The effect of warming on the CO_2 emissions of young and old organic soil from a Sitka spruce plantation.

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Abstract
Under strictly controlled laboratory conditions we investigated the response of soil respiration to increasing temperature. Soil fractions from a Sitka spruce (*Picea sitchensis* (Bong.) Carr.) plantation were sampled to represent "fresh" (i.e. shallower and containing more labile substrates) and "old" (i.e. deeper and presumed to contain more recalcitrant substrates) carbon sources. The soils were incubated at temperatures between 5 - 30 °C, with CO_2 efflux measured using a tunable diode laser. "Fresh" soil showed substantially higher CO_2 effluxes than "old" soil, whilst respiration from "fresh" soils was more sensitive to temperature in the range 5 - 10 °C. After a prolonged (56 day) incubation at 20 °C the response of soils to increasing temperature was re-tested over the same temperature interval. The CO_2 fluxes from both "fresh" and "old" soils were lower than the initial measurements, but the sensitivity to temperature had increased in both "fresh" and "old" soils.

Key Words
Temperature sensitivity, heterotrophic respiration, labile and recalcitrant carbon.

Introduction

Soil organic matter plays a major role in the carbon cycle. The emission of CO_2 from organic matter stored in soils is one of the largest fluxes in the global carbon cycle, so small changes in the size of this flux can have a large effect on atmospheric CO_2 concentrations (Schlesinger and Andrews 2000) and thus constitute a powerful positive feedback to the climate system. Approximately 1500 Gt of organic carbon is stored in the world's soils to a depth of 1 m, with a further 900 Gt between 1-2 m (Kirschbaum 2004). Of particular concern is the fact that soils of high latitudes include many peatlands and other organic soils, and store approximately one third of soil carbon globally (Biasi *et al.* 2005), whilst global warming is expected to be more pronounced at these high latitudes (IPCC 2007). The temperature sensitivity of soil respiration has been a topic of intense debate over recent years, as summarised by Davidson and Janssens (2006). There is evidence to suggest that under higher temperatures soil carbon decomposition will increase, thus resulting in increased CO_2 emissions from heterotrophic respiration (Knorr *et al.* 2005). However there is a contrasting opinion that soil carbon decomposition will be rather insensitive to temperature (Giardina and Ryan 2000), being mostly determined by the supply rate of substrate. Much of the debate considers the temperature sensitivity of the labile versus recalcitrant fractions of the soil carbon. As a large component of SOM is made up of such recalcitrant material, the temperature sensitivity and potential availability as a substrate for microbial respiration of this pool are of acute importance with respect to climate change (Biasi *et al.* 2005).

Materials and methods

Site description and soil sampling
Samples for incubation were collected within Harwood Forest, Northumberland, England (55° 12′ 59" N, 2° 1′ 28" W), a forest consisting of mainly even-aged stands of Sitka spruce (*Picea sitchensis* (Bong.) Carr.). The dominant soil type found in Harwood forest is peaty gley, a soil that is seasonally waterlogged (Zerva *et al.* 2005). Sampled soils were separated into shallow ("fresh") (5 – 15 cm, O_L layer) and deep ("old") (20 – 30 cm, A layer) samples and transported back to the laboratory where they were stored until preparation for incubations began. Average soil C content was 39.1 % in the "fresh" samples, and 21.7 % in the "old" samples, whilst ^{14}C dating of samples aged the "fresh" samples between ~0 – 200 years, and the "old"samples at ~2100 years.

Incubation experiment and respiration measurements
Before the incubation experiment began, all soils were sieved to 4 mm. They were weighed and placed into modified 500 ml Erlenmeyer flasks. Each flask held approximately 500 g of soil at field moisture content. Flasks (n = 6) were then placed into a temperature-controlled waterbath. The initial incubation temperature was 5 °C, and once respiration rates had stabilised at this temperature for ~48 hours the temperature was

increased up to a maximum of 30 °C, before the temperature was decreased back down to 5 °C. At each temperature step, respiration was measured for ~48 hours after rates had stabilised. The total time course of the initial incubation experiment was 22 days. After the initial experiment flasks containing the soils were incubated at 20 °C for 56 days, after which the same incubation from 5 - 30 °C was repeated.
Total heterotrophic soil respiration was determined using a tunable diode laser absorption spectrometer (TGA 100A, Campbell Scientific Inc., Logan, Utah, U.S.A.), using methods described in detail in Bowling *et al.* (2003). Respiration from each flask was calculated using the difference in CO_2 concentrations measured from the reference and sample flasks (containing soil), and the total dry weight of the soil in each flask.

Calculation of Q_{10}
Q_{10} can be defined as the factor by which respiration rate increases for a temperature interval of 10 °C. This relationship between soil respiration and temperature was defined by using the following approach from Fang *et al*. (2005): Mean respiration rates were first fitted with Exponential and Arrhenius models:
$F = ae^{bT}$ (Exponential), where F is respiration rate, a and b are fitted parameters and T is the temperature.
$F = ae^{-E/(RT)}$ (Arrhenius), where F is the respiration rate, a is a constant, E is the activation energy, R is the universal gas constant and T is the absolute temperature (K).
Q_{10} was then determined for the models, as well as the actual data using:

$Q_{10} = \frac{F_{T+10}}{F_T}$, where F_T and F_{T+10} are respiration rates at temperatures of T and T+10.

The relative increase in respiration rate $(\Delta F/\Delta T)/F_T$ was calculated from the derivative of a fitted polynomial equation, using observed values of temperature (T) and respiration rate (F), as per Lloyd and Taylor (1994).

Results
Effect of temperature on CO_2 flux from "fresh" and "old" organic matter
During the initial incubation experiment, heterotrophic soil respiration from both the "fresh" and "old" soils increased significantly as the temperature was increased from 5 - 30 °C, with the flux from the "fresh" soils ~2.4 times greater than from the "old" soils (Figure 1). The temperature sensitivity (Q_{10}) of soils during the initial incubation experiment (across the entire measured temperature range) was higher in the "fresh" soils compared to the "old" soils (2.38 and 2.18 respectively), irrespective of the method of obtaining Q_{10}.

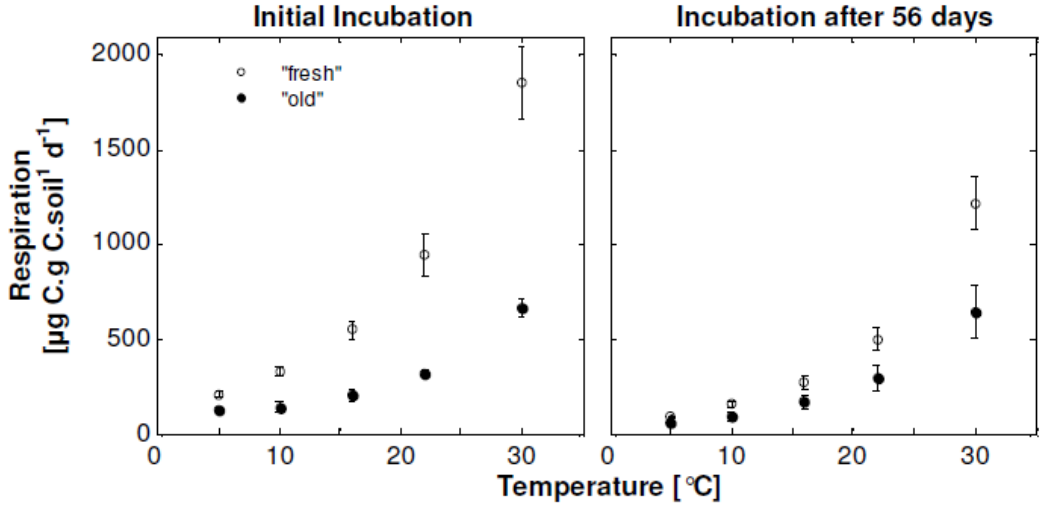

Figure 1. Mean respiration rates of "fresh" and "old" soil organic matter samples incubated from 5 - 30 °C. Initial incubation results and incubation results after 56 days at 20 °C are on the left and right panels respectively. Respiration rates are expressed as per mass of carbon, and error bars are one standard error of the mean (n = 3).

Following constant incubation at 20 °C for 56 days, heterotrophic soil respiration from both "fresh" and "old" soils still responded significantly to increasing temperature, however respiration had decreased in the "fresh" and "old" soils compared to the initial incubation experiment by factors of ~2 and ~1.5 respectively. Fluxes from the "fresh" soils were still significantly higher than the "old" soils although this difference was smaller than during the initial incubation experiment (Figure 1). The measured Q_{10} across the entire temperature range increased after incubation at 20 °C. The Q_{10} of the "fresh" samples was still higher than the "old" (2.77 and 2.51 respectively), however both samples had higher Q_{10} values than that of the initial experiment.

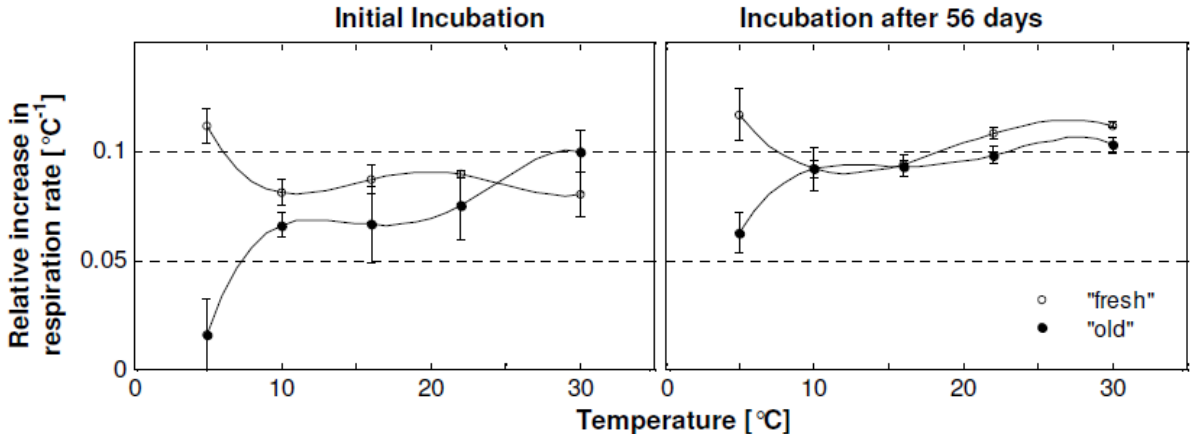

Figure 2. The relative sensitivity of soil respiration to changes in soil temperature, during the initial incubation and incubation after 56 days at 20 °C, calculated using rates adjusted for percentage carbon and bulk density. Smoothed curves have been fitted to values calculated as the derivative of the polynomial fit (see methods), and error bars are one standard error of the mean (n = 3).

To explore the temperature sensitivity of respiration, it is widely acknowledged that the Q_{10} is not a very precise parameter as it averages across a broad range of temperatures. We therefore used the relative increase in respiration, defined by Lloyd and Taylor (1994). During the initial incubation it showed a significant difference between "fresh" and "old" samples at 5 °C ($p < 0.01$), and a significant response to temperature between 5 - 10 °C ($p < 0.01$). After the initial decrease from the "fresh" samples, both samples showed a slight increase in the relative increase in respiration rate in the range 10 - 30 °C (Figure 2). Following incubation at 20 °C for 56 days, the relative increase in respiration rate showed a significant difference between "fresh" and "old" samples at 5 °C ($p < 0.01$), and a significant response to temperature between 5 - 10 °C ($p < 0.01$)(Figure 2). The relative increase in respiration however remained relatively constant for the "fresh" samples, whilst the "old" samples showed an increase with temperature.

Discussion

Respiration after initial and 56 day incubations

The effect of temperature on soil respiration from both the "fresh" and the "old" samples was clearly apparent, with CO_2 flux showing a near-exponential increase with temperature during both the initial incubation, and incubation after 56 days at 20 °C. This relationship was first described by Lundegårdh (1927) and has since been studied and quantified for various soil types from different environments (Kirschbaum 1995). Raw respiration rates measured in the present study were comparable to those from similar studies (Andrews *et al.* 2000; Fang *et al.* 2005). Respiration from the "old" samples was significantly lower than the "fresh" samples. This can be explained by the presence of a high proportion of recalcitrant carbon in the "old" samples. It has been shown that stores of carbon at depth are usually more resistant to decomposition by soil microbes due to their inherent physical properties and chemical constituents (Fierer *et al.* 2003), and recalcitrant soil fractions enriched with resistant alkyl carbon structures increase with soil depth and age (Lorenz *et al.* 2007). Following incubation at 20 °C for 56 days, respiration rates had dropped in both the "fresh" and "old" samples. There was however a much more substantial drop in the "fresh" samples. This is in agreement with studies that have shown that there is a decline in soil respiration rate as incubation time increases (Winkler *et al.* 1996; Reichstein *et al.* 2000; Fang *et al.* 2005). It has been shown that declines such as this are due to a depletion of the most labile substrates, and are greater at higher temperatures (Grisi *et al.* 1998; Fang *et al.* 2005). Given the assumption that the "fresh" samples contained more labile carbon, mineralization of this carbon after the prolonged incubation at 20 °C appears to be responsible for the significant decline in respiration from the "fresh" samples.

Temperature sensitivity of "fresh" and "old" samples

The Q_{10} data from the incubations show that the temperature sensitivity of soil respiration was higher in the "fresh" compared to the "old" samples, using the observed as well as modelled data. After incubation for 56 days at 20 °C, Q_{10} increased for both the "fresh" and "old" samples. Fang *et al*. (2005) hypothesised that Q_{10} values should decrease after a long incubation if the recalcitrant carbon was unresponsive to temperature variations, with a more consistent Q_{10} suggesting that the temperature dependence of recalcitrant carbon is similar to that of labile carbon. Our results support the latter view, with the temperature sensitivity of both

"fresh" and "young" being very similar after incubation for 56 days at 20 °C. The relative increase in respiration rate is a term first introduced by Lloyd and Taylor (1994). It expresses the decline in carbon per unit of carbon in the sample. In the present data, the term was significantly higher in the "fresh" samples compared to the "old" samples, and especially so in the range 5 - 10 °C. This has large implications for the fate of labile soil carbon from coniferous forests in temperate climates, given that 5 - 10 °C is a very frequent temperature range. However at higher temperatures the relative sensitivity of the fresh soil samples remained more or less stable, whilst the sensitivity of the old samples increased with temperature up to 30 °C. A similar pattern was evident following the 56 day incubation at 20 °C. However the relative temperature sensitivity for both the "fresh" and the "old" samples was higher than during the initial incubation. Assuming that a large proportion of the labile carbon substrates had been mineralized during the 56 day incubation, this result suggests that the recalcitrant carbon is more responsive to temperature than the labile carbon, a result supported by Fierer *et al*. (2003), however opposed by others (Giardina and Ryan 2000; Thornley and Cannell 2001). Our results support the view that labile and recalcitrant carbon (corresponding to "fresh" and "old" carbon) respond similarly to warming, but after 56 days of incubation, indications suggest that recalcitrant fractions could actually be more sensitive to mineralization, particularly at higher temperatures. The implications of this result are of great importance to the understanding and prediction of the carbon cycle response to climate change in coniferous forests.

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