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ORIGINAL PAPER

Effects of drying/rewetting on soil aggregate dynamics and implications for organic matter turnover

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Abstract

Drying and rewetting (D/W) of soil have significant impacts on soil organic matter (SOM) turnover. We hypothesised that frequent D/W cycles would release the labile organic matter locked away in soil aggregates, increasing the priming effect (PE) (acceleration or retardation of SOM turnover after fresh substrate addition) due to preferential utilisation by microbes. ^{13}C-labelled lignocellulose was added to the soil, and the effects of 0, 1, or 4 cycles of D/W were evaluated at 5 °C and 25 °C after a 27-day incubation of undisturbed soil cores from a temperate forest (*Araucaria araucana*). Following the incubation, macroaggregates (> 250 μm), microaggregates (250–53 μm), and silt + clay materials (< 53 μm) were separated. For each aggregate size class, three organic matter (OM) fractions (light (fPOM < 1.6 g cm^{-3}), occluded (oPOM 1.6–2.0 g cm^{-3}), and heavy (Hf > 2.0 g cm^{-3}) were determined. D/W cycles caused macroaggregates to increase and a decrease in microaggregates (> 15%) at warm temperatures, and preferential use of the novel particulate organic matter (^{13}C labelled), formerly protected fPOM. CO_2 efflux was three times higher at 25 °C than at 5 °C. The D/W cycles at 25 °C had a strong negative impact on cumulative CO_2 efflux, which decreased by approximately − 30%, induced by a negative PE of −50 mg C kg^{-1} soil with 1 D/W cycle and − 100 mg C kg^{-1} soil with 4 D/W cycles, relative to soil under constant soil moisture receiving ^{13}C-labelled lignocellulose, but no cycles. Increasing the temperature and the number of D/W cycles caused a decrease in substrate use efficiency of particulate lignocellulose. In conclusion, D/W cycles at warm temperatures accelerated OM turnover due to preferential use from fPOM, increasing macroaggregates at the expense of microaggregates. A novel pathway of OM release and PE due to the D/W cycles is discussed.

Keywords Soil priming effect · Particulate soil organic matter · Drying and rewetting cycles · Aggregate stability · Carbon turnover

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Introduction

Drying/rewetting (D/W) cycles lead to gains or losses in soil carbon (C) from soil organic matter (SOM), effects that are enhanced under extreme climatic events (Kim et al. 2012). However, soil C turnover is dependent upon other environmental conditions, e.g. temperature (Davidson and Janssens 2006). Small changes in mean annual temperature can have significant effects on soil CO_2 release (Billings and Ballantyne IV 2013). Soil organic C turnover is further modified by topography, vegetation, and soil type (Balser and Firestone 2005; Vargas et al. 2010). Other factors, such as physical protection of organic matter (OM) (von Lützow et al. 2007) or the frequency of D/W cycling during dry seasons, also play critical roles in soil C dynamics (Hibbard et al. 2005).

Cycles of D/W are assumed to affect the overall functions of soils in terrestrial ecosystems and to affect soil emission of greenhouse gases such as CO_2, methane, and nitrous oxides (Corti et al. 2002; Lal 2004; Vicca et al. 2014). Increasingly frequent D/W cycles could therefore cause a breakdown of aggregates (slacking), exposing the physically protected OM to microbial decomposition (Adu and Oades 1978; Appel 1998; Oztas and Fayetorbay 2003). Greater intensities of drought could intensify negative impacts on CO_2 flow and microbial activity (Sinha and Cherkauer 2010; Meisner et al. 2015). After rewetting, an increase in gas fluxes occurs via the Birch effect (Birch 1958). The Birch effect is driven by the labile particulate organic matter (POM), determined by density fractionation as the light fraction (fPOM < 1.6 g cm^{-3}), which consists mostly of pieces of plant residue and fungal hyphae. These materials can be occluded POM (oPOM 1.6–2.0 g cm^{-3}), protected by the aggregates (Christensen 1992; von Lützow et al. 2007). The CO_2 efflux from the soil can decline with successive D/W events as a result of an increasingly limited pool of labile substrates (Schimel and Mikan 2005; Fernández et al. 2006; Goldberg et al. 2008).

The addition of fresh organic matter to soils results in a C cycle phenomenon known as the priming effect (PE) (Bingemann et al. 1953). The PE is a strong, short-term change in the turnover of SOM caused by an input of fresh OM (Jenkinson et al. 1985; Kuzyakov et al. 2000). It is calculated as the difference between unlabelled CO_2 efflux and labelled CO_2 from ^{13}C- (or ^{14}C) added to the soil (Oades 1988; Jarvis et al. 2007). Priming can be positive (acceleration) or negative (retardation) depending on the quantity and quality of fresh input (Kuzyakov 2010; Garcia-Pausas and Paterson 2011). Although the effect is considered a short-term phenomenon, Fontaine et al. (2011) demonstrated that priming could have long-lasting effects. Hence, under frequent D/W cycles, the PE can have a significant impact on the decomposition of OM fractions, triggering CO_2 efflux from native SOM in the ecosystem (Magid and Kjærgaard 2001; Gregorich et al. 2006).

In terms of the protection of OM in the aggregates, there is a hierarchical order from the largest particles to the smallest particles (Tisdall and Oades 1982; Oades 1984; Six et al. 2000). This protection is disrupted by D/W cycles (Denef et al. 2001a, 2001b), which increase the accessibility of microorganisms to the soil C. Because the fPOM contains the highest amount of labile C, providing a rich source of energy for microorganisms, disruption of the aggregates by D/R cycles can result in high CO_2 emissions (Mikha et al. 2005; Borken and Matzner 2009; Shi et al. 2014).

A new perspective on C release and PE due to the D/W cycle is introduced in this study. Drying and rewetting cycles are hypothesised to lead to the preferential use of new, unprotected, and labile organic matter over native C, resulting in negative PE values. Quantifying this effect under the application of ^{13}C-labelled fPOM to soils will facilitate (a) differentiating the degree of physicochemical protection of the SOM in various aggregate size classes and (b) estimating the substrate use efficiency, i.e. the relative proportion of added fPOM-C that is incorporated into microbial biomass.

Temperate forests in Chile have experienced increasing temperatures and more frequent extreme climatic events, such as severe droughts (Garreaud et al. 2017; Urrutia-Jalabert et al. 2018). In light of the effects of these events on soil moisture content, it is important to understand the impact of D/W on SOM turnover in these ecosystems. Three hypotheses were tested: (i) priming of native C is induced by the amendment of fresh C-input, but D/W cycles release OM, which primarily consists of the fPOM from disrupted aggregates (Fig. 1). Therefore, comparing the difference in the PE between 0 cycle and D/W cycles will allow us to quantify the effect of D/W on the actual PE. (ii) Native SOM decomposition will be retarded (negative PE) due to the preferential use of new OM by microorganisms (Fig. 1). And, (iii) a cumulatively more negative PE is expected with an increased number of D/W cycles. The aim of this study was to evaluate the effects of two frequencies of D/W events on the PE, soil aggregate size class distribution, and their OM fractions, dependent upon temperature in a temperate forest soil.

Materials and methods

Study site and sampling

Soil samples were collected from an Inceptisol (Soil Survey Staff 2014) developed under an ancient temperate forest with a dominant tree canopy of *Araucaria araucana* (Molina) K. Koch in Nahuelbuta National Park (37°47′S, 72°59′W), Chile. Important soil properties are provided in Table 1, and a more detailed description of the site can be found in Bernhard et al. (2018) and Oeser et al. (2018). Undisturbed cores (PVC 5-cm diameter × 5-cm length) were taken from the uppermost soil

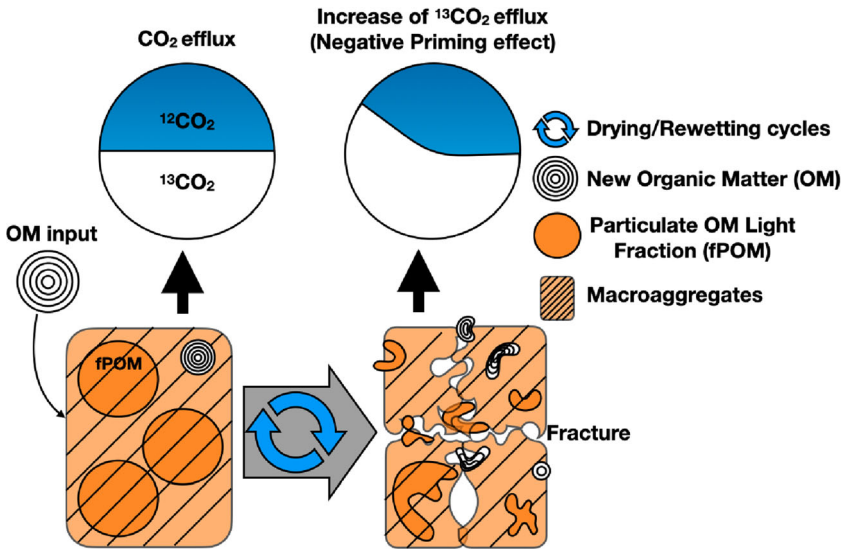

Fig. 1 Schematic illustration of the impact of drying/rewetting (D/W) events on the soil C dynamics and CO_2 efflux after fresh C addition. D/W cycles breakdown soil macroaggregates and release labile particulate organic matter (fPOM) that was formerly protected. Increasing number of D/W cycles raises microbial respiration from decomposition of new organic matter of the POM fraction rather than using older, more stabilised OM, thus generating a negative PE

horizons after litter removal. Cores were stored at 4 °C and immediately transported to the laboratory of Agricultural Soil Science of Georg-August University of Göttingen, Germany.

Microcosm experiment

CO_2 effluxes were determined during the incubation period of 27 days. This timespan was selected because D/W-induced differences in mineralisation of fPOM were expected directly after the D/W cycles (Schimel and Mikan 2005; Goldberg et al. 2008). The PE and substrate use efficiency (SUE) (for details see below) were assessed to compare the microbial incorporation of the ^{13}C-labelled amendment into the new organic matter. Aggregate size distribution and density fractions from each aggregate class were determined to categorise the SOM pools via different degrees of C protection.

The microcosm experiment consisted of 28 undisturbed core samples (~ 78.5 g dry soil, bulk density 0.8 ± 0.1 Mg m^{-3}) pre-incubated for 4 days at field capacity (0.34 m^3 m^{-3}, − 33 kPa). Following incubation, the cores were placed on a ceramic pressure plate within a closed acrylic chamber, modified from Poll et al. (2010), and equipped with a septum for gas sampling (Fig. 2). Briefly, approximately 3 mg of ^{13}C uniformly labelled lignocellulose milled residue (maize derived, isotopic purity 97 atm % ^{13}C (IsoLife –Stable Isotope Labelled Plant Products for the Life Sciences,

Table 1 Properties and standard deviation (±) of studied soil (0–8-cm depth)

Variable	Units	Value	
pH water		4.3 ± 0.3	Acid soil (1:2.5 water)
pH $CaCl_2$		3.3 ± 0.2	Acid soil (1:2.5)
Soil C	g kg^{-1} soil	106 ± 9.9	Total soil carbon at 0–8-cm depth
Soil N	g kg^{-1} soil	5.0 ± 0.5	Total soil nitrogen 0–8-cm depth
Soil C:N		21	0–8-cm depth.
Litter C:N		60	*Araucaria araucana* litter 0–2 cm
Al_p	g kg^{-1} soil	6.4 ± 2.2	Pyrophosphate extractable Al
Fe_p	g kg^{-1} soil	3.5 ± 1.9	Pyrophosphate extractable Fe
Al_o	g kg^{-1} soil	8.7 ± 2.8	Oxalate extractable Al
Fe_o	g kg^{-1} soil	6.7 ± 1.4	Oxalate extractable Fe
Si_o	g kg^{-1} soil	0.3 ± 0.2	Oxalate extractable Si
Al_d	g kg^{-1} soil	12.2 ± 1.6	Dithionite extractable Al
Fe_d	g kg^{-1} soil	4.7 ± 0.3	Dithionite extractable Fe
Al_p/Al_o		0.8	> 0.5 organo-mineral nature
$Al_o + 0.5Fe_o$	%	1.3	> 2 andic properties
Al_K	$cmol_+$ kg^{-1}	6.8 ± 2.5	Exchangeable Al
CEC_e	$cmol_+$ kg^{-1}	9.0 ± 1.6	Effective cation exchange capacity

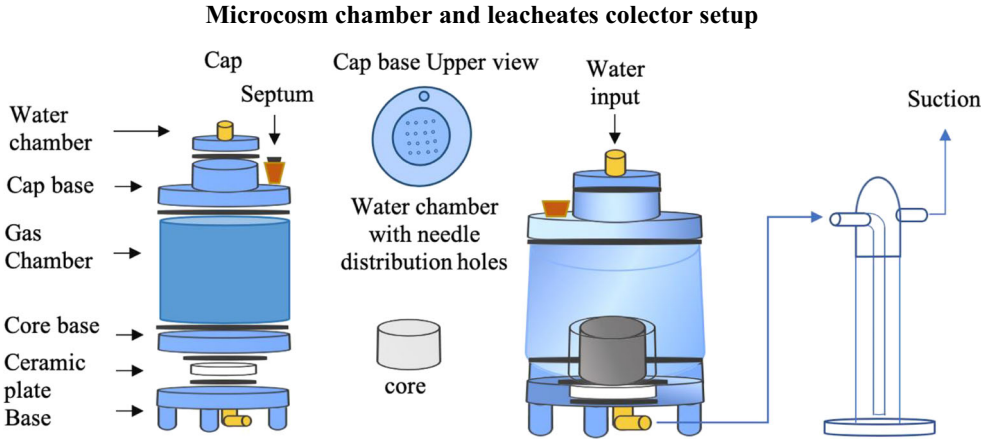

Fig. 2 Microcosm chambers (acrylic materials) setup for the drying and rewetting cycles and CO_2 collection. Note: The top of the main chamber has a small additional chamber to which several irrigation needles were connected to apply the irrigation water uniformly

Wageningen, Holland)) were suspended in 10 ml of distilled water and spread uniformly on top of each core using several injections with a syringe. Drying and rewetting cycles consisted of 3 days of drying followed by 3 days of wetting. Dry conditions were achieved using a vacuum pump (Leroy-Somer™) from the bottom of the ceramic plate, reaching − 80 kPa for 3 h. Rewetting was conducted by watering the core soil on the top and leaving the soil to equilibrate for 30 min until the moisture content reach field capacities. This was achieved using 12 needles connected to another pump (model ISM404B, ISMATEC™). Microcosms received either 1 or 4 cycles. Control soils with labelled lignocellulose additions were subjected to zero D/W cycles and observed alongside the other treatments. In addition to determining the natural isotopic abundance of ^{13}C, moist soil cores without labelled lignocellulose additions were also incubated. All treatments were replicated four times.

CO_2 sampling

CO_2 gas samples were collected during 27 days of incubation from the first day of each drying or rewetting (12 h apart) period and thereafter, with one sample collected for each day until the next drying. All samples were collected via a 10-ml syringe through the septum on top of the microcosm container (Fig. 2). The gas samples were injected into a vacutainer (Exetainer, Labco Limited, 12 ml) and stored at 5 °C until measurement. After sampling, each acrylic flask was ventilated with CO_2-free air. At the end of the 27-day incubation period, the soil was carefully extracted from each core for further analyses.

Aggregate size classes

Aggregate size distribution was determined by dry sieving. Soil was air-dried at 40 °C and sieved through 250 μm and 53 μm meshes on the Vibratory Sieve Shaker AS 200 (Retsch, Germany) for 5 min, at an amplitude of 1.5 mm. Three aggregate size classes were obtained: macroaggregates (> 250 μm), microaggregates (250–53 μm), and silt + clay size particles (< 53 μm). The D/W cycles impact soil aggregate turnover, and differences in aggregate size composition between soils with 1 and 4 cycles and soils with constant moisture (0 cycle) were regarded as the proportional effects of the D/W cycles.

Organic matter density fraction

Organic matter fractions were obtained by density fractionation from each aggregate size class using sodium polytungstates (SPT) (Gunina and Kusyakov 2014). Three OM density fractions were obtained, dried at 40 °C, and weighed: light fraction (fPOM, < 1.6 g cm^{-3}), occluded fraction (oPOM, 1.6–2.0 g cm^{-3}), and heavy fraction (Hf > 2.0 g cm^{-3}). The effect of D/W on the gain (negative values) or loss (positive values) of aggregate mass and its associated C was obtained using the difference between the 0 cycle, which received labelled residue but no D/W cycling, and the 1 cycle or 4 cycle treatments. For the aggregate calculations, the same subtraction for the proportional change in the OM density fractions was utilised.

Priming effect

The priming effect (PE) was calculated as defined by Guenet et al. (2010):

$$\mathrm{PE} = \left(\frac{A_{\mathrm{lignin}} - A_{\mathrm{sample}}}{A_{\mathrm{lignin}} - A_{\mathrm{soil}}}\right) \times Q_{\mathrm{sample}} - Q_{\mathrm{soil}} \quad (1)$$

where A_{lignin}, A_{sample}, and A_{soil} represent the isotopic abundance of ^{13}C-lignocellulose residue added to the soil, the isotopic abundance of the CO_2 from the amended soil core sample with labelled lignocellulose, and the isotopic abundance of the CO_2 from non-amended (natural) soil core sample, respectively. Q_{sample} and Q_{soil} represent the quantity of released CO_2 in the microcosm headspace of freshly C amended soil and the

CO_2 in the headspace of non-amended soil, respectively. Equation 1 was used to calculate the priming of SOM induced by the amendment of lignocellulose. The D/W cycles were assumed to release fPOM, which primarily consists of lignocellulose. Therefore, the difference in PE between soil with D/W cycles and soil with no D/W cycles allowed us to quantify the effect of D/W cycles on priming (PE_c).

Soil analyses

Soil C and nitrogen (N) contents were determined by dry combustion using a CN Elemental analyser (CHN NA 1500, Carlo Erba). Microbial biomass C (MB-C) was determined by the difference in extractable C in 0.5 M K_2SO_4 of fumigated (chloroform free of ethanol) and unfumigated soils and multiplied by the factor 2.64, used by Vance et al. (1987a, 1987b).

$^{13}C/^{12}C$ isotope ratio

The carbon isotope ratios ($^{13}C/^{12}C$) of all fractions, CO2, MB-C, and bulk soil samples were measured at the Centre for Stable Isotope Research and Analysis (KOSI) of Georg-August-University of Göttingen, Germany. The CO2 concentration and the carbon-isotope ratio were measured in a gas chromatograph combustion isotope ratio mass spectrometer (GC-C-IRMS). Soil C contents were measured using an elemental analyser (Vario EL II, Germany), and the isotopic ratio was measured using an elemental analyser in dual-element analysis mode (Carlo Erba 1108, Milano, Italy). The C isotope ratio was expressed relative to the international Pee Dee Belemnite (PDB) limestone standard as $\delta^{13}C$.

Substrate use efficiency

The SUE was calculated at the end of the incubation as the ratio between labelled microbial biomass ($^{13}C_B$), $^{13}CO_2$ respired, and $^{13}C_B$ (Spohn and Chodak 2015):

$$SUE = \frac{^{13}C_B}{^{13}CO_2 + ^{13}C_B} \quad (2)$$

where SUE estimates the relative proportion of the labelled MB-C to respiration.

Statistical analysis

Two-way ANOVA was performed to analyse the effects of temperature and D/W cycles on CO_2 efflux, PE, aggregate size, OM-C fraction, and microbial biomass-C and its ^{13}C-lignocellulose distribution. The normality of the variances was tested by the Shapiro-Wilk test, and the homogeneity of variance was tested by Levene's test. The data abnormally distribution was log transformed until comparison data presented similar variance. Least significant difference (LSD) and post hoc Tukey tests ($p < 0.05$) were performed to compare mean values between variables. All analyses were conducted using SPSS statistical software v23.0.0.0 (SPSS Inc., Chicago, IL, USA). Figures were developed with DataGraph 4.3 Visual Data Tools, 2006–2018, Inc.

Results

Soil weight and C recovery (%) following dry sieving varied between 92 and 99%, respectively. The recovery of soil-labelled ^{13}C fluctuated between 6 and 52% and varied between 5 and 39% in the ^{13}C MB-C. Leachates were minimal and fluctuated between 0 and 7% (Table 2). The total recovered lignocellulose-derived labelled ^{13}C ranged from 73 to 99% (Table 2).

Aggregate size classes

The D/W-induced change in the distribution of aggregate size classes and their C contents was obtained by subtracting D/W 0 cycle results from the aggregate size class abundance from that of the 1 or 4 D/W cycle treatment (Fig. 3). Macroaggregates (> 250 μm) were the most abundant aggregate size class in the investigated soils (609–785 g kg^{-1}), followed by microaggregates (250–53 μm) (201–308 g kg^{-1}) and silt + clay particles (< 53 μm) (12–23 g kg^{-1}) (Table S1, Supplementary Materials). Drying and rewetting had minimal influence on the mass of the aggregate size classes and their C content at 5 °C (Fig. 3a). At 25 °C, however, macroaggregate weight (Fig. 3b) and labelled C (Fig. 3f) increased (positive value) after 1 D/W cycle, and no significant differences were detected for 4 D/W cycles (Table S4, Supplementary Materials). The same was true for labelled C at 5 °C (Fig. 3e).

Density fractionation

Drying and rewetting cycles did influence the quantity of organic C, including labelled C (Fig. 4; Tables S2, S5, Supplementary Materials). The interaction between temperature and D/W cycles influenced the distribution of C and lignocellulose-derived ^{13}C among the various OM fractions (Tables S3, S5, supplementary Materials). The quantity of D/W cycles did not have significant effects at 5 °C, but the total C and lignocellulose-derived ^{13}C content always increased with 1 cycle and decreased with 4 cycles at the expense of heavy fraction, which lost the respective mass or C (Fig. 4).

Table 2 Total recovery (%) of soil weight, soil C, and labelled C after dry sieving

	Weight	Soil C	NB-^{13}C-^{1}	MB-^{13}C^{2}	$^{13}CO_2$	^{13}C-leached	Total
5 °C							
0 cycle	97	95	21	39	13	0	73
1 cycle	99	92	32	20	33	3	88
4 cycles	100	106	47	20	17	5	89
25 °C							
0 cycle	93	92	48	5	43	0	96
1 cycle	99	117	52	14	33	0.3	99
4 cycles	92	72	6.4	26	60	7	99

[1] Non-biomass

[2] Microbial biomass

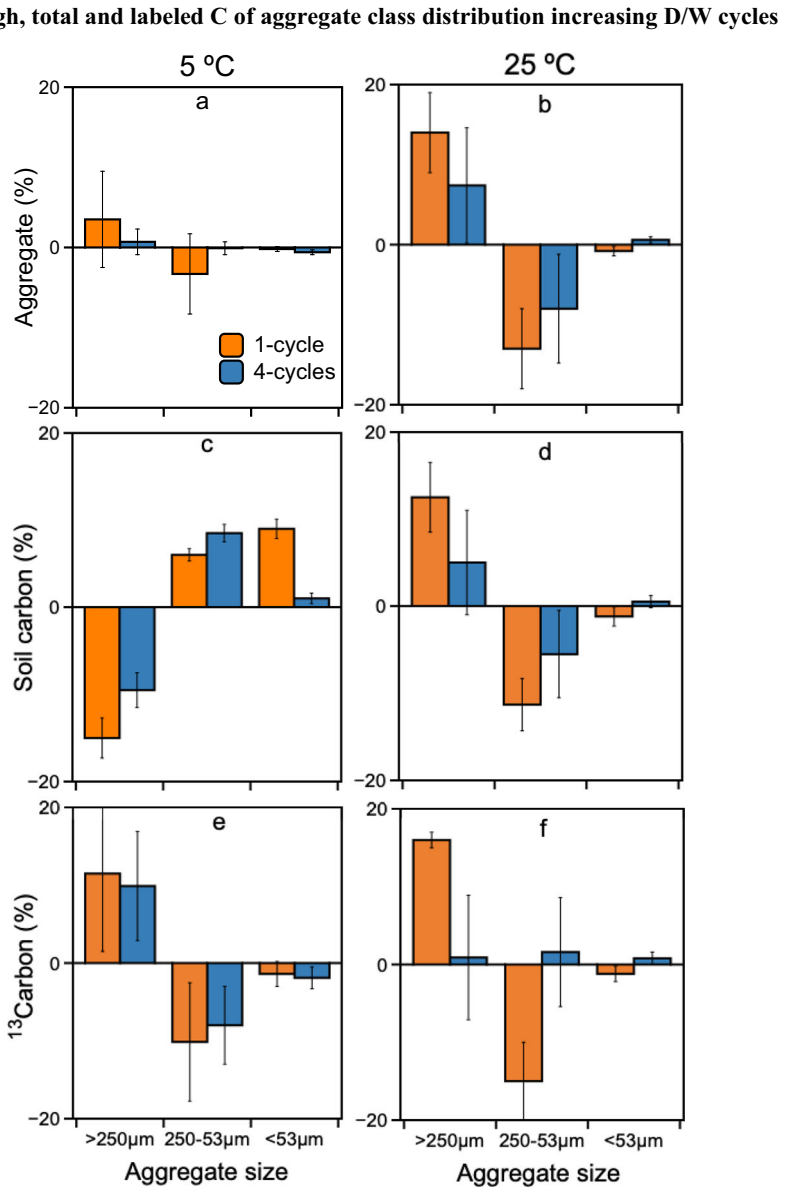

Fig. 3 Proportional change effect of aggregate size classes (macroaggregates > 250 µm, microaggregates 250–53 µm, and silt + clay size < 53 µm) obtained by subtracting zero cycles (no cycle + labelled residue) to 1 cycle D/W or 4 cycles D/W. Soils amended with lignocellulose are displayed after 27 days of incubation at 5 °C (left) and 25 °C (right), whereas relative weight (**a** and **b**), total C content (**c** and **d**), and lignocellulose-derived ^{13}C incorporation (**e** and **f**) of the aggregate size classes is shown. Bars indicate standard errors of the means

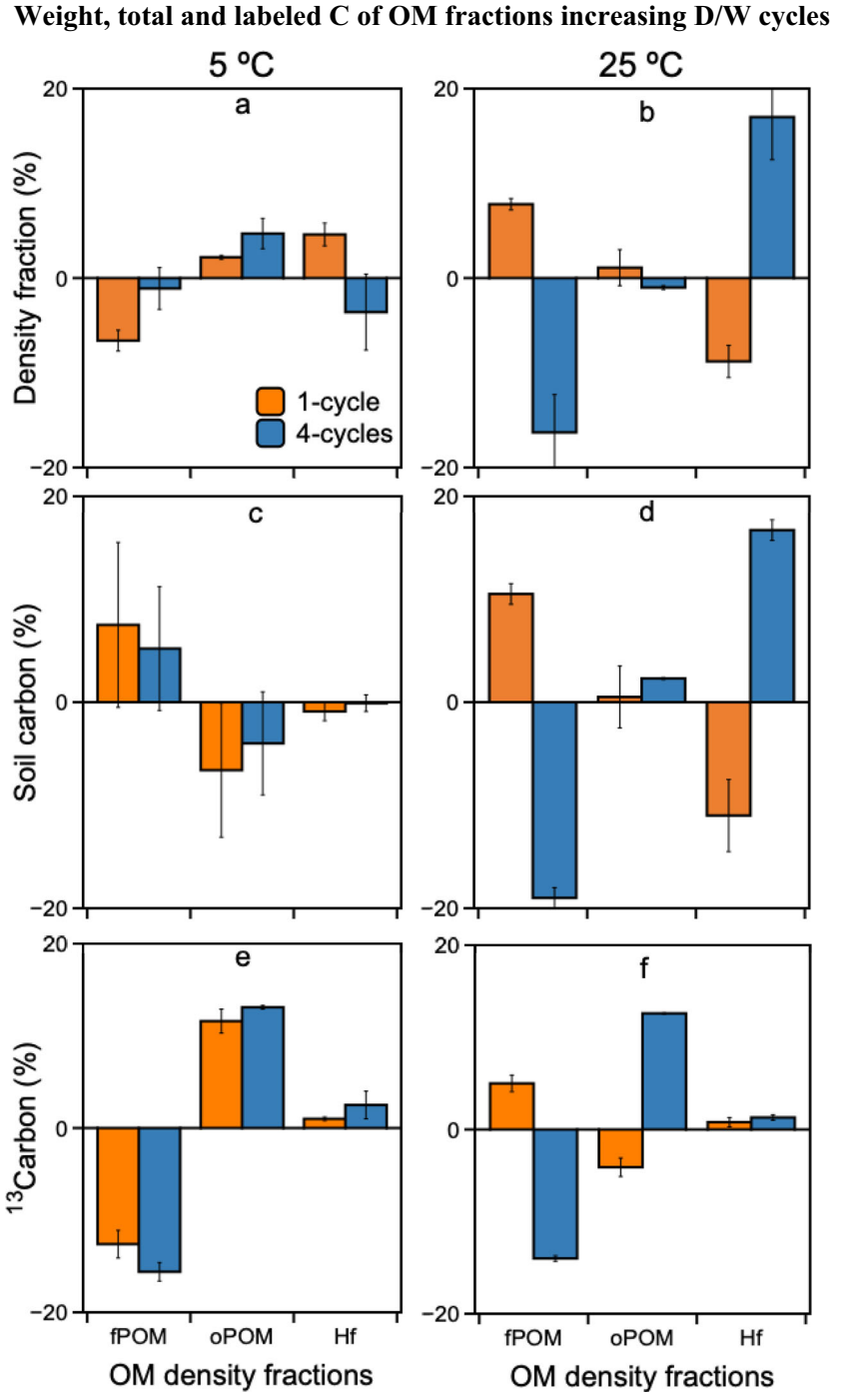

Fig. 4 Proportional change effect of organic matter particles (POM) from the entire soil; OM fraction from the different aggregates was reunited as light fraction < 1.6 g cm $^{-3}$ (fPOM), occluded fraction 1.6–2.0 g cm-^{3} (oPOM), and heavy fraction > 2.0 g cm^{-3} (Hf) obtained by subtracting the zero cycles (no cycle + labelled residue) to 1 cycle D/W or 4 cycle D/W. Soils amended with lignocellulose after 27 days of incubation at 5 °C and 25 °C are presented regarding the relative weight of the OM fraction (**a** and **b**), their total C content (**c** and **d**), and their lignocellulose-derived ^{13}C incorporation (**e** and **f**). Bars indicate standard errors of the means

CO_2 effluxes

Soil respiration was responsive to temperature, as demonstrated by the accumulated total CO_2 and labelled $^{13}CO_2$ efflux in the undisturbed cores (Table S6, Supplementary Materials). On average, the total amount of CO_2 released at 25 °C was approximately three times that released at 5 °C (Fig. 5). The mineralisation of lignocellulose-derived ^{13}C was roughly 2.5 times higher at 25 °C than that at 5 °C.

D/W cycle effects were isolated at each temperature by one-way ANOVA. After day 18, the total CO_2 efflux was significantly higher for soils exposed to 1 D/W cycle than those exposed to 4 cycles or provided with constant moisture content (0 cycle) at 5 °C ($p < 0.05$) (Fig. 5a). Lignocellulose mineralisation displayed the same pattern as the total CO_2; it was higher in soils exposed to only a single D/W cycle, compared with those experiencing 0 or 4 cycles (Fig. 5c). Soil Incubated at 25 °C with no D/W cycles had a higher total

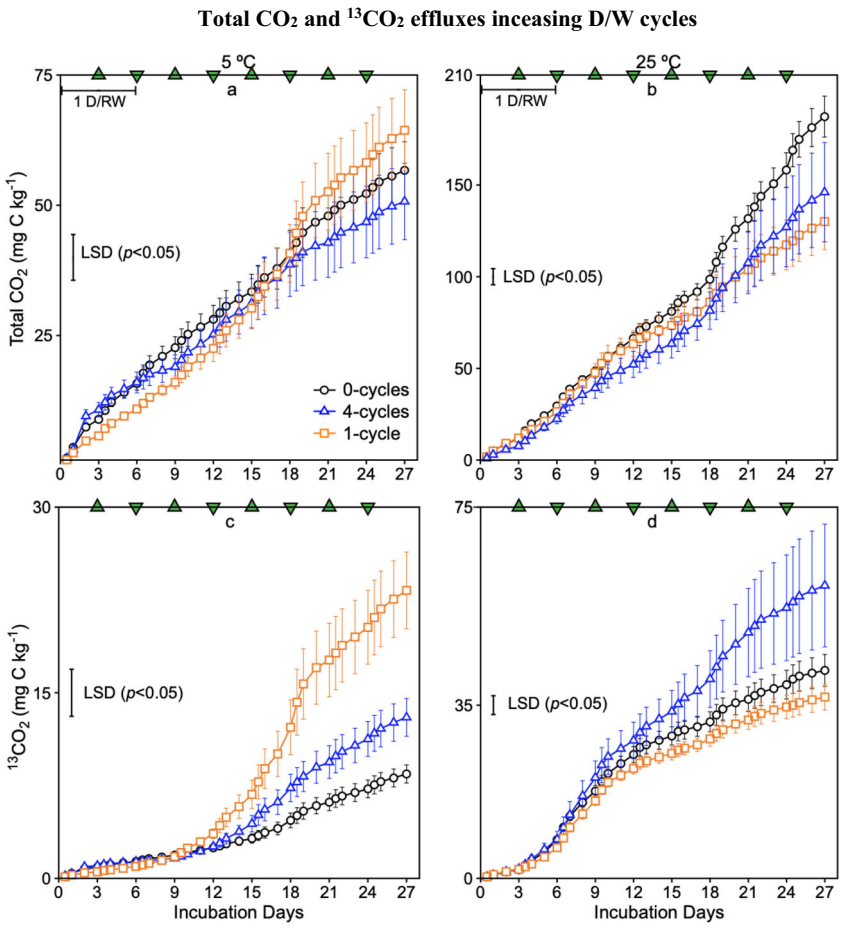

Fig. 5 Total CO_2 evolved during 27 days of incubation at 5 °C (**a**) and 25 °C (**b**) from soil with lignocellulose addition and D/W (0 cycle, 1 cycle, and 4 cycles). Dry period (triangle) started on day 3 and continued for another 3 days of incubation. The wet period (inverted triangle) started on day 6 until the next drying. $^{13}CO_2$ efflux through 27 days of incubation at 5 °C (**c**) and 25 °C (**d**). Small bars on the data point indicate standard errors of the mean. Large bars indicate the least significant differences (LSD) ($p < 0.05$)

CO_2 efflux than those of soils with 1 or 4 D/W cycles after 18 days of incubation ($p < 0.05$) (Fig. 5b). In the warmer soil, the release of lignocellulose ^{13}C was the highest when exposed to 4 D/W cycles (cf. Fig. 5 b and d).

Priming effect

The PE response varied with the temperature, and differences between D/W treatments began to become evident after 18 days of incubation (Fig. 6). Only the 0 D/W cycle soil at 5 °C showed a positive PE, although it was not significantly different from zero PE; soils with D/W cycles showed a negative PE, and the soil with 4 D/W cycles was the only treatment significantly different from zero at the end of the incubation time (Fig. 6a). At 25 °C; however, the PE was always negative and soils exposed to D/W, regardless of the number of cycles, showed the most negative values ($p < 0.05$) (Fig. 6b). At 5 °C PEc, the differences between soil with 1 or 4 D/W cycles and 0 cycle were significant between 0 and 18 days and at the end of the incubation (Fig. 6c). However, at 25 °C the differences were expressed from day 9 and were not perceptible at the end of the incubation (Fig. 6d).

Microbial biomass and substrate use efficiency

Temperature and D/W cycles had significant impacts on microbial biomass ^{13}C incorporation (cf., Tables 2 and 3) and SUE (Table 3; Fig. 7; and Table S7, Supplementary Materials). High SUE occurred preferentially under lower temperatures and was on average two times higher ($p < 0.05$) at 5 °C than at 25 °C (Fig. 7). Drying and rewetting had a decreased effect on SUE values at 5 °C (Fig. 7a), but at 25 °C, D/W cycles did not induce any significant effects on SUE (Fig. 7b).

Discussion

Aggregates and particulate organic matter

Physical protection of SOM by aggregates is an important mechanism for C stabilisation; differentiating the degree of physicochemical protection afforded to the SOM by various aggregate size classes remains challenging. Drying and rewetting cycles were investigated in terms of their disruptive effects on the degradation and formation of macroaggregates (> 250 μm) and microaggregates at (250–53 μm) (i.e. the

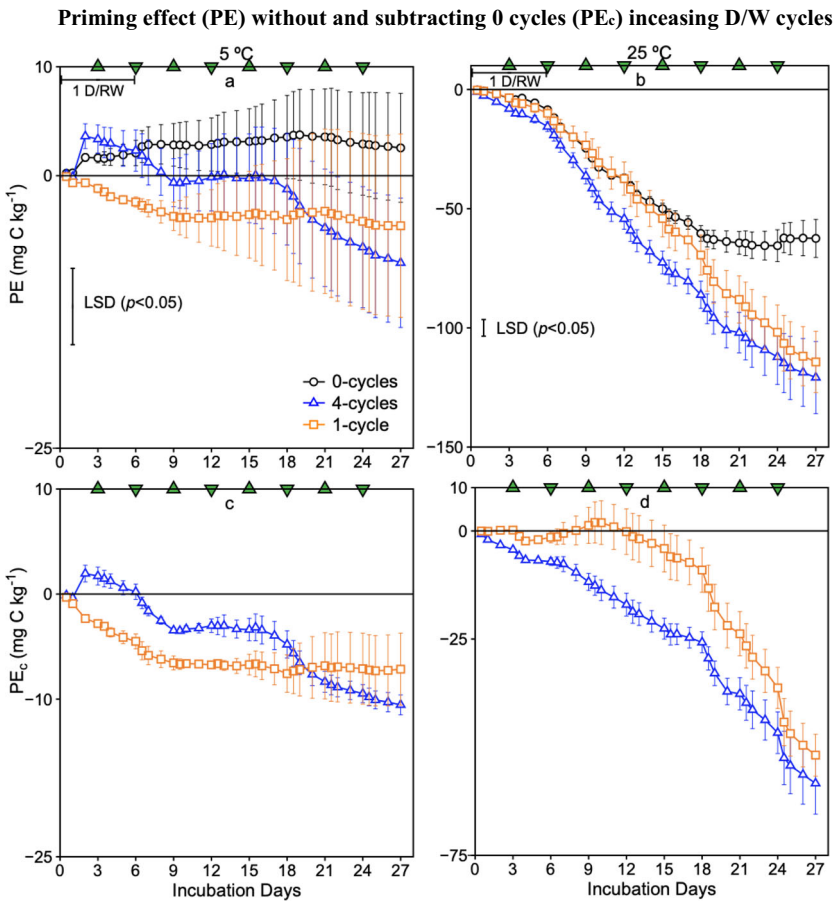

Fig. 6 Priming effect (PE) through 27 days of incubation at 5 °C (**a**) and 25 °C (**b**) for soil with lignocellulose addition. Dry period (triangle) started on day 3 and continued for another 3 days of incubation. The wet period (inverted triangle) started on day 6 until the next drying. Relative priming effect as affected by drying and rewetting (PEc), calculated by substratcing the zero cycles (no cycle + labelled residue) to 1 cycle D/W or 4 cycles D/W, is shown for 27 days of incubation at 5 °C (**c**) and 25 °C (**d**) for soil with lignocellulose addition. Small bars on the data point indicate standard errors of the mean. Large bars indicate the least significant differences (LSD) ($p < 0.05$)

macroaggregate turnover) and the associated C dynamics in the respective aggregate size classes found in a temperate forest. Soil with D/W cycles experienced accelerated macroaggregate turnover at the expense of the microaggregates size class, particularly at warmer temperatures of 25 °C (Fig. 3b).

Table 3 Total microbial biomass C (MB-C), MB-^{13}C, and standard error of the mean (±) of four replicates. Different lowercase letters in each column and within each temperature indicate significant differences ($p < 0.05$). Different capital letters in each column and between temperatures indicate significant differences ($p < 0.05$)

Drying and rewetting	Microbial biomass C	
	Total MB-C (mg C kg^{-1})	MB-^{13}C
5 °C		
0 cycle	456 ± 61aA	15 ± 4.0 aA
1 cycle	372 ± 28 aB	7.5 ± 1.0 bB
4 cycles	346 ± 51 aB	7.6 ± 3.0 bB
25 °C		
0 cycle	317 ± 48 aC	2.0 ± 1.5 bD
1 cycle	313 ± 25 aC	5.4 ± 1.1 aC
4 cycles	345 ± 57 aBC	9.8 ± 4.0 aB

Generally speaking, we found strongly contrasting effects between the two temperature treatments, indicating a systematic process underlying influence of temperature. Although we did not determine the microbial community composition, fungal growth could be significantly reduced at low temperatures and fungal hyphae development could be stunted at higher temperatures. Fungi can function as binding agents in soil (Denef et al. 2001a), and at high temperatures, fungi could represent a significant portion of the microbial biomass and could have key function in building and stabilising macroaggregates (Denef et al. 2001a). After 27 days of incubation at 25 °C, the proportion of microaggregates' weight (Fig. 3b), their C content (Fig. 3d), and lignocellulose-derived ^{13}C (Fig. 3f) decreased in soils exposed after 4 D/W cycles, but the effect was not observed after 1 D/W cycle (Fig. 3b–f). Increasing the number of D/W events could therefore have a negative impact on microaggregate formation, while novel protected OM within macroaggregates could contribute to its formation. Density fractionation indicated a depletion of the fPOM and an increase in Hf, supporting the acceleration of macroaggregate turnover (Fig. 4b, d) and increasing the ^{13}C fraction in the oPOM (Fig. 4f). Microaggregates were depleted by accelerated turnover and the formation of new macroaggregates, which only occurred in the short term under enhanced D/W cycles

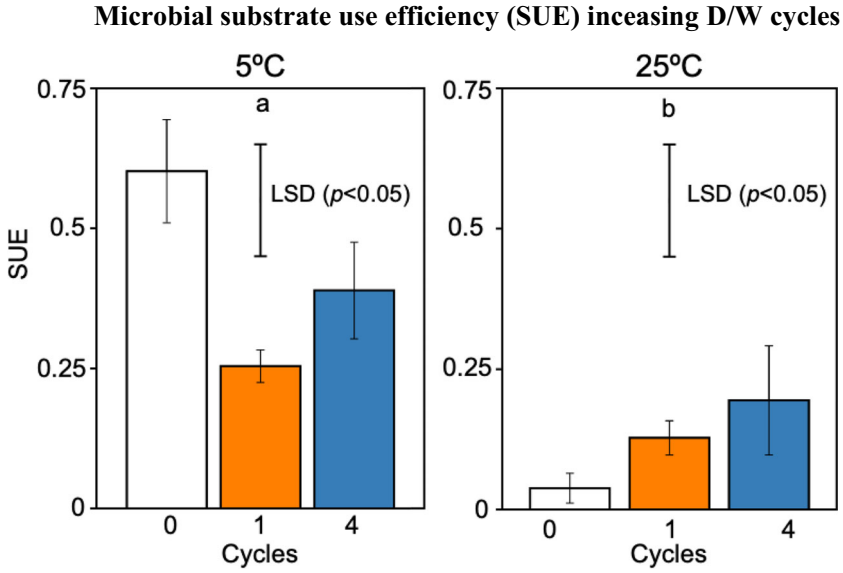

Fig. 7 Substrate use efficiency (SUE) of ^{13}C-lignocellulose at 5 °C (**a**) and 25 °C (**b**) estimated after 27 days of incubation of the D/W treatments, 0 cycle, 1 cycle, and 4 cycles. Small bars indicate standard errors of the mean. Large bars indicate the least significant differences (LSD) ($p < 0.05$)

(Denef et al. 2001a; Dorodnikov et al. 2011; Gunina and Kusyakov 2014).

CO_2 efflux

Drying and rewetting cycles affected the cumulative C mineralisation at 25 °C. The total CO_2 emitted throughout the 27 days of incubation was strongly reduced compared to the CO_2 produced by soil at optimum moisture content (0 cycle). Thus, rewetting does not compensate for the lower mineralisation during drought periods but rather has a medium-term impact (Fig. 5). Cumulative mineralisation is linked to the intensity and duration of drying and the accessible pool of organic C during drying and rewetting (Borken and Matzner 2009). Therefore, under field conditions, increasing droughts could result in reduced C mineralisation, whereas increasing spring/summer precipitation could accelerate C losses from physically protected organic matter. In our laboratory study, drying and rewetting cycles caused higher microbial respiration of new organic matter added to the soil (Fig. 5). This effect for $^{13}CO_2$ became evident after 15 days of incubation at both temperatures (Fig. 5c and d). *Araucaria araucana* litter fall displayed a C:N ratio of 60 (Table 1) with a high lignin:N ratio (70–90), which is generally associated with a low mineralisation rate (Diehl et al. 2003; Bertiller et al. 2006). The lignocellulose-rich OM decomposed at a rate between 50 and 150 mg C kg soil^{-1} day^{-1}, comparable to other rates determined through similar incubations of Chilean forest soils (Matus et al. 2008; Muñoz et al. 2016) or Mediterranean forest soils (Almagro et al. 2009; Guntiñas et al. 2013). Despite the recalcitrance of the fresh substrate, there was significant C mineralisation from this material, supported by the negative PE value (Fig. 6d).

Priming effect

At 5 °C, there was a small but significant PE induced by the lignocellulose amendment, while at 25 °C a stronger negative PE was produced. The PE was negatively correlated with respired ^{13}C ($r = -0.59$, $p < 0.04$, $n = 12$). This result indicates that when less organic C is consumed from native SOM by microorganisms (negative PE), more fresh ^{13}C is mineralised. This correlation clearly demonstrates the preferential C use of the substrate, which is, in this study, a representative compound of the soil's fPOM fraction. These results were also supported by the PE_c, the difference in PE between 1 or 4 cycles and 0 cycle (Fig. 6). In other studies, where complex OM was added in the form of leaf and stem residues (^{13}C-labelled wheat residues), the results also showed intensive mineralisation of the added OM, yielding a negative PE for extended periods (Shahbaz et al. 2017); with the addition of other materials, a temporary negative PE (up to 40 days) was observed (Wang et al. 2015), likely due to preferential utilisation of the added substrate and thus a pool substitution (Shahbaz et al. 2017). This mechanism was effectively revealed by the SUE, particularly at 5 °C (Fig. 7), because the lignocellulose was incorporated into the microbial biomass by a well-adapted microbial community (Borken and Matzner 2009). Soil microbial communities are resilient and able to quickly recover after wetting in soils with high SOC stock (Canarini et al. 2017). At 25 °C, however, lignocellulose-derived C could be invested for highly energy demanding processes, e.g. for enzyme synthesis, and less C was converted into structural cell components (Ågren and Bosatta 1987; Blagodatsky et al. 2000; Davidson and Janssens 2006; Manzoni et al. 2012). This finding is in accordance with other studies, which obtained similar results, i.e. a decreasing C use efficiency with increasing temperature between 2 and 28 °C

(Manzoni et al. 2012; Qiao et al. 2019). This phenomenon can likely be associated with a change in metabolism rather than a change in the microbial community structure (Manzoni et al. 2012; Bölscher et al. 2017; Di Lonardo et al. 2017). When the number of D/W cycles was increased on undisturbed soil, fPOM was negatively affected by warming and the acceleration of aggregate turnover. Warming and aggregate turnover could have significant implications for temperate forests facing global change. Faster macroaggregate turnover and depletion of fPOM may prevent large stabilised SOM from decomposing, leading to a lack of C stabilisation after repeated D/W cycles.

Conclusions

One drying-rewetting (D/W) cycle disrupted approximately 15% of the aggregates after 27 days. The fine particulate fraction of organic matter (fPOM, < 1.6 g cm^{-3}) released from aggregates disrupted by D/W contained the most physically exposed C (microbially available) as compared to the other C pools. This fPOM, which we traced by added ^{13}C-labelled lignocellulose, was decomposed preferentially, covering microbial energy demand but not converted to microbial biomass and therefore not contributing to long-term stabilisation in the form of necromass residues. Increasing the number of D/W cycles caused a negative priming effect (PE), i.e. preferential utilisation of the added ^{13}C-labelled lignocellulose released by D/W cycles rather over other OM fractions. A new pathway is proposed for C release by aggregate disruption, resulting in negative PE due to D/W cycling. This scenario was reflected by low substrate use efficiency (SUE), i.e. microbes preferentially respiring the accessible fPOM, particularly at a high temperature. Consequently, the D/W cycles at 25 °C significantly increased microbial activity, which primarily regulated fPOM decomposition.

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