Soil heterotrophic respiration is insensitive to changes in soil water content but related to microbial access to organic matter

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A B S T R A C T

While most models describing soil organic matter dynamics relate the turnover of soil organic matter to its chemical structure, there is increasing evidence that microbial accessibility to the organic matter is predominant in controlling its stability and its decay. This finding has major implications for forecasting the impacts of land management and climate change on soil organic carbon cycling and there is a need for further research to understand the role of microbial accessibility. Further progress is problematic because of difficulties in partitioning total soil respiration (R_S) into its components soil heterotrophic respiration (R_H) and soil autotrophic respiration (R_A) in undisturbed ecosystems. To overcome this problem, we used an improved natural abundance of ^{13}C technique to partition R_S into R_H and R_A at one and six months after irrigation and addition of nitrogen fertiliser treatments was imposed in a grassland ecosystem.

Addition of nitrogen had no significant effect on the components of soil respiration compared with the values for the control. Irrigation resulted in differential effects on R_H and R_A, leading to strong differences in the proportion of R_H contributing to R_S (fR_H) with (mean ± standard error) 0.65 ± 0.09 and 0.30 ± 0.06 for the non-irrigated and irrigated plots, respectively, six months after the treatments began. R_S and R_A were strongly correlated and both showed strong linear relationships with gravimetric soil water content (W_S) resulting in strong differences between irrigation treatments. Soil temperature (T_S) and the amount of dissolved organic carbon were also correlated with both R_S and R_A. In contrast, R_H was not related to variation in W_S and T_S but was correlated with the amounts of particulate organic matter carbon, a labile fraction of carbon defined as physically unprotected, and specific surface area, an indicator of soil protection capacity. There were, however, no differences in the labile carbon fraction and specific surface area between the irrigation treatments. We showed that R_H was insensitive to irrigation and remained constant throughout the entire experimental period with a mean value of 1.7 ± 0.2 µmol m^2 s^{-1}.

Our findings support for the growing evidence that microbial accessibility to substrate, rather than its chemical structure, is predominant in regulating soil organic matter decomposition.

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1. Introduction

Soil organic matter has long been known to be critically important to maintain ecosystem services, including sustainable production of food and fibre, water retention and biodiversity (Jenny, 1941; Miller and Donahue, 1990; Powlson et al., 2011). Findings from the past few decades have supported the concept that the chemical structure of soil organic matter regulates its microbial degradation and that the existence of compounds in the soil, referred to as 'humic substances', is inherently recalcitrant to microbial degradation (Schmidt et al., 2011; Lehmann and Kleber, 2015). However, recent research is challenging this contention, with findings showing that the chemical structure of organic matter is unrelated to its residence time (Marschner et al., 2008; Kleber and Johnson, 2010; Schmidt et al., 2011). The emerging interpretation is that microbial access to substrate is regulating soil organic matter cycling, with chemical recalcitrance restricted to a marginal role (Schmidt et al., 2011; Dungait et al., 2012; Lehmann and Kleber, 2015). The idea of limited substrate availability to microbes within the soil matrix casts doubt on major assumptions used in models that address the response of soil carbon exchange to climate change, especially the description of the response of soil organic matter decay to temperature (Davidson and Janssens, 2006) and water status (Moyano et al., 2013). New experimental approaches to characterise the relative importance of chemical recalcitrance and physical protection of soil organic matter

in regulating the stability and decay of soil organic matter are required (Schmidt et al., 2011; Dungait et al., 2012; Lehmann and Kleber, 2015).

In terrestrial ecosystems, the rate of soil respiration (R_S) is the largest component (60–90%) of CO_2 losses from the soil to the atmosphere (Longdoz et al., 2000) and is the result of two processes: root and rhizosphere respiration (autotrophic respiration, R_A), and microbial decomposition of soil organic matter (heterotrophic respiration, R_H). Because R_A has little effect on long-term changes in soil organic matter (Kuzyakov, 2006), understanding the variables regulating R_H, independent from those regulating R_S and R_A, is critically important to forecast future changes in soil organic matter stocks and, subsequently, changes in the atmospheric CO_2 concentration. Empirical evidence for concluding the dominance of chemical recalcitrance in regulating soil organic matter turnover is derived mainly from studies involving laboratory incubations on samples removed from the soil (Kirschbaum, 1995; Davidson and Janssens, 2006; Manzoni et al., 2012). Alternatively, observations have been made from field studies using techniques that disturb the soil environment and remove the autotrophic component to measure R_H, for example by trenching, shading or burning the vegetation (Kuzyakov, 2006). These techniques potentially overlook the direct effects of the roots and the rhizosphere on R_H (Subke et al., 2006; Paterson et al., 2009). Soil structure is linked intimately to the processes that stabilise organic matter and protect it from microbial degradation. These mechanisms include the formation of aggregates that isolate the substrate and its binding to silt and clay particles (Six et al., 2000, 2002). These stabilisation mechanisms create conditions in which the substrate concentration located near to decomposers is reduced within the soil matrix (Davidson and Janssens, 2006; Dungait et al., 2011). The formation of aggregates and their stability result from complex interactions within the soil matrix, involving the whole soil biota, including roots (Bronick and Lal, 2005). Zakharova et al. (2014) showed that physical disturbance of soil resulted in the release of previously protected labile sources of carbon that became accessible for microbial degradation. Modifying the aggregation structure of the soil through physical extraction, including sieving and/or root removal, creates an artificial environment in which microbial access to chemically labile organic matter is temporarily unlimited (Zakharova et al., 2014). Thus, results from studies that modify soil structure, or supply the soil with substrate for microbial degradation, must be interpreted with caution, because they are likely to underestimate the importance of organic matter protection in regulating soil organic matter decomposition.

Application of stable carbon isotope techniques have provided the opportunity to investigate the variables regulating R_H in field conditions while avoiding disturbance of soil structure (Kuzyakov, 2006; Subke et al., 2006; Paterson et al., 2009). These methods are based on measurable differences in the ^{13}C isotopic signatures ($\delta^{13}C$) of the CO_2 respired from R_H and R_A ($\delta^{13}CR_A$ and $\delta^{13}CR_H$, respectively). Most studies to date have used C_3/C_4 plant isotopic shifts to amplify the difference between $\delta^{13}CR_A$ and $\delta^{13}CR_H$. In C_3 ecosystems $\delta^{13}CR_H$ is typically 2–4‰ enriched compared with the values of $\delta^{13}CR_A$ (Bowling et al., 2008). This difference has been shown to be measurable (Midwood et al., 2008) and extends the application of the natural abundance of ^{13}C to C_3 systems more generally (Millard et al., 2010; Graham et al., 2012; Snell et al., 2014; Moinet et al., 2016).

Considerable effort has been undertaken to relate fractions of soil organic matter that can be separated chemically or physically to theoretical pools of carbon of biological relevance, with different turnover times (Wander, 2004; von Lützow et al., 2007). Isolating fractions representing a passive carbon pool has proven to be particularly difficult, but labile fractions have been identified with more success (von Lützow et al., 2007). This has been achieved using water soluble organic matter fractions, including dissolved and hot water extractable organic matter (Ghani et al., 2003; Gregorich et al., 2003). These methods assume that easily degradable substrate will be more water soluble than other fractions of soil organic matter (McLauchlan and Hobbie, 2004). Thus, the 'lability' of the carbon isolated through this method is defined by its chemical structure.

To relate fractions more closely to bioavailability, particulate organic matter can also be isolated by physical fractionation on the basis of particle size. Different particle sizes represent different aggregate levels providing different degree of physical protection to organic matter (Six et al., 2002). Small particle sizes (53–2000 μm) are defined as the organic matter not bound to mineral particles (Gregorich et al., 2006), which define higher level of organic matter protection (Six et al., 2002). Coarse (250–2000 μm, macro-organic matter) and fine (53–250 μm, particulate organic matter) fractions can be distinguished (Willson et al., 2001; Wander, 2004). Six et al. (2002) defined the coarse fraction as unprotected and the fine fraction as the first level of physical protection. Here, the lability of the carbon is defined by its degree of physical protection, with decreasing particle size providing higher degree of protection (e.g. reduced lability) by isolation from microbial biomass and reduced oxygen diffusion. These labile fractions (e.g. macro-organic matter and particulate organic matter) often show correlation with total soil organic carbon content (McLauchlan and Hobbie, 2004) and the proportions of each fraction have been used as early indicators to forecast changes in soil organic matter levels under different land management practices and environmental conditions (Ghani et al., 2003; Gregorich et al., 2006). Specific surface area of the soil can also been measured as an indicator of physical protection to organic matter (Parfitt et al., 2001; Kahle et al., 2002) and was related to the mean residence time of added labile carbon in soils of different mineralogy (Saggar et al., 1999). Parfitt et al. (2001) provided a rapid easy method to measure specific surface area in similar soils in New Zealand, based on the water content of air-dried soil samples. As specific surface area largely resides in the clay fraction (Parfitt et al., 2001), this may provide a higher degree of protection compared to the fine and coarse particle size fractions defined above and thus provides an easy indicator to estimate the degree of protection. This is the first study where an approach is proposed to relate estimates of R_H and R_A in an undisturbed pure C_3 grassland to both environmental fluctuations and indicators of physical soil protection of soil organic matter. We partition the components of R_S and estimate values of R_H, R_A and the fraction of R_S attributable to R_H, fR_H, using the natural abundance ^{13}C technique in a factorial field experiment with treatments that manipulated water and nitrogen availability, with relevance to the widespread pastoral agriculture intensification in New Zealand, where irrigation and addition of nitrogen fertiliser are applied. We relate estimates of R_H and R_A to chemically (hot water extractable carbon) and physically (macro and particulate organic matter) defined labile pools of carbon as well as soil specific surface area, an indicator of organic matter protection capacity. Our objectives were to (i) observe the effects of the treatments on respiration rates and labile fractions of soil organic matter and (ii) test the hypothesis that R_H, as opposed to R_A, is under the control of both environmental fluctuations and the availability of soil organic matter.

2. Materials and methods

2.1. Site description

The measurements were made at a field site located at Ashley Dene Farm, Lincoln, Canterbury, New Zealand (latitude 43.40° S, longitude 172.20° E, elevation 35 m above sea level). The site was flat and had been managed under extensive sheep farming for more than 50 years prior to the experiment, with no irrigation and no input of nitrogen fertiliser. The soil was a deep stony silt loam, excessively drained and described as a mixture of Balmoral and Lismore according to New Zealand classification (Hewitt, 2010).

2.2. Experimental design

The experimental design consisted of six circular plots with a radius of 2 m (area 12.5 m^2). Three plots were selected randomly for irrigation (treatment I_1), and the three remaining plots were left unirrigated (treatment I_0). Within each plot, half was selected randomly for the