 WFPS. The relationship between CO_2 flux and moisture once average moisture was below 0.20 WFPS shows a significant exponential relationship between mean flux and mean WFPS ($r^2 = 0.92$) (Fig. 3a). When soil moisture was above 0.60 WFPS (Fig. 3b), the decline in fluxes was best described by an exponential decline ($r^2 = 0.88$, $P < 0.001$) between flux and soil moisture.

3.4 The influence of temperature on CO_2 flux

Clear exponential relationships were observed between CO_2 flux rates and temperature at 5 cm depth for samples over the course of a diurnal air temperature cycle across moisture contents ranging from 0.11 to 0.58 WFPS (Fig. 4). The magnitude of the effect of temperature on soil respiration was influenced by the moisture content and wetting classification (RW vs. SS). Soils that were dry but rewet (0.11 RW) experiences a much higher increase in CO_2 flux with a change in temperature then the steady-state conditions (0.11 SS), and respired on par with rewet soils at a higher moisture content (0.34 RW). If a soil was wet to above 0.40 WFPS, the flux-temperature relationships followed an intermediate trajectory that did not depend on wetting status (i.e. 0.42 RW and SS). If the soil was very wet (0.54 WFPS), flux-temperature relationships were in the same range as those for dry SS soil. Results from regression fits with Eq. (2) for the plots in Fig. 4 are listed in Table 2. All flux temperature relationships were significant at $P < 0.0001$.

A general estimate of temperature sensitivity, Q_{10}, for all samples (constant, diurnal and deep) was calculated from fluxes before and after a 10 °C rise in the climate chamber air temperature using Eq. (3) and were related to the sample WFPS (Fig. 5). No significant difference in Q_{10} (overall mean = 2.19, $n = 12$, SE = 0.07) for any of the samples and treatments across moisture was observed (one way ANOVA, $P > 0.05$) for a range of Q_{10} values from 1.73 to 2.66 (constant), 1.88 to 2.68 (diurnal) and 1.29 to 3.23 (deep).

3.5 In situ respiration-temperature relationships

A total of 159 surface CO_2 flux measurements were taken at the field site root exclusion plots in 2007 and 2008 (combined).

Surface CO_2 fluxes for 2007 ranged from 0.96 $\mu mol\,m^{-2}\,s^{-1}$ to 8.82 $\mu mol\,m^{-2}\,s^{-1}$, with a mean of 3.98 $\mu mol\,m^{-2}\,s^{-1}$ (SE = 0.4) and a median of 3.16 $\mu mol\,m^{-2}\,s^{-1}$. Surface CO_2 flux for 2008 ranged from 0.61 $\mu mol\,m^{-2}\,s^{-1}$ to 5.34 $\mu mol\,m^{-2}\,s^{-1}$ with a mean of 2.1 $\mu mol\,m^{-2}\,s^{-1}$ (SE = 0.1) and a median of 1.78 $\mu mol\,m^{-2}\,s^{-1}$.

Temperature was the main factor controlling CO_2 at the root exclusion plots. Field CO_2 surface flux temperature relationships from the root exclusion plots show exponential relationships (Fig. 6) through the 2007 and 2008 growing seasons with a correlation coefficient (r^2) of 0.85 ($P < 0.0001$). Flux measurements taken within days of a rainfall were generally elevated relative to other periods. When all measurements taken on days within 5 days of a rainfall event (classified as RW) were removed from the regression, the exponential relationship between mean flux and mean soil temperature improved to an r^2 of 0.99 ($P < 0.0001$). The Q_{10} (calculated using Eq. 2) changed little (from 3.06 to 3.10) with the RW samples removed.

4 Discussion

4.1 Moisture sensitivity of SOM decomposition in shallow soil cores

The challenge in decoupling temperature and moisture-driven CO_2 flux responses was dealt with by employing an incubation approach that held one variable constant while varying the other(s). Overall, the results of this study support the general consensus that the optimal soil moisture for heterotrophic respiration exists at intermediate water contents, which represents a balance between solute diffusion through continuous soil water films on the lower end and limits upon rates of gas transport on the upper end of the moisture spectrum (Skopp et al., 1990; Howard and Howard, 1993). Based on the results from Figs. 2–6, the optimum moisture level for soil respiration under steady-state moisture conditions for the studied soils generally ranged from 0.20 to 0.60 WFPS. Within this intermediate range, a plateau of CO_2 flux was observed (Fig. 2). These results are consistent with those of Schjonning et al. (2003); Pumpanen et al. (2003) and Schindlbacher et al. (2008) who identified a range of 25 to 45% volumetric water content as optimal for microbial activity. Not all studies identify such a broad optimal moisture range, though. Optimum soil moisture for microbial processes for a spectrum of soil types have been identified at 50–60% water holding capacity (Linn and Doran, 1984; Howard and Howard, 1993) while Grant and Rochette (1994) found an optimum respiration at 0.6 to 0.7 of total porosity, and Illeris et al. (2004) observed the highest respiration rates and temperature sensitivity at 25% VWC. Differences in soil structure and texture, methodology and the choice of soil moisture metric may result in

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inconsistencies among studies; this suggests that reported optimal moisture contents are site- and study-specific.

Under the experimental conditions of this study, the relationship between CO_2 surface flux and water content for shallow soils displayed threshold behaviour. Below a lower and above an upper threshold, CO_2 flux is dependent on moisture, while within an intermediate moisture range, soil water content was no longer the dominant factor controlling of respiration, and instead, variation in CO_2 flux depended mainly on temperature. Recent studies have documented similar results (Liu et al., 2002; Xu et al., 2004; Rey et al., 2005; Ball et al., 2009). A threshold type relationship is consistent with the nature of soil spatio-temporal dynamics (Di Domenico et al., 2007); according to the analytical model of (Manzoni et al., 2004), a change in the system dynamics as the system changes from dry to adequately watered, and then again when the soil is saturated.

In soils drier than the optimum range, heterotrophic respiration under steady-state conditions decreases with soil moisture, such that below 0.20 WFPS, CO_2 flux is correlated exponentially with moisture (Fig. 3). Respiration has been observed in other studies to decrease in incubated soils (in both mineral and organic horizons) with increasing water potential (Orchard and Cook, 1983; Skopp et al., 1990). Studies suggest that as soils dry, a decrease in microbial biomass is correlated with the length of drying, and this would reduce heterotrophic soil respiration (Schimel et al., 1999). A lower threshold in a similar range (below 0.20 WFPS) has been identified in field studies; Knohl et al. (2008) found that once soil moisture dropped below 23% VWC in a beech forest water limitations were apparent, and Rey et al. (2002) observed a lower threshold of 20% VWC. Others have found it to be near 15% VWC (Xu and Qi, 2001a; Yuste et al., 2003; Xu et al., 2004; Inclan et al., 2007; Almagro et al., 2009) or even lower (Davidson et al., 1998; Jassal et al., 2008). Below a water-holding capacity of 0.123 (volumetric water content), Yuste et al. (2003) used a linear model to predict the effect of soil water content on soil respiration, restricted to measurements where no rewetting occurred. Below the optimum water content threshold, soil water films are discontinuous and solute diffusion is thought to cease (Schjonning et al., 2003). This point is thought to represent a moisture level in the soil at which WFPS within the soil matrix suddenly becomes disconnected (Moldrup et al., 2001).

As the soils were wetted above the optimum range, CO_2 flux declined rapidly. This upper threshold of 0.60 WFPS represents the field capacity for these soils, and thus is a point beyond which water begins to impede gaseous transport. Above the optimum range, water fills pores between aggregates and air-filled pore space becomes discontinuous. In situ, observed rapid declines in diffusivity near saturation have been suggested to be the result of preferential recruitment of large pores for diffusion (Risk et al., 2008a). Maintaining the natural soil structure in this study (with intact cores) meant that the pore network remained largely unaltered from in situ conditions, and could explain why we observed such sharp changes near threshold moisture contents.

4.2 Moisture sensitivity of SOM decomposition in deep soil cores

In contrast to shallow soils, CO_2 flux from deep soil cores was an order of magnitude lower (Fig. 2b). A lower and upper threshold at 0.20 and 0.60 WFPS (Fig. 2–4) was observed, but the differences in flux within the optimum range were not significant. This may be attributed to different controls on heterotrophic respiration for surface and subsurface soil horizons; Davidson et al. (2006b) found that the water content was a predictor of CO_2 production only in the organic horizon of sandy loam soil in a mixed deciduous forest, and below this depth, flux did not vary significantly with water content. Similarly, Fierer et al. (2003a) found that surface soils were more sensitive to drought, while the subsurface was controlled by temperature and nutrient inputs.

The decline in flux rates after extraction was more pronounced for deep than shallow soil cores, as also observed by Reichstein et al. (2005) in their intact soil core incubations. In our study, the deep soils would not have contained labile decaying root structures, so the reason for the decline in flux would be different than in the shallow soil microcosms. We speculate that the microbial community in the deep microcosms may have been particularly sensitive to the large initial decline in moisture content, which dipped below 0.06 WFPS in most samples during this equilibration period before moisture adjustment. Without data on the microbial biomass, however, it is difficult to ascertain whether this contributed to the decline in CO_2 flux rates.

It has been observed that SOM in deep soils can be spatially heterogenous and inaccessible (von Lutzow et al., 2006; Chabbi et al., 2009), making this SOM unavailable for microbial processing, regardless of the soil moisture status. Furthermore, deep SOM is generally thought to be dominated by lower quality substrate which requires more energy to decompose (Bosatta and Agren, 1999; Paul and Clark, 1996). Perhaps substrate availability was a clear controlling factor in deep soils: it is known that SOM in deeper layers are mostly associated with the organomineral fraction (Diochon and Kellman, 2008), a less bioavailable C pool due to strong mineral interactions with organic matter. Recent evidence demonstrates that SOM in deep soil is indeed protected from decomposition by a suite of physical factors, which may be more important than inherent substrate quality (Gillabel et al., 2010; Risk et al., 2008b; Xiang et al., 2008). A lack of response from the deep soil could also be related to the nature of the moisture inputs. In situ inputs would have been leachate from rainfall events at the surface with dissolved organic matter (DOM), but recent evidence points to enhanced decomposition of deep soil C with inputs of labile C (Fontaine et al., 2007), and water itself may not be capable of stimulating microbial activity (Salome et al., 2009), especially if nutrient status and substrate quality are also limiting factors. It is possible that the moisture sensitivity cannot be adequately detected with this experimental setup for deep SOM, especially since CO_2 fluxes were low. Further work in this area is required.

4.3 CO_2 flux-temperature relationships

Results from analysis of high frequency CO_2 flux data (every 15 min) of surface soils under a diurnal temperature regime demonstrate a high correlation between CO_2 flux and temperature (Fig. 5). All samples with a moisture content below 0.4 WFPS respired at a higher magnitude if rewetted compared to those in steady-state. Within an intermediate moisture range, but above 0.40 WFPS, steady-state and rewet samples respired similarly. For soils in steady-state below 0.20 WFPS, and above 0.60 WFPS, the magnitude of the flux response to temperature was lower than at intermediate water contents. The observed flux magnitude depended on soil moisture content, and this was consistent with the results summarized in Fig. 2 for soils at constant temperature. The CO_2 flux-temperature relationship can thus be influenced by soil moisture in two ways: the moisture content and the wetting history.

Despite extended drying, we did not observe the expected decoupling of fluxes from temperature at low moisture contents reported by some studies (Davidson et al., 1998; Lavigne et al., 2004; Jassal et al., 2008). Even though we observed a drastic reduction in moisture and a clear relationship between moisture and flux, the daily pattern in respiration rates at low moisture contents were still driven by diurnal temperature changes (data not shown). Shallow soils of coniferous forests are populated by fungi and actinomycetes, which are indeed better adapted to drought conditions than bacteria (Orchard and Cook, 1983; Fritze et al., 2000), and so perhaps the microbial communities of these soils are able to tolerate extended drought stress. In addition, water vapour moves through soil diurnally with temperature, and this moisture could have been enough to sustain a low level of microbial activity. For instance, Dirks et al. (2010) found that in chronically dry soils, water vapour movement determines the daily variation in flux.

Temperature sensitivity

This study isolated the temperature sensitivity of SOM decomposition in the absence of confounding disturbance effects. While the methodology does not entirely reproduce field conditions (i.e. no constant supply of readily decomposable substrate), the use of intact soil cores allowed for a more realistic examination than incubations of processed soil.

The temperature sensitivity estimates calculated from these results were generally lower than those obtained in other long term intact soil core incubations, such as Reichstein et al. (2005), but were in a similar range as the results of Yuste et al. (2007).

Values of Q_{10} determined here were also lower than those found in other studies at the ecosystem scale (Raich and Schlesinger, 1992; Xu and Qi, 2001b) and in other laboratory studies (Kirschbaum, 2000; Reichstein et al., 2000; Fierer et al., 2005; Fang and Moncrieff, 2001). Indeed, factors that influence substrate availability, such as physical disturbance and substrate accessibility (Davidson et al., 2006a), are purported to create apparent responses instead of a true temperature sensitivity.

Low temperature sensitivity values (near 2) across a full range of soil moisture contents was also unexpected. Soils are thought to be less sensitive to temperature at low moistures (Yuste et al., 2007), with temperature sensitivity increasing up to an intermediate optimum moisture range and then decreasing again at higher moistures (Craine and Gelderman, 2011; Illeris et al., 2004; Jassal et al., 2008). However, some other studies found little to no change in Q_{10} with soil moisture for incubated samples (Reichstein et al., 2005; Rey et al., 2005). Perhaps factors other than soil moisture affected the incubated soils' response to temperature that differed from field studies. For instance, many in situ temperature sensitivity estimates would have included the contribution from roots, which respond to covarying temperature and moisture changes, and affect readily decomposable substrate supply through root exudate delivery. It is likely that the isolated heterotrophic response to temperature as determined from root-free soil cores is distinct from the response from in situ temperature sensitivity estimates: indeed, this experiment may have successfully separated the temperature sensitivity from factors that create an apparent response.

Although deep soils did not exhibit the responses to moisture additions observed in shallow soils, a relationship was observed between temperature and flux for deep soils. Small daily temperature shifts in the constant temperature chamber resulted in no observable change in flux, but the 10 °C shift at the end of the experiment produced a measurable change, with a temperature sensitivity in the same range as the shallow soils. No overall increases in temperature sensitivity compared to surface soils were observed for deep soils (Fig. 2). The temperature sensitivity has been predicted from modeling studies, based upon theoretical responses of SOM to temperature (Davidson and Janssens, 2006), to be greater for subsurface soils than shallow horizons (Liski et al., 1999; Fierer et al., 2003a). In many experimental observations, however, it has been found to be lower than (Gillabel et al., 2010) or similar to that of surface soils (Fang and Moncrieff, 2005; Reichstein et al., 2005). Certainly, it has been found that the Q_{10} increases for subsurface soils due to the differing sensitivity of the microbial community through depth to temperature changes (Fierer et al., 2003b). However, Conant et al. (2008) and Reichstein et al. (2005) observed that soils which were more depleted in organic matter, such as deep soils, were more sensitive to temperature. This trend was not, however, noted in these soils under the experimental conditions employed.

Many reasons can be suggested for the low temperature sensitivity of deep soil microcosms. Deep soil contains a much higher proportion of recalcitrant substrates, such as humic acids, with a lower substrate availability, and so according to enzyme theory, the temperature sensitivity should be high, as long as substrate release itself is temperature sensitive (Larionova et al., 2007; Gershenson et al., 2009). However, other factors can control substrate availability: coniferous soils contain a high proportion of waxy OM which have lower C/N ratios (Gleixner, 2005) and can become water-repellent upon drying, thus reducing availability (Borken and Matzner, 2009). Rewetting did not seem to improve substrate availability for deep soils, and if SOM was hydrophobic, water additions could not have mobilized substrate in the manner proposed by Xiang et al. (2008). Another possible reason for insensitivity to temperature is nutrient limitations at depth: Fierer et al. (2003a) noted that the addition of N or P increased respiration rates by 450%. Finally, the role of physical protection in attenuating responses of SOM decomposition to temperature, as discussed in Section 4.2, must be considered as a key factor controlling subsoil C dynamics.

4.4 Comparing field and microcosm CO_2 flux

Soil CO_2 fluxes from the microcosm experiment were in the same range as those from the field site. Initial respiration rates were slightly higher than the field fluxes, but this difference could be explained by higher temperatures (by 10 °C) in the climate chamber and by the contribution by decaying root structures to the labile C pool (Reichstein et al., 2005).

Fluxes decreased quickly over a period of 20 days, leveling off over time, in a manner that could not be explained by temperature or moisture. After that initial large decay during the equilibration period, any declines in flux could be accounted for by changes in moisture levels. This trend has been observed in other studies with intact cores and has been attributed to the rapid decomposition of severed fine root structures (labile C) in organic horizons (O'Connell, 1990; Reichstein et al., 2005). After this equilibration period, the response of flux can be assumed to be primarily from native SOM instead of substrate released as a result of extraction artifacts. Overall, the similarity in fluxes between field and lab points to minimal disturbance incurred from the extraction.

The seasonal temperature sensitivity estimate, Q_{10} (calculated with Eq. 3), for root exclusion plots was 3.10 (with rewetting events removed from the data), but the temperature sensitivity estimates determined from the climate-controlled chamber were close to 2. While temperature sensitivity estimates from field root exclusion sites are higher, the surface CO_2 fluxes from these field sites are in the same range as the incubations. We interpret this to mean that the observed temperature sensitivity of SOM decomposition is artificially inflated due to processes that are functioning only in situ. Temperature-related processes that control substrate accessibility should be considered (Davidson et al., 2006a), including the activity of soil fauna, and other biological processes that influence nutrient turnover. For instance, perhaps the small amount of ground vegetation and associated fungi on the surface of the root exclusion plots, while absent directly under the PVC collar where CO_2 flux was measured, played a role in altering the response of SOM decomposition to temperature. If incubated soil cores consistently underestimate the temperature sensitivity of root exclusion plot soils, this difference in temperature sensitivity needs to be quantified and should be taken into account for scaling purposes.

Relevance to in situ processes

Rewetting of the shallow soil surface layers results in a higher soil flux for up to 5 days. Fluxes from trenched and clear cut soils, which likely experience surface drying and high subsurface moisture due to decreased root uptake, can be susceptible to a higher dependency on water content, since high pulses of CO_2 result from rainfall events, and very low or negative fluxes can result from saturation of the soil profile. This should be taken into account for ecosystem modelling along forest landscape gradients, and more work should be performed to quantify rewetting effects. Throughout the year these forest soils will be within the optimum moisture range, with only surface soils possibly dropping below the lower moisture threshold. This was apparent from the relationship between soil respiration and temperature (Fig. 7). The removal of points immediately after rainfall events improved the fit for exponential flux temperature relationships.

5 Conclusions

Overall, this study demonstrates that for soil moisture conditions experienced by most sites in this region, flux-temperature relationships alone can be used to reasonably estimate heterotrophic respiration. It is only at extremes that moisture exerts a more important control upon soil respiration.

This incubation approach is a valid intermediate between field root exclusion plots and standard laboratory soil incubations. Heterotrophic respiration from soil cores are consistent with the surface flux observed at the field sites, yet allow for the controlled manipulation of a single variable at a time. Soil cores retain the intact soil structure and thus mimic realistic physical controls on SOM decomposition, a factor which is particularly important for obtaining realistic estimates from deep soils.

This study has thus provided interesting and valuable insight into the threshold nature of the relationship between moisture and SOM decomposition. Although labour intensive, this approach is recommended for those trying to understand soil processes that might be altered by the conditions of standard laboratory incubations.

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Table 1. Important physico-chemical site characteristics for Shallow and Deep soil layers from a 20 yr old red spruce plantation at Abraham's Lake, Nova Scotia. Numbers in brackets indicate 1 standard error (SE). Soil moisture indicators were derived from core samples used in this study. All other data from (Diochon, 2009).

Property (units)	Shallow	Deep
Depth (cm)	0–25	25–50
Bulk Density (g cm^{-3})	0.98 (0.03)	1.32 (0.01)
C Storage (Mg C ha^{-1})	12.3 (1)	29.4 (8)
% C	3.0 (0.4)	1.2 (0.3)
N Storage (Kg N ha^{-}1)	722 (70)	2040 (400)
% N	0.19 (0.02)	0.13 (0.03)
C/N Ratio	17.0 (0.8)	13.8 (1)
pH	3.97 (0.08)	4.15 (0.10)
Soil Texture	sandy loam	sandy loam
Field Capacity (vol/vol)	0.37 (0.04)	0.27 (0.02)
Porosity (vol/vol)	0.58 (0.03)	0.40 (0.04)

Table 2. Regression fits and model coefficients (a and b) for a 2 parameter exponential model of CO_2 flux (R_h) data versus temperature (T) for one sample with a diurnal cycling across a moisture range, where is $R_h = ae^{bT}$. SS indicates steady state conditions, and RW indicates a recent rewet. All regressions are significant at $P < 0.0001$.

Moisture	a	b	r^2
0.11 SS	0.241	0.0913	0.98
0.11 RW	0.404	0.0900	0.98
0.34 RW	0.431	0.0863	0.93
0.40 RW	0.534	0.0610	0.89
0.40 SS	0.483	0.0653	0.83
0.58 SS	0.291	0.0846	0.94

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Fig. 1. Experimental set-up in one chamber at the Phytotron facility. Soil microcosms were placed in on trolleys in the climate chamber in triplicate groups that represent the four moisture treatment groups.

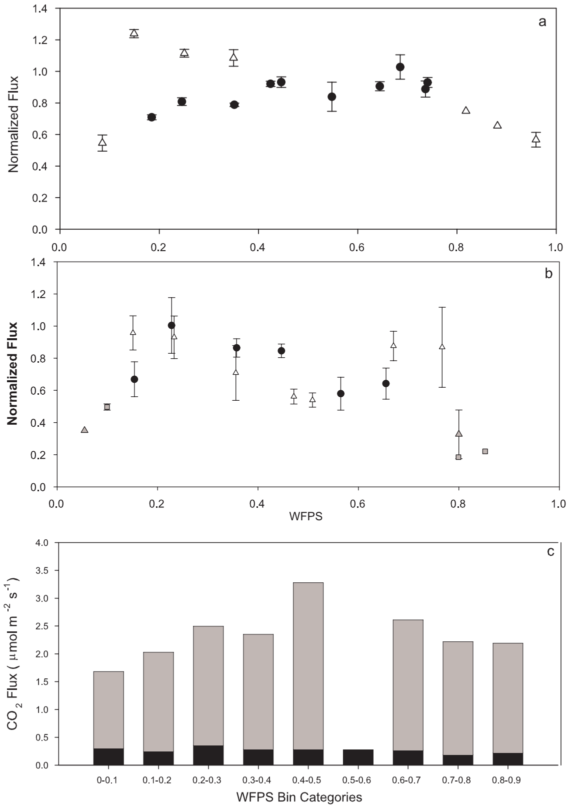

Fig. 2. Normalized carbon dioxide (CO_2) flux for binned data for Shallow **(a)** and Deep **(b)** samples during rewetting (open triangles) and steady-state (filled circles) conditions. Bin widths are 0.1 WFPS. Error bars represent 1 SE. Total flux contribution from Shallow (upper portion, grey) and Deep (lower portion, black) are shown in **(c)**. Deep fluxes are usually less than 10% of the combined total flux. Note that in **(c)** there is no bar for the shallow soil 0.5–0.6 WFPS bin due to absence of data for this range.

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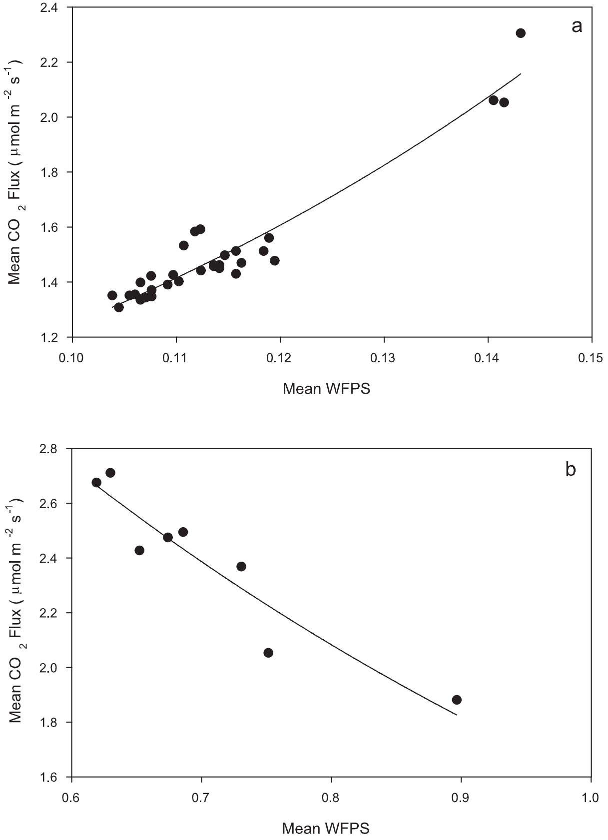

Fig. 3. Relationship between mean CO_2 flux and mean moisture content (WFPS) for moisture groups ($n = 3$) when the average moisture content was **(a)** under 0.20 WFPS and **(b)** above 0.60 WFPS. The regression fits for the exponential relationships in **(a)** ($R = 0.3494\,e^{12.72\,M}$, $r^2 = 0.92$) and **(b)** ($R = 6.1944\,e^{1.325\,M}$, $r^2 = 0.89$) are both significant at $P < 0.0001$.

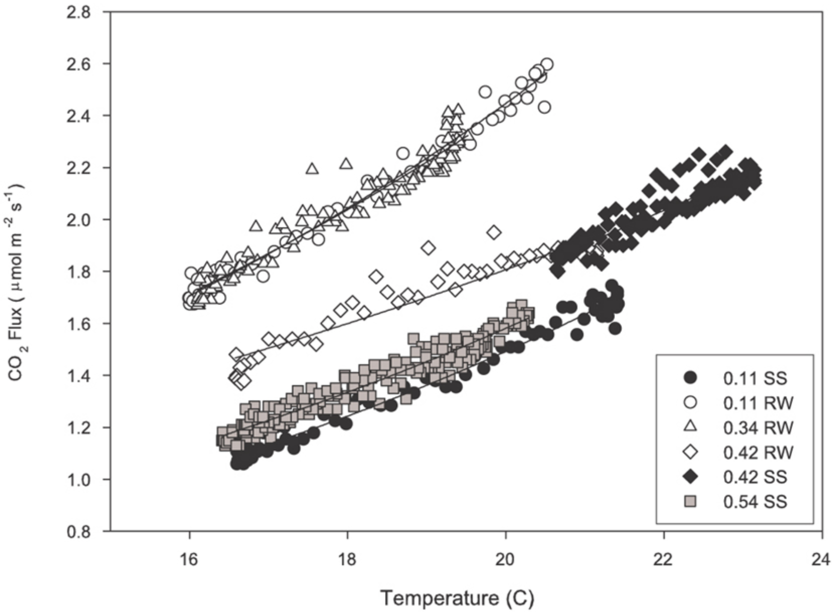

Fig. 4. Response of CO_2 flux to temperature for selected moistures (WFPS) and conditions (RW is rewet and SS is steady-state conditions) for one sample exposed to a diurnal temperature cycle. All regressions are significant to $P < 0.0001$. Regression results and parameters are listed in Table 2.

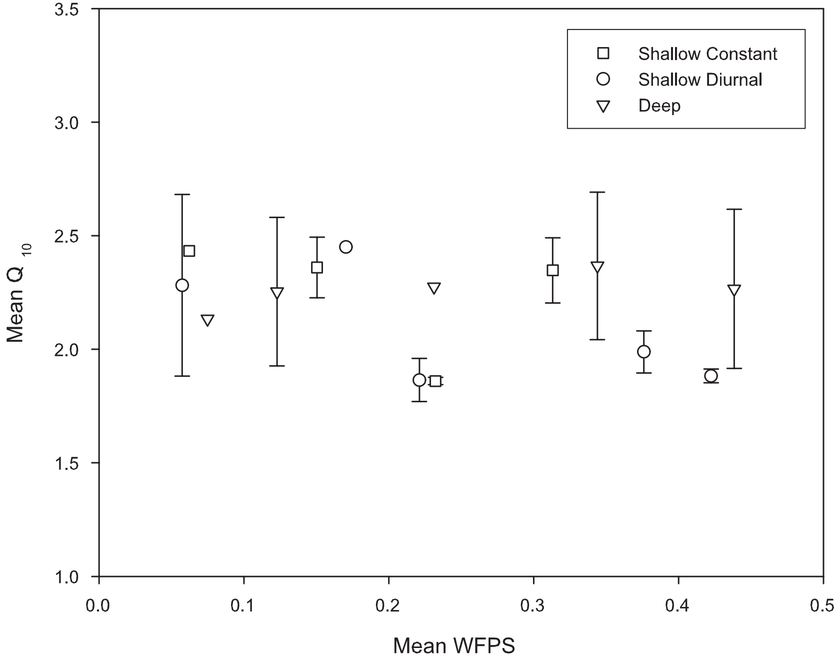

Fig. 5. Temperature sensitivity of soil respiration for constant (squares), diurnal (circles) and deep (triangles), assessed as: mean Q_{10} as a function of RWC for all moisture groups ($n = 3$). Error bars represent 1 SE. Q_{10} estimates across moisture, depth and temperature regime were not significantly different (ANOVA, $P > 0.05$).

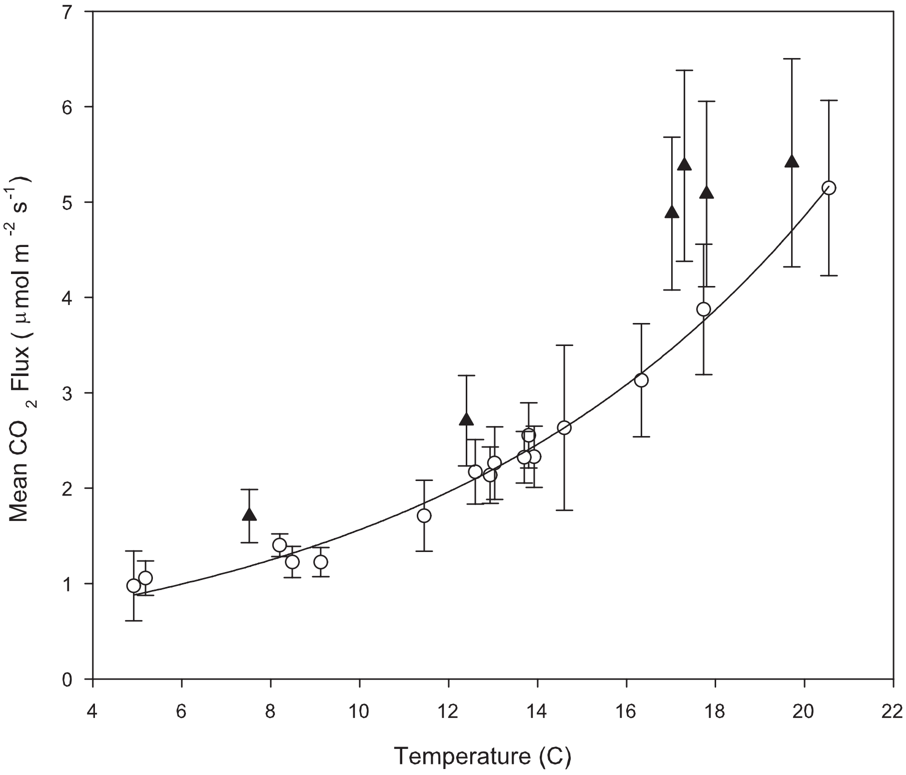

Fig. 6. Response of mean CO_2 flux to mean soil temperature for root exclusion plots at Abraham's Lake for the growing season (May to November), 2007 and 2008. Each point is a mean of 6 root exclusion plots and error bars represent 1 SE. Filled triangles are mean fluxes for days immediately after a rainfall event and are not included in the nonlinear regression between mean flux and mean soil temperature ($r^2 = 0.99$, $P < 0.0001$).