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Soil microbial populations in deep floodplain soils are adapted to infrequent but regular carbon substrate addition

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ABSTRACT

Floodplain soils provide an important link in the land-ocean aquatic continuum. Understanding microbial activity in these soils, which can be many metres deep, is a key component in our understanding of the role of floodplains in the carbon (C) cycle. We sampled the mineral soil profile to 3 m depth from two floodplain sites under long-term pasture adjacent to the river Culm in SW England, UK. Soil chemistry (C, nitrogen (N), phosphorus (P), soil microbial biomass (SMB), moisture content) and soil solution (pH, dissolved organic C (DOC) and N, nitrate, ammonium, water extractable P) were analysed over the 3 m depth in 6 increments: 0.0–0.2, 0.2–0.7, 1.0–1.5, 1.5–2.0, 2.0–2.5, and 2.5–3.0 m. ^{14}C-glucose was added to the soil and the evolution of $^{14}CO_2$ measured during a 29 d incubation. From soil properties and ^{14}C-glucose mineralisation, three depth groups emerged, with distinct turnover times extrapolated from initial k_1 mineralisation rate constants of 2 h (topsoil 0.0–0.2 m), 4 h (subsoil 0.2–0.7 m), and 11 h (deep subsoil 1.0–3.0 m). However, when normalised by SMB, k_1 rate constants had no significant differences across all depths. Deep subsoil had a 2 h lag to reach maximal $^{14}CO_2$ production whereas the topsoil and subsoil (0.2–0.7 m) achieved maximum mineralisation rates immediately. SMB decreased with depth, but only to half of the surface population, with the proportion of SMB-C to total C increasing from 1% in topsoil to 15% in deep subsoil (> 1.0 m). The relatively large SMB concentration and rapid mineralisation of ^{14}C-glucose suggests that DOC turnover in deep soil horizons in floodplains is limited by access to biologically available C and not the size of the microbial population.

1. Introduction

Carbon (C) dynamics in deep soil are some of the most poorly understood components of the global C cycle, despite an estimated 75% of the C found in the top 3 m of soil occurring below 0.2 m (Jobbágy and Jackson, 2000; Rumpel and Kögel-Knabner, 2010). Subsoil soil organic carbon (SOC) has predominantly been considered older (i.e., large radiocarbon age), more stable and chemically recalcitrant than that of topsoil (Wordell-Dietrich et al., 2017), with decomposition rates increasing with depth down the profile. However, many existing SOC decomposition models tend to simplify decay rates to one pool, which can lead to an underestimation of the amount of C observed at depth (Jenkinson and Coleman, 2008). Subsoils have been suggested as having the potential to store additional C due to reduced microbial activity at depth, but there is debate surrounding the stability of C in subsoil (Kramer et al., 2013; Jones et al., 2018). Recent studies have reported little difference in the decomposability of topsoil SOC compared with subsoil SOC, with stability potentially linked to the physical environment rather than the molecular recalcitrance of subsoil SOC (Fontaine et al., 2007; Gregory et al., 2016; Heitkötter et al., 2017; Jones et al., 2018). Subsoils vary in oxygen availability, moisture content (MC), mineralogy, metal concentrations, quantity and quality of SOC and microbial population abundance when compared to topsoil, and increasing spatial heterogeneity, i.e., physical separation of decomposers to available substrate, which may all contribute to observed stability (Salomé et al., 2010; Chaopricha and Marín-Spiotta, 2014; Wordell-Dietrich et al., 2017; Jones et al., 2018).

Deep soils are characterised by having SOC radiocarbon ages of many thousands of years (e.g. 2500 y at 0.6–0.8 m; Fontaine et al., 2007). However, rapid accretionary environments, such as floodplain soils, can be much younger (e.g. > 250 y for the top 0.6 m; Lair et al., 2009). Some floodplain soils can extend beyond 8 m in depth and the age can vary greatly depending on soil conditions (Lair et al., 2009; Zehetner et al., 2009; Chaopricha and Marín-Spiotta, 2014). Floodplains are dynamic, complex systems characterised by large spatial and temporal variation in physical and chemical characteristics, e.g. in

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water flow, channel migration, sediment transportation and nutrient retention (Raymond and Bauer, 2001; Graf-Rosenfellner et al., 2016). They are also productive ecosystems due to the continual input of fresh, nutrient rich sediments resetting soil formation to an early phase of OC accumulation with rapid accumulation of labile C and nitrogen (N; Zehetner et al., 2009). However, the biogeochemical processes occurring in these systems remain poorly understood.

There is debate over the survival of C in floodplain systems with Wang et al. (2014) reporting 2–14 times slower turnover of SOC in depositional areas, with buried SOC in saturated riparian soils remaining stable for thousands of years (Chaopricha and Marín-Spiotta, 2014). By contrast, Hoffmann et al. (2013) suggested rapid turnover and reduced C sequestration rates. The complexity of floodplain C dynamics is also increased by the additional lateral and vertical fluxes of C from erosion, flooding and sediment deposition (Regnier et al., 2013; Jansen et al., 2014) and by enhanced vertical movement of dissolved OC (DOC) due to flushing of C from upper soil horizons (Morel et al., 2009). Furthermore, the co-transport of nutrients is likely to affect the stoichiometry of depositional soils in favour of mineralisation. Carbon storage in deeper soils is suggested to be due to the limitation of easily available substrate (Fontaine et al., 2007; Salomé et al., 2010; Heitkötter et al., 2017; Jones et al., 2018). Indeed, microbial hotspots in deep unsaturated subsoils have been reported in areas of preferential DOC flow (Gocke et al., 2017). Therefore, riparian soils with regular inputs of DOC during flood events may have enhanced mineralisation potential in the hyporheic zone (Marín-Spiotta et al., 2014).

Carbon storage in subsoils may also be driven by the vertical transport of DOC, which is subsequently chemically protected (Kramer and Gleixner, 2008; Müller et al., 2016). Alternating redox conditions in periodically inundated soils can lead to anoxic conditions, which, in turn, can lead to reduced decomposition rates, increased SOC and DOC accumulation and increased denitrification (Bräuer et al., 2013; Hanke et al., 2013; Ding et al., 2017). Furthermore, the predicted increases in temperature and precipitation from the altering of the North Atlantic storm track and intensification of the global hydrological cycle due to climate change may alter the redox state from increased flushing and/or waterlogging (Orme et al., 2017). This might result in high intensity erosion events, changes to soil microbial activity, and may also cause enhanced nitrification, denitrification respiration, methanogenesis rates and increased DOC transport through soils (Keller and Bridgham, 2007; Beniston et al., 2015; Poblador et al., 2017).

Despite the potential significance of floodplain soils in the terrestrial C cycle, they are acknowledged to be under-represented in empirical studies (Bullinger-Weber et al., 2014). Riverine systems are dynamic and likely to become more so with future climate change, with Worrall et al. (2004) reporting an increase of 0.02 Mt C y^{-1} in the UK riverine DOC flux of 0.86 Mt C y^{-1}, and Sandford et al. (2013) reporting a 91% increase in DOC in UK rivers and lakes over the past 20 years, with the coincident increasing supplies of biologically available C and other macronutrients (e.g. N and phosphorus (P)). Therefore, it is important to measure the response of microbial activity to DOC in this largely unquantified environment. We test the hypothesis that deep floodplain soil systems support a relatively large metabolically alert microbial population able to respond rapidly to substrate supply. Our study was based on a rapidly accreting mineral soil under permanent pasture, undergoing regular flood inundation (approx. 8 times per year, with floodwaters typically receding within 24 h; Walling and Bradley, 1989; Simm and Walling, 1998; Walling et al., 2006). The hypothesis was tested using measurements of soil microbial biomass (SMB), basal respiration and the addition of a ^{14}C-labelled simple sugar (glucose) under aerobic laboratory conditions as a general proxy for microbial activity in a dynamic temperate grassland floodplain soil profile.

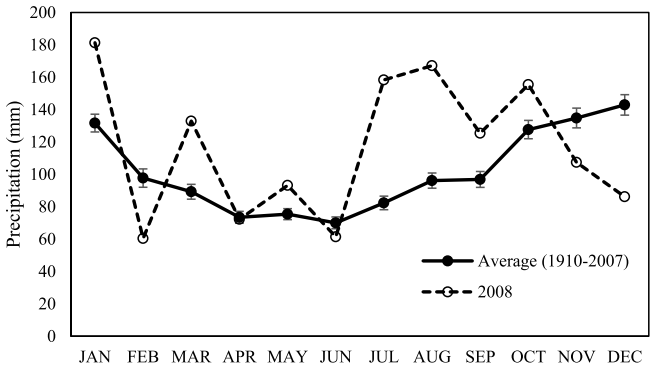

Fig. 1. Average precipitation for the SW of England and S Wales for 1910–2007 (errors are SEM) and precipitation (mm) for 2008 (data from: Met Office, 2017).

2. Materials and methods

2.1. Field sites

The field sites were two active channel riparian grassland sites (Smithincott: 50°33′50.2″ N, 3°20′34.8″ W and Rewe: 50°47′15.2″ N, 3°29′20.0″ W) on the river Culm in SW England, UK that are permanent pasture grazed by cattle in the summer. The river has a catchment of 276 km^2, with a mean altitude of 140 m a.s.l., dominated by sandstone and marl lithology, with a mean precipitation of 952 mm and an estimated sediment yield of 25 t km^{-2} y^{-1} (Walling et al., 2006). However, 2008 was a notably stormy year with elevated rainfall (Fig. 1); during which SW England experienced a 15% increase in recorded precipitation above the annual average (from 1910 to 2007), with 65% greater precipitation than average in the three months prior to sampling (Met Office, 2017).

2.2. Soil sampling

Soil cores were sampled in October 2008. At Smithincott, 7 cores were sampled along a transect perpendicular to the bank, with the primary transect 30 m from the river channel, with 4 cores sampled at 10 m intervals and a secondary transect of 3 cores 10 m perpendicular to the bank; all cores were sampled 25 m apart. At Rewe, 5 cores were sampled at 20 m intervals along a transect from 15 m from the bank to a maximum distance of 85 m from the channel.

Soil cores were extracted from 0.0 to 3.0 m depth and divided into 6 depth increments: 0.0–0.2 (n = 12), 0.2–0.7 (n = 12), 1.0–1.5 (n = 10), 1.5–2.0 (n = 10), 2.0–2.5 (n = 6) and 2.5–3.0 m (n = 6). Topsoil (0.0–0.2 m) and subsoil (0.2–0.7 m) cores were sampled using a percussion hammer (0.1 m diameter; Wacker Neuson Ltd, Stafford, UK), directly adjacent to deep subsoil cores (1.0–3.0 m), sampled using a pneumatic corer (0.03 m diameter; Geoprobe, DT22 Soil Sampling System, KS, USA) to reduce compaction effects in the top metre. The cores were sealed in plastic tubes and stored at 4 °C for 1 week prior to analysis.

As per Fontaine et al. (2007), Heitkötter et al. (2017) and Wordell-Dietrich et al. (2017), topsoil and subsoil were sieved, under aerobic conditions, prior to analysis through a large mesh (7 mm) to maintain soil aggregate structure, to homogenise the samples and remove large roots and stones. Sieving through mesh of this size does not significantly affect soil microbial activity or the intrinsic DOC dynamics of the soil (Jones and Willett, 2006). The sieved soil samples were subdivided into four equal portions for mineralisation, respiration, analyses of soil properties and soil solution extractions and stored in gas permeable bags at 4 °C.