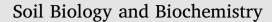
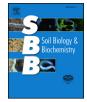
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Drying and rewetting conditions differentially affect the mineralization of fresh plant litter and extant soil organic matter



Luis Lopez-Sangil^{a,b,*}, Iain P. Hartley^c, Pere Rovira^d, Pere Casals^d, Emma J. Sayer^e

^a Department of Evolutionary Biology, Ecology and Environmental Sciences, Universitat de Barcelona, Av. Diagonal 643, Barcelona, 08028, Spain

^b Crops, Environment & Land Use Research Centre, Teagasc, Johnstown Castle, Co. Wexford, Ireland

^c Geography, College of Life and Environmental Sciences, University of Exeter, Amory Building, Rennes Drive, Exeter, EX4 4RJ, UK

^d Forest Sciences Centre of Catalonia (CTFC), Ctra. Sant Llorenç de Morunys, km 2, Solsona, 25280, Spain

^e Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ, UK

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ABSTRACT

Drought is becoming more common globally and has the potential to alter patterns of soil carbon (C) storage in terrestrial ecosystems. After an extended dry period, a pulse of soil CO2 release is commonly observed upon rewetting (the so-called 'Birch effect'), the magnitude of which depends on soil rewetting frequency. But the source and implications of this CO₂ efflux are unclear. We used a mesocosm field experiment to subject agricultural topsoil to two distinct drying and rewetting frequencies, measuring Birch effects (as 3-day cumulative CO_2 efflux upon rewetting) and the overall CO_2 efflux over the entire drying-rewetting cycle. We used ¹⁴Clabelled wheat straw to determine the contribution of fresh (recently incorporated) plant litter or extant soil organic matter (SOM) to these fluxes, and assessed the extent to which the amount of soil microbial biomass + K₂SO₄-extractable organic C (fumigated-extracted C, FEC) before rewetting determined the magnitude of Birch effect CO₂ pulses. Our results showed a gradual increase in SOM-derived organic solutes within the FEC fraction, and a decrease in soil microbial biomass, under more extreme drying and rewetting conditions. But, contrary to our hypothesis, pre-wetting levels of FEC were not related to the magnitude of the Birch effects. In the longer term, rewetting frequency and temperature influenced the overall (31-day cumulative) amount of CO2-C released from SOM upon rewetting, but the overall ¹⁴CO2-C respired from fresh straw was only influenced by the rewetting frequency, with no effect of seasonal temperature differences of ~ 15 °C. We conclude that the mineralization of fresh plant litter in soils is more sensitive to water limitations than extant SOM in soils under drying-rewetting conditions. Moreover, we found little evidence to support the hypothesis that the availability of microbial and soluble organic C before rewetting determined the magnitude of the Birch effects, and suggest that future work should investigate whether these short-term CO₂ pulses are predominantly derived from substrate-supply mechanisms resulting from the disruption of the soil organo-mineral matrix.

1. Introduction

When a dried soil is rewetted, an immediate sharp increase in CO_2 efflux typically follows. This peak of CO_2 efflux upon rewetting is referred to as the 'Birch effect' (Birch, 1958; Jarvis et al., 2007), which has a mean, albeit variable, duration of 3–4 days (Kim et al., 2012). It has been observed in a wide range of terrestrial ecosystems and under laboratory conditions, and may represent a substantial proportion of the total annual CO_2 efflux in arid, semi-arid and Mediterranean soils (Borken and Matzner, 2009; Kim et al., 2012). Previous work has shown that the Birch effect can be attributed to a large increase in the microbial mineralization (respiration) of soil organic matter and the

release of CO₂-C into the atmosphere (Casals et al., 2011), but the specific sources of organic C that contribute to this CO_2 flux are less clear.

A number of experiments have shown that many factors can modulate the magnitude of soil C release by the Birch effect. Respiration peaks only occur when there are substantial differences between preand post-rewetting soil water content (Chowdhury et al., 2011), and the amount of soil organic matter (SOM) mineralized upon rewetting normally declines with increasing number of previous drying-rewetting (D-RW) cycles (Mikha et al., 2005; Wu and Brookes, 2005), which suggests that the mineralization of SOM after rewetting is related to the number and extent of previous soil desiccations (Williams and Xia, 2009; Unger

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^{*} Corresponding author. Current address: Crops, Environment & Land use Research Centre, Teagasc, Johnstown Castle, Co. Wexford, Ireland. *E-mail address*: Luis.Lopez-Sangil@teagasc.ie (L. Lopez-Sangil).

et al., 2010; Chowdhury et al., 2011). The availability of SOM to soil microorganisms before rewetting is also thought to regulate the magnitude of the rewetting response (Casals et al., 2009), and soil temperature and/or water content after rewetting may also play a role (Cable et al., 2011; Suseela et al., 2012). The relative importance of these multiple factors and their interactions are still a source of great uncertainty for predicting the magnitude of soil respiration responses to the expected extension of dry periods in many ecosystems (Wetherald and Manabe, 2002; Borken and Matzner, 2009; Falloon et al., 2011; Suseela et al., 2012).

Several mechanisms are thought to contribute to the post-rewetting increase in SOM mineralization, and many of them are closely related to the supply of organic substrates in the soil solution: i) release of intracellular compounds from microbial cell lysis after severe soil desiccation, and subsequent respiration by surviving microbes (Bottner, 1985); ii) microbial release, re-uptake and respiration of intracellular osmolytes, to cope with the sudden increase of soil water potential upon rewetting (Kieft et al., 1987; Halverson et al., 2000; Fierer and Schimel, 2003); iii) spatial redistribution of soil microorganisms and/or organic solutes upon rewetting, due to increased mobility of microbes or substrate within soil pores (Van Gestel et al., 1993; Xiang et al., 2008); iv) desorption of soluble SOM from a plethora of organo-mineral complexes (Kalbitz et al., 2000; Lopez-Sangil and Rovira, 2013); and v) aggregate disruption and exposure of previously occluded SOM particles during the drying phase or upon rewetting (Denef et al., 2001). The relative contribution of these mechanisms is poorly understood and likely to be modulated by factors such as soil structure or depth within the profile, which determine levels of water retention and rewetting abruptness under D-RW conditions (Xiang et al., 2008; Sanaullah et al., 2011; Rovira and Vallejo, 1997). For instance, desiccation and rewetting extremes decline with soil depth (Sanaullah et al., 2011; Lopez-Sangil et al., 2013), which may promote specific mechanisms over others as they exhibit different sensitivities to physical disturbance (Borken and Matzner, 2009; Williams and Xia, 2009).

The relationship between SOM decomposition rates and the size of the soil microbial biomass is the subject of much debate, but it is also directly relevant to C dynamics during D-RW cycles (Coleman and Jenkinson, 1996; Shen et al., 1997; Probert et al., 1998; Sato and Seto, 1999; Franzluebbers et al., 2000; Bapiri et al., 2010). A major portion of the soil microbial biomass can be in a dormant or in a completely nonviable state in dry soil, and consequently the supply of available substrates (rather than the size of microbial biomass) could be a better predictor of the magnitude of SOM mineralization upon rewetting (Wang et al., 2003). The amount of soluble (i.e., extractable) organic C has been proposed as an indicator of substrate availability for soil microbes (Boyer and Groffman, 1996), and this C fraction may help to explain the dynamics of SOM mineralization during D-RW cycles (Wang et al., 2003; Casals et al., 2009). Improving our understanding of these relationships could refine our modeling tools and land-use strategies for reducing soil C release to the atmosphere.

A potential way to address some of these uncertainties is to assess separately the contributions of fresh organic matter (recently incorporated) and extant SOM (more stable) as potential C sources of the Birch effect. Distinguishing between these two substrates can enhance our mechanistic understanding of soil C respiration sources (Bottner, 1985; Casals et al., 2000), and can provide modelers with information about how the mineralization of different organic substrates in soil may respond distinctly to changes in pedoclimatic conditions. Although fresh plant litter decomposition exhibits a lower sensitivity to temperature than SOM due to its lower recalcitrance (Bosatta and Agren, 1999), previous work shows that, contrastingly, it can be very susceptible to water limitations (Rovira and Vallejo, 1997; Magid et al., 1999). This susceptibility is not necessarily related to substrate quality (Sanaullah et al., 2012), but could be a result of decreased substrate availability during desiccation, or greater drought sensitivity of litterdecomposing microbes, although the mechanisms involved are still speculative. Moreover, it is still uncertain how soil temperature and moisture interact to control the mineralization of distinct substrates during Birch effects.

In this study, we hypothesized that 1) the amount of C that is available to microbes (i.e., readily accessible) before rewetting will explain the magnitude of CO_2 release during subsequent Birch effects; and 2) the mineralization of extant soil organic matter would be less affected by extended drought periods than that of fresh plant litter inputs. To test these hypotheses, we assessed the effect of extended drought periods on microbial biomass and soluble (i.e., extractable) organic C fractions in a Mediterranean agricultural soil, and its subsequent impact on soil CO_2 emissions. By incubating soil horizons mixed with ¹⁴C-labelled wheat straw at different depths, we aimed to identify which soil C sources are mostly affected by D-RW conditions and more able to explain the observed Birch effect CO_2 pulses.

2. Material and methods

2.1. Experimental design and straw ¹⁴C-labelling

We assessed the influence of two distinct drying-rewetting frequencies on two different simulated soil profiles, using the mesocosm incubation design described in Lopez-Sangil et al. (2013). We constructed 44 mesocosms, each consisting of a PVC cylinder (12-cm inner diameter, 24-cm height) with a funnel, a 2.7-µm glass microfiber filter and a nylon tube attached to the bottom to collect possible leachates (Fig. 1). Each mesocosm was packed with 560 g agricultural topsoil (henceforth, 'topsoil') and 2635 g mineral subsoil (see section 2.2), simulating a 20-cm depth soil profile. Both soils were air-dried, homogenised and sieved (2-mm) before filling the mesocosms. To trace the carbon from recent plant litter inputs, the topsoil in each mesocosm was thoroughly mixed with homogeneously ¹⁴C-labelled wheat straw $(0.42 \text{ g straw kg}^{-1} \text{ soil; fragment size } 2 \text{ mm} - 50 \mu\text{m}; 2550.9 \text{ Bq mg}^{-1}$ C). The initial total organic C content of the labelled topsoil was $25.35 \text{ mg C g soil}^{-1}$, of which 0.62% was labelled straw (equivalent to 2 kg straw ha⁻¹). The topsoil formed a 4-cm deep horizon (bulk density = 1.24 g cm^{-3}) and a 7-mm pore nylon mesh separated the topsoil from the mineral subsoil $(1.61 \,\mathrm{g \, cm^{-3}})$ while maintaining hydraulic conductance. As the intensity of drying-rewetting cycles declines with soil depth (Sanaullah et al., 2011; Lopez-Sangil et al., 2013), we accounted for differences in drying-rewetting disturbance with depth by distinguishing two 'depth treatments': the topsoil horizon was placed on the surface of 22 mesocosms (0-4 cm; 'surface mesocosms'), whereas in the other 22 mesocosms, the topsoil formed a subsurface horizon at 10-14 cm depth ('subsurface mesocosms'; Fig. 1).

2.2. Soil substrates

The agricultural topsoil was a clay loam Haplic Calcisol (IUSS Working Group WRB, 2006) with an organic C content of 2.52% and carbonate content of 37.9%. It was collected from the upper 10–15 cm of a maize cropland (*Zea mays* L.) in north-eastern Spain (42°16′51″N; 2°58′37″E). The mineral subsoil was a sandy loam with very low organic C and carbonate concentrations (0.12% and 0.8% respectively), obtained from a nearby quarry. Further details are given in Lopez-Sangil et al. (2013).

2.3. Incubation and irrigation frequencies

The mesocosms were subjected to two different drying-rewetting frequencies and incubated for 366 days under field conditions. To maintain natural daily and seasonal variation of soil temperature, we incubated the mesocosms at the experimental field site of the University of Barcelona, sunken in the ground so that the surface of the mesocosm soil profile was levelled with the surrounding soil. A plastic cover protected the area from rainfall, increasing air temperature by 2–3 °C.

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