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Microbial utilization of low molecular weight organic carbon substrates in cultivated peats in response to warming and soil degradation

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Abstract

Peatlands store vast amounts of carbon (C) within the global terrestrial biosphere. Drainage and cultivation of peat soils lead to rapid soil degradation and C losses, and this may worsen under warming as the soils are no longer protected by anaerobic conditions. To predict the rates of soil C loss and design effective mitigation strategies, it is important to understand what controls organic matter mineralization in these soils. Using the 0-10 cm soil depth of thick and thin (degraded) agricultural peat soils, we investigated the fate of low molecular weight organic substrates (LMWOS) and how the microbial biomass consuming these substrates responded to temperature. We incubated the soils under increasing temperatures (4, 10, 20, and 30 °C) for 72 h. Either ^{14}C-labelled glucose or amino acids were added to the soils and their speed of breakdown, partitioning into anabolic/catabolic processes and microbial C use efficiency (CUE) were determined. The total $^{14}CO_2$ loss from soil increased significantly with increasing temperature during 72-h incubation, regardless of peat layer thickness. Warming altered the dynamics of LMWOS mineralization by changing C allocation and turnover rate of different pools . The half-life of LMWOS decreased more than 50% when temperature increased from 4 to 30 °C for both substrates. CUE was always higher for thin than thick peat soil and both declined by 0.002–0.005 $°C^{-1}$ with temperature increase. Thin peat decreased substrate C allocation into the fast cycling pool compared to the thick peat, but had no overall effect on pool turnover rate. Our work suggests that climate warming will accelerate C mineralization and turnover in drained peat soils, with larger effects expected in thick peat soil. This study provides an important initial step in characterizing the response of the microbial utilization of labile C to temperature change and soil degradation in cultivated peatlands.

Keywords: C sequestration; Climate warming; Dissolved organic matter; Histosol; Turnover rate

1. Introduction

Peatland soils represent a vast store of global C, amounting to ca. 455 Gt (Gorham, 1991). Around three quarters of peatlands are located in the middle and high latitudes of the Northern Hemisphere areas, which are predicted to experience significant climate warming (Grogan and Jonasson, 2005; Davidson and Janssens, 2006). Warming-induced acceleration of C losses through enhanced mineralization of peat deposits could result in positive feedback and exacerbate climate change (Davidson and Janssens, 2006; Dorrepaal et al., 2009; Evans et al., 2019). Much of the work to date on warming-induced changes in peatland C cycling has focused on undrained ecosystems with natural vegetation cover, and most commonly on ombrotrophic bog peats (e.g. Freeman et al., 2001; Weltzin et al., 2003; Clark et al., 2009; Bragazza et al., 2012; Ward et al., 2013). Comparatively little work has been undertaken on the impact of warming on more modified systems, most notably drained, nutrient-enriched fen peats. Additionally, in temperate peatlands drained for agriculture, a similarly high temperature-sensitivity has been widely assumed in policy-related assessments of the future vulnerability of these areas to climate change (e.g. Graves and Morris, 2013). However, the empirical basis for these assessments is weak, and a greater understanding of the mechanisms that regulate C dynamics and turnover in agriculturally drained fen peatlands under increasing soil temperatures is important to inform future management for both climate change mitigation and adaptation.

Soil microorganisms mediate key processes involved in the cycling of C and other nutrients (Nguyen and Henry, 2002). Soil microbial activity and consequently soil respiration are typically limited by the availability of organic substrates (Demoling et al., 2007). The majority of dissolved organic matter is made up of high molecular weight organic compounds (van Hees et al., 2005). These must first be broken down

into low molecular weight organic substances (LMWOS) available for transportation into the cell prior to microbial use (Glanville et al., 2012). Although LMWOS typically represent <10% of total dissolved organic matter, they are relatively more labile and have very fast turnover rates (van Hees et al., 2005; Boddy et al., 2007). Therefore, LMWOS appear to dominate the total CO_2 flux from soil (up to 30%) and strongly affect nitrogen (N) cycling at the global scale (van Hees et al., 2005). However, little is known about the temperature dependence of LMWOS mineralization. Developing a detailed, mechanistic understanding of the temperature and soil type dependence of LMWOS dynamics is therefore critical to predicting C turnover responses to climate warming and peat degradation.

CO_2 fluxes originating from SOM mineralization are also controlled by how the microbial community partitions the LMWOS between catabolic (i.e. energy yielding processes associated with CO_2 production) and anabolic (i.e. microbial biomass growth) pathways (Jones et al., 2018). Carbon use efficiency (CUE) is a parameter commonly used to quantify the proportion of C source that is converted into new microbial biomass (del Giorgio and Cole, 1998). Although CUE is generally thought to decrease with increasing temperature (Devêvre and Horwáth, 2000; Tucker et al., 2013; Schindlbacher et al., 2015), a few studies have demonstrated a limited response to temperature changes (e.g. Dijkstra et al., 2011; Hagerty et al., 2014). Changes to microbial CUE in response to warming and soil degradation could have significant influences on soil CO_2 emissions (Öquist et al., 2017). However, it remains unclear how CUE response to changing temperatures and soil conditions in the drained, cultivated fen peats. Therefore, it is important to better understand how environmental variables alter CUE, in order to reliably quantify associated feedback effects, and their impact on warming and land degradation.

Quantifying the dynamics and turnover of LMWOS is vital when investigating the impacts of environmental change on peatland mineralization. Warming induces an immediate change in microbial activity and the effects of this on C turnover and dynamics are often short-lived (Luo et al., 2001; Walker et al., 2018). When the effects of warming are evaluated longer-term, CO_2 release decreases in most cases, returning to pre-warming rates as substrate depletion reduces microbial biomass and constrains microbial activity (Walker et al., 2018) or as the temperature sensitivity of soil respiration acclimatizes under warming (Luo et al., 2001). The response of cultivated peat soils to warming is further complicated by altered availability of C and nutrient sources, for example, due to fertiliser application and alterations in the rate and form of C input from crops compared to natural wetland vegetation, which are likely to influence microbial growth and CUE (Manzoni et al., 2012; Sinsabaugh et al., 2013, 2016). Given these considerations, we compared the microbial utilization of LMWOS in thick and thin fen peat soils under short-term (72 h) warming using ^{14}C labelling approach (trace amount of addition lead to minimal effect on the intrinsic C pool, whilst enable to separately investigate the size and turnover rate of substrate pools). The objectives of this study were: 1) to assess changes in the dynamics and turnover of LMWOS (glucose and amino acids) in response increasing temperatures; 2) to investigate the influence of peat degradation on the rate of LMWOS cycling; and 3) to quantify the effects of LMWOS type, temperature increase and peat soil degradation on microbial CUE.

2. Materials and methods

2.1. Site description and soil sampling

The study site was located in Fenland region of East Anglia, UK (52°31'N,

0°23'E). The climate regime is classified as temperate oceanic with a mean annual temperature of 13 °C (range -6 to 25 °C) and mean annual rainfall of 612 mm (Taft et al., 2017). The site is comprised of a flat lowland eutrophic fen, under intensive rotational horticultural production (e.g. lettuce, celery, sugar beet, wheat), with >1.5-m depth organic layer overlying carbonatic clay (Oxford Clay) (Musarika et al., 2017). Most of the area has been drained since at least the 17th century, and as a result of peat oxidation and subsidence much of the original thick peat has reduced to a thin (< 40 cm) residual layer of organic matter intermixed with underlying mineral soil, referred to as 'wasted' peat (Holman, 2009). It should be noted that these thicker peats are still undergoing rapid C loss at rates of ca. 1.5 cm y^{-1} (Taft et al., 2017). To investigate the effect of differences in peat degradation on microbial C transformation processes, we selected soil samples from paired thick and thin peat sub-sites. These two kinds of peats were termed 'thin peat' and 'thick peat' based on their organic C contents. The exact thickness of the thin peat layer was not measured due to the diffuse boundary with the underlying mineral soil. At each sub-site, topsoil (0-10 cm) was collected from four sampling points (replicates) located at least 10 m apart. Soil samples were stored in gas-permeable plastic bags at 10 °C (approximate field temperature during sampling) until the start of substrate mineralization experiments (1 week after collection).

2.2. Soil properties

Soil bulk density was determined by the core method (Blake and Hartge, 1986). Soil volumetric water content was calculated using the measured gravimetric water content (80 °C, 48 h). Soil pH was measured in a 1:2.5 (w/v) distilled water extract using a standard calomel electrode (Hanna Instruments Ltd., Leighton Buzzard, UK). Total organic C and N were determined on oven-dried, ground soil using a TruSpec CN Analyzer (Leco Corp., St Joseph, MI, USA) after removing inorganic C by concentrated

HCl fumigation. Water extractable parameters were measured with 3 g fresh soil in 1:2.5 (w/v) slurries of soil and deionized water, which were shaken for 16 h and centrifuged at 3800 *g* for 5 min. Extractable organic C and N were analysed using a Multi N/C 2100/2100 analyser (AnalytikJena AG, Jena, Germany). Extractable phenolics were assayed colorimetrically using the Folin-Ciocalteu reagent (F9252; Sigma-Aldrich Inc.) according to Velioglu et al. (1998). Extractable phosphate (P) was measured using the molybdate blue method described in Murphy and Riley (1962). The microbial community was determined by phospholipid fatty acid (PLFA) analysis as described by Bartelt-Ryser et al. (2005). To measure the Q_{10} value for soil respiration in the bulk soil, we incubated 30 g fresh soil in 430 cm^3 containers at 4, 10, 20, and 30 °C for 72 h, and measured soil CO_2 emissions using an EGM-5 portable infra-red gas analyser (PP Systems Ltd., Amesbury, MA, USA) at 1, 31 and 61 minutes after closure of the containers, and Q_{10} values were calculated based on Karhu et al. (2014).

2.3. Low molecular weight organic substrate mineralization

The mineralization rate of LMWOS was investigated following the methods of Boddy et al. (2007) and Gunina et al. (2017). Briefly, fresh soil (2 g) was added into a 50 ml centrifuge tube, placed into incubators at 4, 10, 20, or 30 °C and equilibrated for 5 h prior to substrate addition (Boddy et al., 2008; Blagodatskaya et al., 2016). The range of temperatures used was chosen to reflect the current annual temperature range of the study site, which typically rises to around 25 °C, as well as the potential for higher peak summer temperatures in response to climate change. Next, 200 µl of either ^{14}C-glucose or a ^{14}C-amino acid mixture (< 10 nM; 16 kBq ml^{-1}; Amersham Biosciences UK Ltd, Chalfont St. Giles, UK) was injected into the soil, equivalent to 0.15 ng glucose-C g^{-1} dry soil for the thick peat and 0.09 ng glucose-C g^{-1} for the thin peat. The amino acid mixture was an equimolar mixture of 15 uniformly ^{14}C-labelled

L-amino acids (alanine, arginine, aspartic acid, glutamic acid, glycine, histidine, isoleucine, leucine, lysine, phenylalanine, proline, serine, threonine, tyrosine and valine; pH 5.60). These substrates were chosen as they are central to C and N cycling in soil, they represent the major breakdown products of cellulose and protein, and are present in high amounts within crop residues entering these soils. A low substrate concentration was chosen to reflect ambient, steady state concentrations in the soil (i.e. the pulse addition aims to label the intrinsic substrate pool but is insufficient to induce microbial growth). Subsequently, a $^{14}CO_2$ trap (1 M NaOH 1 ml) was placed into the closed container to capture evolved CO_2. The NaOH traps were changed at 1, 3, 5, 7, 10, 24, 32, 48, 72 h after LMWOS addition to measure the production of $^{14}CO_2$. This sampling schedule was selected as many previous studies measuring the dynamics of LMWOS-C turnover by microbial biomass show that partitioning is quasi-complete after 72 h (ca. 96% for glucose and 82% for amino acids; Jones et al., 2018). After trap removal at 72 h, the amount of available ^{14}C remaining in the soil was quantified by extracting the soil with 10 ml of 0.05 M K_2SO_4 (Glanville et al., 2016). ^{14}C activity of the NaOH traps and K_2SO_4 extractions was measured by liquid scintillation counting (Wallac 1409 scintillation counter) with Optiphase-3 alkali compatible scintillation cocktail (Wallac EG&G Ltd., Milton Keynes, UK).

2.4. Calculations

^{14}C contained in the LMWOS can be partitioned into two pools once it is taken up from the soil by the microbial community: (1) the fast cycling C pool, where substrate-C is immediately used for catabolic processes, rapidly influencing the $^{14}CO_2$ flux; (2) the slow cycling C pool which constitutes the remaining ^{14}C immobilized within the microbial biomass (i.e. used for cell growth, maintenance, and ultimately necromass turnover, of which the latter two lead to $^{14}CO_2$ production; Glanville et al.,

2012, 2016; Jones et al., 2018). The slow and fast cycling processes should occur simultaneously. Therefore, substrate mineralization was described by a two-process, double first order decay model as follows:

$$S = a_1 e^{-k_1 t} + a_2 e^{-k_2 t} \quad (1)$$

where S is the ^{14}C remaining in the soil, a_1 and a_2 are pool sizes for the fast and slow mineralization phases, k_1 and k_2 are the rate constants for a_1 and a_2, and t is time (Glanville et al., 2016; Gunina et al., 2017).

The half-life ($t_{1/2}$) of the fast and slow cycling pools were calculated as Eq. (2) and referred to $t_{1/2}$- fast and $t_{1/2}$-slow, respectively (Gunina et al., 2017).

$$t_{1/2} = \frac{\ln(2)}{k} \quad (2)$$

Due to uncertainty between the connection of pools a_1 and a_2 and isotopic pool dilution in pool a_2, unlike pool a_1 the $T_{1/2}$ values for pool a_2 are indicative rather than absolute (Glanville et al., 2016). The total amount of substrate was modelled as the sum of the fast and slow cycling pools. When half of the LMWOS was respired as CO_2 the amount of substrate remaining ($S_{1/2}$) was defined as:

$$S_{1/2} = \frac{a_1 + a_2}{2} \quad (3)$$

The half-life of the LMWOS (i.e. combined loss from pools a_1 and a_2) was determined by substituting Eq. (3) into Eq. (1) and solving with a Newton Raphson iteration algorithm, using the fitted parameters from the two-pool model (Glanville et al., 2012).

We calculated CUE using two common methods. The first is the modelling approach using a double exponential kinetic model as Eq. (1). From this, CUE can be calculated as follows:

$$\mathrm{CUE} = \frac{a_2}{a_1 + a_2} \quad (4)$$

This approach is well suited to LMWOS which can rapidly cycle through the microbial

biomass (such as glucose and amino acids) (Glanville et al., 2016; Jones et al., 2018). The second approach to estimating CUE is based on the direct partitioning of substrate C into microbial anabolic processes (i.e. cell growth) and into catabolic processes (i.e. respiration) (Frey et al., 2001; Manzoni et al., 2012). Microbial immobilization of the ^{14}C-substrate ($^{14}C_{imm}$) at the end of the incubation period was estimated as follows:

$$^{14}\mathrm{C}_{\mathrm{imm}} = {}^{14}\mathrm{C}_{\mathrm{tot}} - {}^{14}\mathrm{C}_{\mathrm{K_2}SO_4} - {}^{14}\mathrm{CO_2} \quad (5)$$

where $^{14}C_{tot}$ is the total amount of ^{14}C-substrate added to the soil, $^{14}C_{K2SO4}$ is the amount of ^{14}C recovered in the 0.05 M K_2SO_4 extract and $^{14}CO_2$ is the total amount of $^{14}CO_2$. Then, CUE can be estimated as follows:

$$\mathrm{CUE} = \frac{{}^{14}\mathrm{C}_{\mathrm{imm}}}{{}^{14}\mathrm{C}_{\mathrm{imm}} + {}^{14}\mathrm{CO_2}} \quad (6)$$

It should be noted that the CUE values are only for the C within the glucose or amino acids added (i.e. substrate C use efficiency) and do not account for other C compounds also used by the microbial biomass.

The Q_{10} values on the basis of respiration rates at two temperatures T_1 and T_2 were calculated using the following equation (Karhu et al., 2014):

$$Q_{10} = \left(\frac{R(T_1)}{R(T_2)}\right)^{\frac{10}{(T_2 - T_1)}} \quad (7)$$

where $R(T_1)$ and $R(T_2)$ are respiration rates at two incubation temperatures (T_1 and T_2).

2.5. Statistical analyses

Data were evaluated using three-way ANOVA and Tukey's test, considering LMWOS type, temperature and peat degradation. Analyses were carried out using SPSS (Version 20, SPSS IBM Corp., Armonk, NY, USA). Exponential equations were fitted to the experimental results using a least squares iteration routine with SigmaPlot

12 (SPSS Inc., Chicago, USA). Residuals were checked for a normal distribution using the Shapiro-Wilk test and homogeneity of variance was determined using Levene's test. All differences were considered significant at $P \leq 0.05$.

3. Results

3.1. Soil properties

The bulk density (0-10 cm) of the thick peat soil was significantly lower than the thin peat soil (Table 1; $P = 0.008$), while the volumetric water content was higher in the thick than thin peat soil ($P < 0.001$). The thick peat soil had a higher total organic C, total N, extractable organic C and N contents but a lower C:N ratio compared to the thin peat soil ($P < 0.01$). No differences were detected between the thick and thin peat soils in pH and extractable phosphate ($P > 0.05$). Although the total PLFA was higher in the thick peat soil compared to the thin peat soil ($P = 0.03$), no difference was found in the community components, such as the ratios of fungi-to-bacteria and Gram positive-to-Gram negative bacteria ($P > 0.05$).

3.2. Dynamics of substrate mineralization

The total loss of $^{14}CO_2$ from the soil over the 72-h incubation increased significantly with increasing temperature ($P < 0.001$), regardless of peat degradation and LMWOS type (Figs. 1 and 2). Across all sites and temperatures, significantly more amino acid was mineralized to CO_2 (average 26% of the total ^{14}C added) than glucose (average 14% of the total ^{14}C added; $P < 0.001$). The total losses of $^{14}CO_2$ were always greater in the thick versus the thin peat ($P < 0.001$). The total difference in $^{14}CO_2$ losses between thick and thin soils decreased as temperature increased when glucose was added, but increased when amino acid was added (Figs. 1 and 2). Although increasing

264 temperatures enhanced glucose and amino acid mineralization, the total amount of ^{14}C
265 substrate decomposition yielded relatively lower Q_{10} values (glucose: thick 1.27, thin
266 1.37; amino acid: thick 1.30, thin 1.20; Fig. 2) compared to bulk soil respiratory losses
267 (thick 1.88, thin 1.44; Fig. 3).

268 *3.3. Turnover of low molecular weight organic substrates*

269 A two-pool exponential decay model (Eq. 1) fitted well to the observed data ($r^2 >$
270 0.990). The sizes of both fast and slow cycling pools were significantly affected by
271 incubation temperature, soil degradation, and added substrates (all $P < 0.001$; Table 2).
272 Overall, rising soil temperature increased the relative amount of ^{14}C cycled in the fast
273 cycling pool and decreased ^{14}C cycled in the slow cycling pool (Fig. 4). Additionally,
274 significantly less ^{14}C was portioned to the fast cycling pool in the degraded soil than in
275 the thick peat soil ($P < 0.001$), whilst significantly more ^{14}C was portioned to slow
276 cycling pool in the thin peat soil ($P <0.001$). Furthermore, a smaller proportion of
277 glucose-C (range 6.4-12.3%) was cycled in the fast cycling pool than for amino acid-C
278 (range 12.8-23.3%).

279 Incubation temperature exerted a significant effect on the turnover rate of the fast
280 C pool ($P < 0.001$), however, no clear trend was observed (Fig. 5). A rise in temperature
281 also accelerated the turnover of the slow C pool ($P < 0.001$; Fig. 5). Combining the fast
282 and slow cycling pools together, the half-life of amended LMWOS decreased with
283 increasing temperature (Fig. 6). Peat type, and associated differences in soil properties,
284 did not significantly affect the turnover time of the fast or slow cycling pools ($P > 0.05$;
285 Table 2).

286 *3.4. Microbial carbon use efficiency*

287 The incubation period (72 h) used here was sufficient to allow LMWOS-C to be

partitioned into microbial anabolic and catabolic processes. Substrate CUE was calculated either using a time-independent double exponential kinetic modelling approach (fitting with Eq. 1; method 1) or using a time-dependent approach in which the proportion of metabolised C immobilized is estimated after 72 h (with Eq. 6; method 2). Generally, these two methods showed similar trends of CUE under increasing temperature and soil degradation (Fig. 7). The CUE values of glucose and amino acids calculated with method 1 were 3-9% and 9-19% higher, respectively, than the values from method 2 (Fig. 7). There was a clear trend in decreasing CUE with increasing temperature (0.002-0.005 $^{o}C^{-1}$; Fig. 7). Moreover, the thin peat soil showed higher CUE values than the thick peat soil, indicating more C was used for microbial anabolic processes. Across all samples, the average CUE for glucose (0.909 ± 0.004 and 0.858 ± 0.005 with methods 1 and 2, respectively) was higher than for amino acid (0.826 ± 0.006 and 0.734 ± 0.008; $P < 0.001$).

4. Discussion

4.1. Mineralization of low molecular weight organic substrates

Understanding how temperature affects LMWOS decomposition is important for predicting the influence of climate change on SOM breakdown (Boddy et al., 2008). The positive relationship we observed between temperature and the decomposition rates of LMWOS indicates that temperature has a significant influence on mineralization in cultivated peat soils. This observation agrees with previous findings that ^{14}C-labelled LMWOS are mineralized faster at higher temperatures, albeit these previous observations were in mineral soils from arctic tundra (Boddy et al., 2008). It is also consistent with soil respiration patterns in long-term field warming studies (Luo et al., 2001). The temperature sensitivity (Q_{10} value) of LMWOS mineralization

obtained in this study was 1.20-1.37. It is lower than the Q_{10} from the bulk peat soil (1.44-1.88) in this study, and also lower than the values from other peat soils (e.g. 1.84-3.53; Davidson and Janssens, 2006; Clark et al., 2009). This difference is likely to reflect the microbial utilization of other substrates in bulk respiration measurements (e.g. phenolics, lipids etc), and upstream rate-limiting exoenzyme steps in the decomposition process (e.g. cellulase, protease). In accordance with the kinetic theory of chemical reactions, higher temperature sensitivity occurs in relatively recalcitrant C pools than in labile C pools (Davidson and Janssens, 2006).

Peat layer thickness (a proxy of degradation state) also had a significant influence on mineralization rates of LMWOS and their temperature sensitivities. Smaller amounts of added substrate were mineralized in the thin peat soil, probably due to the lower microbial biomass which may influence reaction rate. The Q_{10} of glucose mineralization was slightly higher in thin than in thick peat soil. As glucose is the most abundant monomer sugar in soils (Gunina and Kuzyakov, 2015), this result suggests increased mineralization and labile C losses from thin peat soil under climate warming. However, thin peat soil showed lower temperature sensitivity for amino acid mineralization than thick soil, with lower mineralization rates, especially at higher temperatures. The percentage decomposition of amino acids was higher than that of glucose. This indicates differential utilization of LMWOS by specific cohorts of the microbial community and/or differential partitioning of the substrates within the microbial cell which consequently turnover at different rates (Boddy et al., 2008).

4.2. Turnover of low molecular weight organic substrates

Disentangling the C allocation into different pools with associated turnover rates can help us to predict the potential response of C cycling to warming and soil degradation in peat soils. The sizes and turnover of fast and slow cycling pools were

clearly temperature dependent. The positive correlation between mineralization of ^{14}C-labelled substrates and temperature is further explained by the increase in the amount of C metabolised in the rapidly respired pool. This is probably because at higher temperatures, microbes prefer to use C for maintenance rather than for storage and growth (Boddy et al., 2008). The turnover rates of both fast and slow cycling pools fall within the range of previous studies in both Arctic and temperate soils (fast cycling pool 0.01 - 0.93 h^{-1}, slow cycling pool 0.14×10^{-3} - 1.66×10^{-3} h^{-1}; Boddy et al., 2007; Creamer et al., 2014). Turnover of the slow cycling pool increased with increasing temperature, whereas no clear trend was found in the fast cycling pool. This result suggests that turnover of C immobilized within the microbial biomass may be more sensitive to soil warming than turnover of fast cycling pool (respired). The half-life of amended LMWOS (fast and slow cycling pools combined) reported in this study (glucose 23-50 days, amino acid 8-21 days) are consistent with previously recorded values for various LMWOS in laboratory and field conditions (Glanville et al., 2012). Substrate half-life decreased with increasing temperature, suggesting that the turnover of LMWOS is temperature sensitive in the peat soils. Overall, it indicates that future warming will potentially increase the turnover of labile organic compounds and resulting C losses through microbial respiration.

Thin, mineral intermixed peat showed significantly lower LMWOS-C allocation into the fast cycling pool compared to thick peat (Fig. 2), indicating that microbial partitioning of incorporated ^{14}C was dependent on soil properties. Additionally, more amino acid-C was used in respiratory processes compared to glucose-C. This reflects the rapid incorporation and deamination of amino acids in cells, leading to the production of keto acids used for respiration (Jones et al., 2005; Boddy et al., 2008).

4.3. Microbial carbon use efficiency

Understanding how CUE varies in response to temperature and soil degradation is vital for predicting edaphic feedback effects on climate change and planning sustainable management of agroecosystems (Manzoni et al., 2012). Our results show that LMWOS type, temperature, and degradation all influence microbial CUE in peatlands. The CUE measured in this study ranged from 0.82-0.94 and 0.64-0.87 for glucose and amino acids, respectively. This is relatively high but still consistent with results obtained in previous studies (CUE ranges from 0.5-0.9 after glucose addition; Öquist et al., 2017; Jones et al., 2018). Regardless of soil degradation status, CUE decreased with warming, which agree with the higher soil respiration measurements obtained at warmer temperatures (Devêvre and Horwáth, 2000). As CUE is a ratio of growth to respiration rates, differences in the temperature sensitivity of these two processes will lead to variations in CUE. Generally, respiration increases more rapidly than growth as a function of temperature and so, CUE tends to decrease with temperature (Devêvre and Horwáth, 2000; Tucker et al., 2013; Schindlbacher et al., 2015). Additionally, respiration processes may keep accelerating at high temperatures, whereas the microbial biomass would reduce due to the substrate depletion caused by promoted microbial activity under warming, particularly in the mineral soils which contain less SOC (Tucker et al., 2013; Walker et al., 2018). The low CUE under warming conditions may lead to a higher CO_2 release with the same amount of substrate consumed, which could potentially increase the temperature sensitivity of substrates or SOM mineralization as well as Q_{10} value. This negative relationship may also result from an increasing C cost of microbial metabolic activity at higher temperatures, with the maintenance of ion gradients across the cell membrane and protein turnover rates increasing energy demands (Dijkstra et al., 2011; Öquist et al., 2017; Sihi et al., 2018). It implies that future temperature increases could deplete SOC in the thin degraded

388 peats due to accelerated microbial activity, potentially decreasing soil nutrient supplies.
389 A similar process will occur in the thick peat, however, this may be accelerated due to
390 the large quantities of available substrate present (SOM depth >1.5 m) and nutrients
391 released during its mineralization.

392 Microbes in the decomposer community need a balanced uptake of C and other
393 nutrients to maintain cellular functions. As a result, availability of nutrients such as N
394 and P can have substantial effects on the rates of microbial growth and respiration
395 (Manzoni et al., 2012). The higher microbial CUE in thin peat is likely attributed to the
396 low extractable C:P ratio (i.e. less nutrient limit in the thin peat soil), suggesting some
397 fundamental stoichiometric controls on decomposer metabolism and CUE (Sterner and
398 Elser, 2002). Another factor affecting CUE is that substrates (i.e. glucose and amino
399 acid), require different metabolic pathways to be completely assimilated, leading to a
400 wide range of possible respiration rates per unit C assimilated (Manzoni et al., 2012;
401 van Hees et al., 2005). Taking our findings together, it suggests that peat degradation
402 adjusts microbial community for higher microbial C acquisition as indicated by
403 increased CUE, which probably prevent the continuously fast losses of C under
404 degradation.

405 The discrepancy in CUE calculated by the two methods probably results from the
406 differential inclusion of microbial turnover in the two CUE calculation methods. An
407 increased temperature is likely to accelerate cell maintenance and microbial turnover,
408 and subsequently promote C release upon microbial death (Hagerty et al., 2014). The
409 released C will either (i) adhere to soil particles and join the SOC pool, or (ii) be
410 metabolized by living microbes, leading to CO_2 release (McGill et al., 1975). The
411 amount of C lost as CO_2 by these processes and the release of immobilized ^{14}C by
412 necromass turnover (extracted by K_2SO_4) will increase over time and thus our estimates

of CUE by method 2 will decrease (i.e. CUE may be underestimate). Standardization of incubation length to minimize underestimation of CUE are needed as it will reduce the influence of experiment duration on the CUE calculation. (Frey et al., 2013; Geyer et al., 2019). Since microbial turnover (i.e. cell growth and maintenance, and ultimately necromass turnover) has been explicitly considered in method 1 (Jones et al., 2018), it is relatively insensitive to incubation temperature and experiment duration compared to method 2. However, time duration may also influence CUE calculated with both methods due to nutrient limitation, particularly when high amounts of C substrate are added in the absence of additional N, P and S. Additionally, shifts in the microbial community, mesofaunal activity or a decrease in soil moisture under warming conditions in the field may also ultimately influence CUE in the longer term (Frey et al., 2001; Hagerty et al., 2014). Based on the short-term measurement period employed here (72 h), the low amounts of C substrate added, the fertile nature of the soils and the constant moisture conditions, we assume these effects of these factors will not greatly influence our estimates of CUE in the peat soils. However, to achieve comparable CUE values with other studies, the temperature and time duration influence on microbial turnover as well as on the effectivity of methods should be considered for future studies, especially for those undertaken in the field.

5. Conclusions

The dynamics of soil LMWOS metabolism examined in this study are relevant to the fate of root and microbial exudates, crop residues, and potentially labile C components produced by the degradation of organic matter preserved in peatlands. Despite their low concentrations in soil, LMWOS play an important role in C cycling and CO_2 emissions due to their rapid turnover. Our study shows that LMWOS cycled

438 rapidly in agricultural peat soils, especially under warmer conditions. Warming altered
439 the dynamics of LMWOS mineralization, increasing C allocation into the rapidly
440 respired pool and accelerating turnover of the slower cycling (microbial growth) pool.
441 Due to the different temperature sensitivities of growth and respiration, CUE decreased
442 with soil warming. Therefore, higher temperature significantly decreased the half-life
443 of LMWOS in soils. This suggests that climate warming will accelerate turnover of
444 LMWOS in peats, ultimately leading to substantial respiratory losses of labile organic
445 components. Microbes in thin peat soil allocated more C into the slow cycling pool
446 increasing CUE compared to thick peat soil. In conclusion, strongly increased
447 mineralization of available organic C and reductions in CUE under climate warming,
448 may lead to intensified degradation of productive, high quality agricultural peat soils.
449

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462

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621

622 **Figure captions**

623 **Fig. 1** Mineralization kinetics following additions of ^{14}C-glucose (a-d) and ^{14}C-amino
624 acid (e-h) to thick and thin peat soil under increasing temperature (4, 10, 20 and 30 °C).
625 The mineralization of ^{14}C low molecular weight organic substrates was fitted with a
626 double first order decay model: $S = a_1 e^{-k_1 t} + a_2 e^{-k_2 t}$. Values are means ±
627 standard errors (n = 4). Note that the x-axis is not crossing the y-axis at value zero.
628 **Fig. 2** Carbon substrate mineralization (% of total added) of ^{14}C-glucose (a) and ^{14}C-
629 amino acid (b) in thick and thin peat soils under increasing temperature (4, 10, 20 and
630 30 °C) after 72-h incubation. The Q_{10} value was calculated on the basis of $^{14}CO_2$ efflux
631 rates with temperature increase of 10 °C. Values are means ± standard errors (n = 4).
632 Lines represent linear regression fits to the experimental data. Note that the x-axis is not
633 crossing the y-axis at value zero.
634 **Fig. 3** Soil CO_2 emission rate in thick and thin peat soils under increasing temperature
635 (4, 10, 20 and 30 °C). The Q_{10} value was calculated on the basis of CO_2 efflux rates with
636 temperature increase of 10 °C. Values are means ± standard errors (n = 4). Lines
637 represent exponential regression fits to the experimental data.
638 **Fig. 4** Sizes of the modelled fast (a, b) and slow (c, d) carbon pools describing the
639 turnover of ^{14}C-glucose and ^{14}C-amino acid in thick and thin peat soils under increasing
640 temperature (4, 10, 20 and 30 °C). Values are means ± standard errors (n = 4). Lines

represent linear regression fits to the experimental data. Note that the x-axis is not crossing the y-axis at value zero.

Fig. 5 Turnover of the modelled fast (a, b) and slow (c, d) carbon pools in thick and thin peat soils under increasing temperature (4, 10, 20 and 30 °C). Values are means ± standard errors (n = 4). Note that the x-axis is not crossing the y-axis at value zero.

Fig. 6 Substrate-C half-life of glucose (a) and amino acid (b) in thick and thin peat soils under increasing temperature (4, 10, 20 and 30 °C). Values are means ± standard errors (n = 4). Lines represent linear regression fits to the experimental data. Note the y-axis has different scale and the x-axis is not crossing the y-axis at value zero.

Fig. 7 Microbial carbon use efficiency of glucose (a, b) and amino acid (c, d) in thick and thin peat soils under increasing temperature (4, 10, 20 and 30 °C). The CUE was calculated by double exponential kinetic model fitting (method 1) and $CUE = {}^{14}C_{imm} / ({}^{14}C_{imm} + {}^{14}CO_2)$ (method 2). Values are means ± standard errors (n = 4). Lines represent linear regression fits to the experimental data. Note that the x-axis is not crossing the y-axis at value zero.

Fig. 8 Conceptual diagram of microbial utilization of low molecular weight organic carbon substrates in cultivated peats in response to warming and soil degradation.

658 **Table 1** Soil properties of thick and thin peats (0-10 cm)

Soil properties	Thick peat	Thin peat	Significance
Bulk density (g cm^{-3})	0.25 ± 0.00	0.61 ± 0.03	**
Volumetric water content (%)	59.3 ± 1.21	44.6 ± 1.44	***
pH	7.59 ± 0.04	7.73 ± 0.05	n.s.
Total organic C (g C kg^{-1})	418 ± 12.8	170 ± 2.3	***
Total N (g N kg^{-1})	25.5 ± 0.88	9.94 ± 0.11	***
C:N ratio	16.4 ± 0.07	17.1 ± 0.05	**
Extractable organic C (g C kg^{-1})	0.58 ± 0.02	0.13 ± 0.01	***
Extractable N (g N kg^{-1})	0.10 ± 0.01	0.02 ± 0.00	**
Extractable phenolics (g kg^{-1})	0.07 ± 0.01	0.02 ± 0.01	*
Extractable P (mg kg^{-1})	3.57 ± 0.50	2.25 ± 0.07	n.s.
Total PLFA (nmol g^{-1})	118 ± 5.4	100 ± 2.9	*
Fungi: bacteria	0.07 ± 0.00	0.07 ± 0.00	n.s.
Gram+ : Gram-	1.01 ± 0.01	1.03 ± 0.01	n.s.

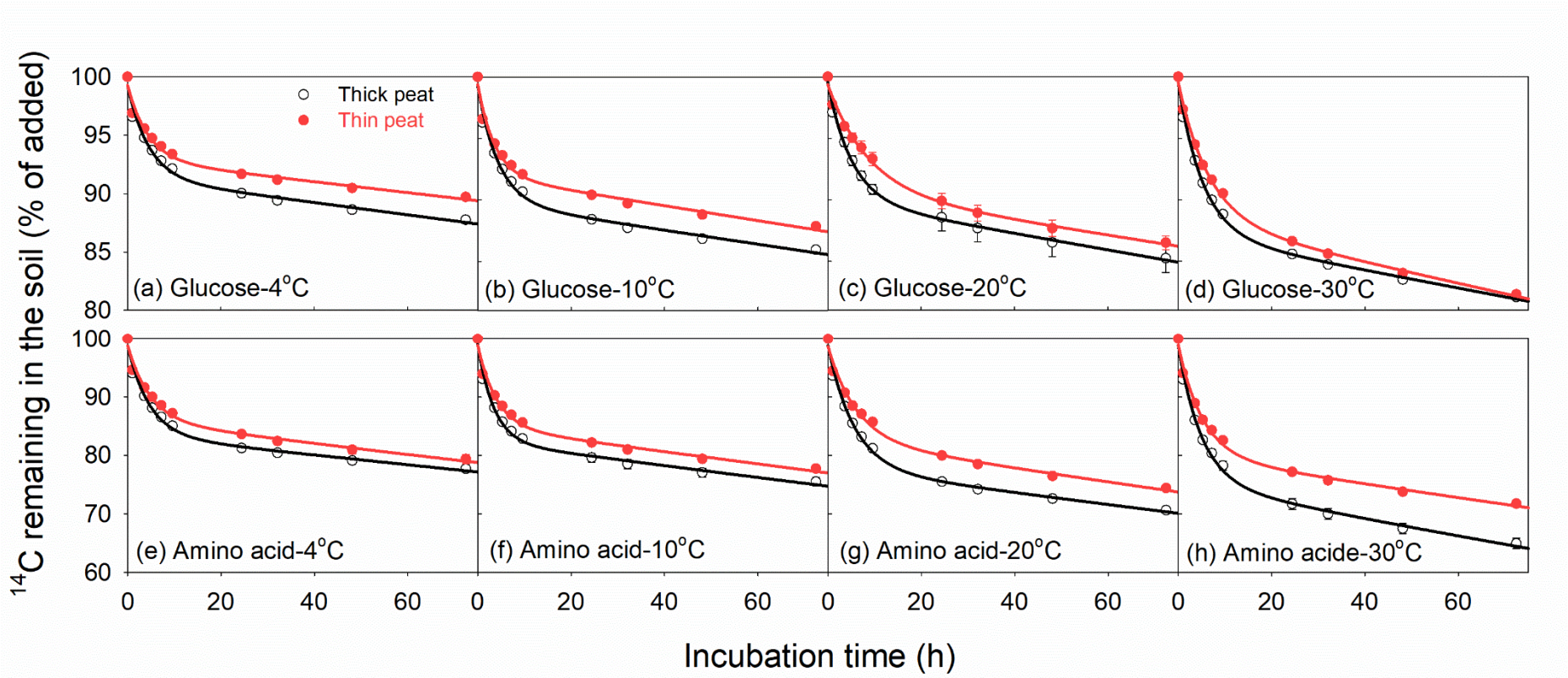
659 Values are means ± standard errors (n = 4). Asterisks within a row indicate significant
660 differences between thick and thin peats (Student's t-test; * $p < 0.05$, ** p <0 .01, ***
661 $p < 0.001$, n.s. not significant).

Table 2 Summary of *P* values from three-way ANOVA analysis of measured variables, with the following predictors: low molecular weight organic substrates (LMWOS; glucose and amino acids), temperature (Temp; 4, 10, 20, and 30 °C), soil (thick and thin peats), and their interactions. *P* values smaller than 0.05 are presented in bold.

	LMWOS	Temp	Soil	LMWOS * Temp	LMWOS * Soil	Temp * Soil	LMWOS * Temp * Soil
^{14}C mineralization	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	0.102	**< 0.001**
Fast pool size	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	0.500	0.104
Slow pool size	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	0.610	0.086
Fast pool turnover	0.217	**< 0.001**	0.121	0.457	0.761	0.260	**0.013**
Slow pool turnover	**< 0.001**	**< 0.001**	0.181	**< 0.001**	0.115	**0.005**	**< 0.001**
Half-life	**< 0.001**	**< 0.001**	**0.012**	**< 0.001**	0.454	0.419	**0.001**
CUE[a]	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	0.508	0.101
CUE[b]	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	0.075	**< 0.001**

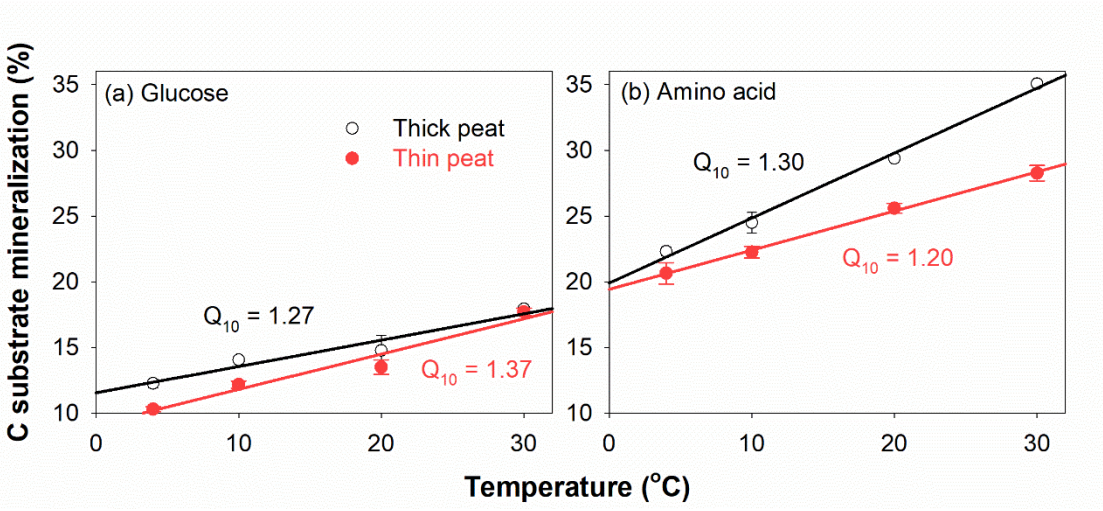
[a] Carbon use efficiency calculated by double exponential kinetic model fitting (method 1)

[b] Carbon use efficiency calculated by $CUE = {}^{14}C_{imm} / ({}^{14}C_{imm} + {}^{14}CO_2)$ (method 2)


Thick peat
Thin peat
(a) Glucose-4°C
(b) Glucose-10°C
(c) Glucose-20°C
(d) Glucose-30°C
(e) Amino acid-4°C
(f) Amino acid-10°C
(g) Amino acid-20°C
(h) Amino acide-30°C
14C remaining in the soil (% of added)
Incubation time (h)

667

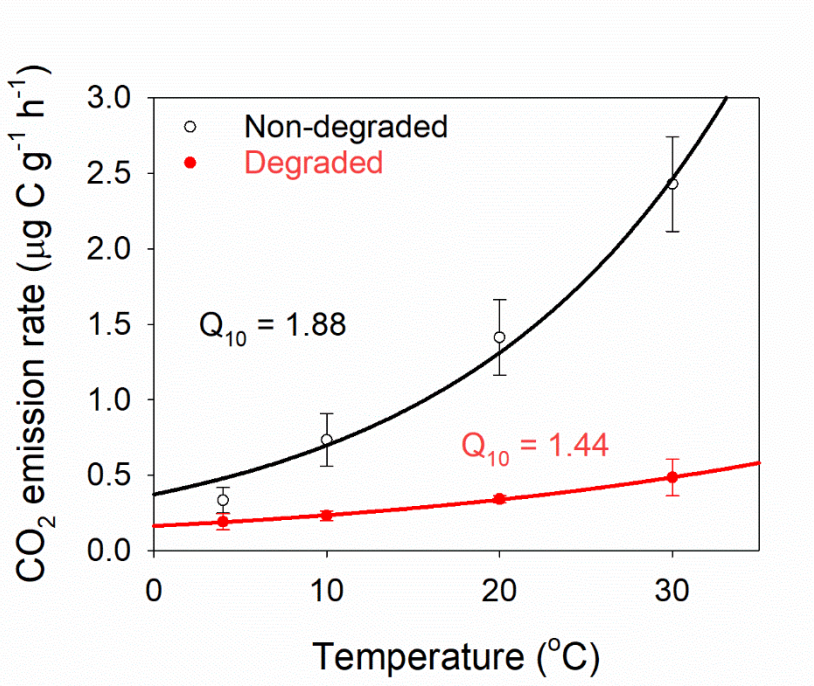
668 **Fig. 1**


C substrate mineralization (%)
(a) Glucose
Thick peat
Thin peat
Q_{10} = 1.27
Q_{10} = 1.37
(b) Amino acid
Q_{10} = 1.30
Q_{10} = 1.20
Temperature (°C)

669

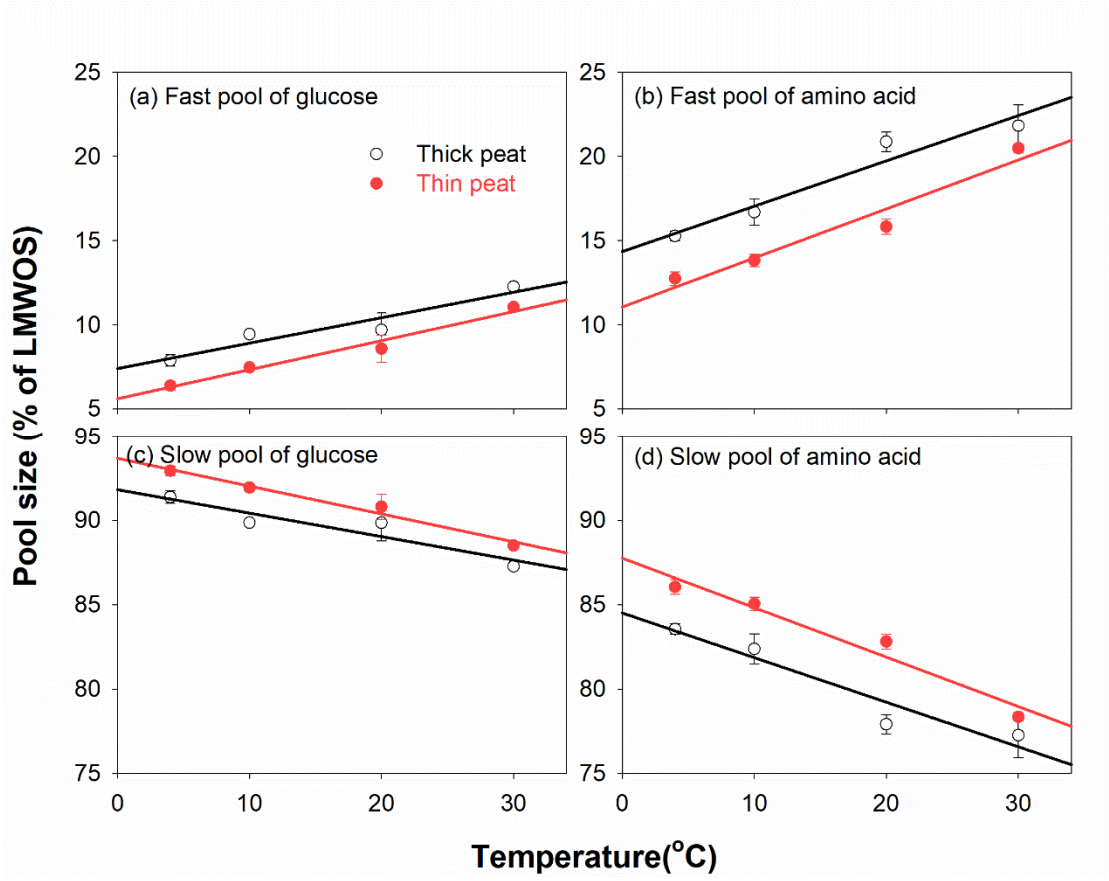
670 **Fig. 2**

671



672

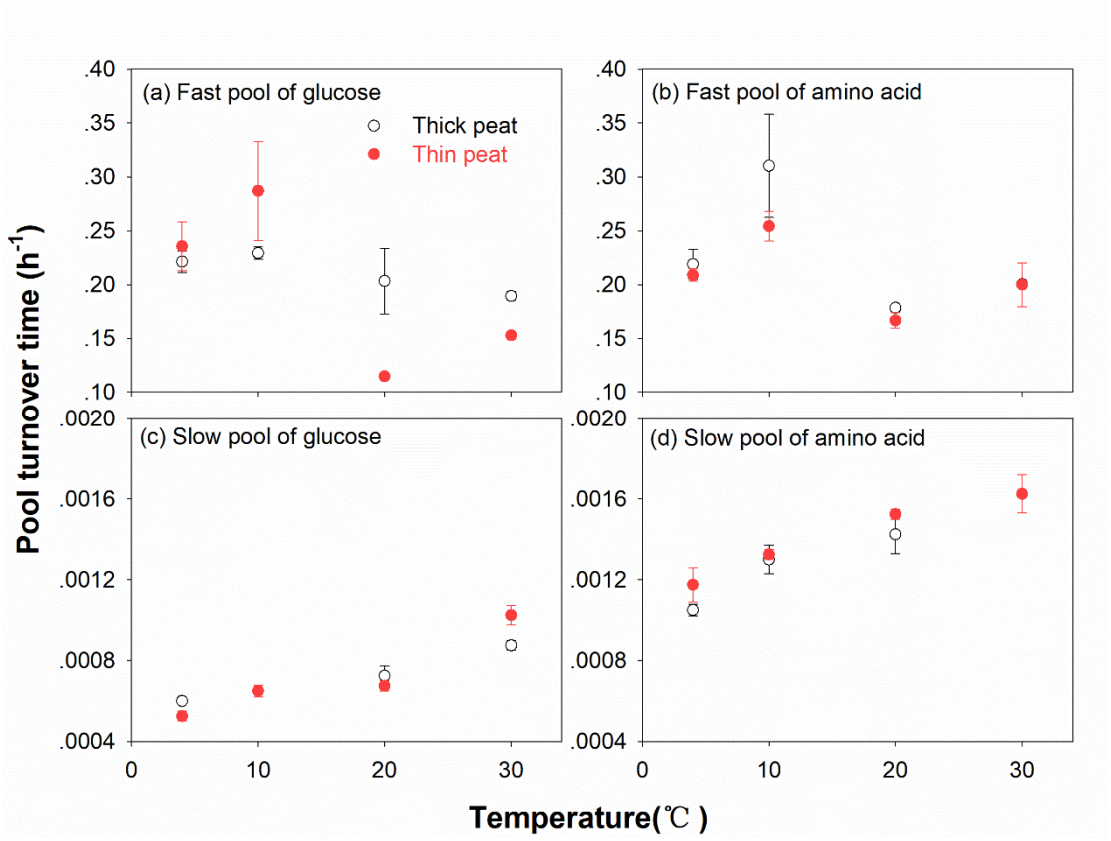
673 **Fig. 3**



674

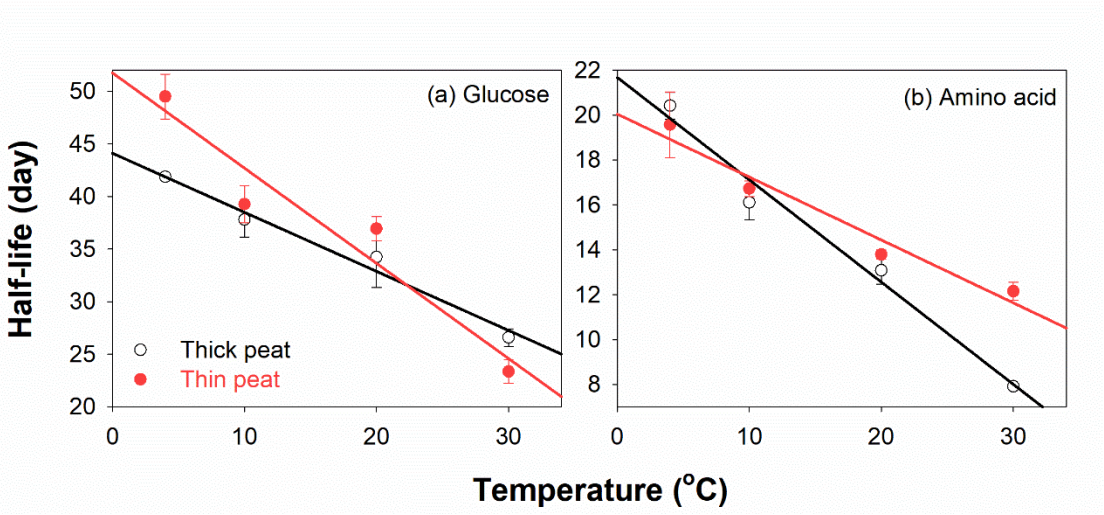
675 **Fig. 4**

676


(a) Fast pool of glucose
Thick peat
Thin peat
(b) Fast pool of amino acid
(c) Slow pool of glucose
(d) Slow pool of amino acid
Pool turnover time (h-1)
Temperature(℃)
.40
.35
.30
.25
.20
.15
.10
.0020
.0016
.0012
.0008
.0004
0
10
20
30

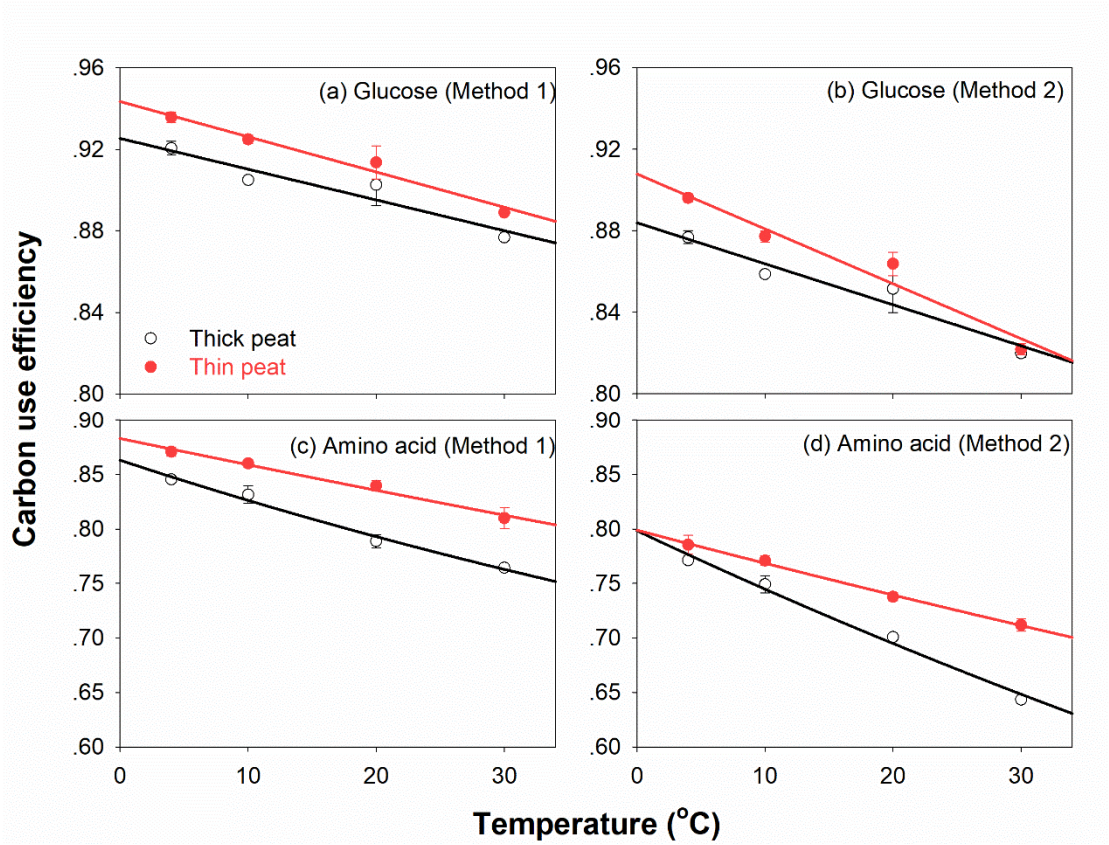
677

678 **Fig. 5**


Half-life (day)
(a) Glucose
(b) Amino acid
Thick peat
Thin peat
Temperature (°C)

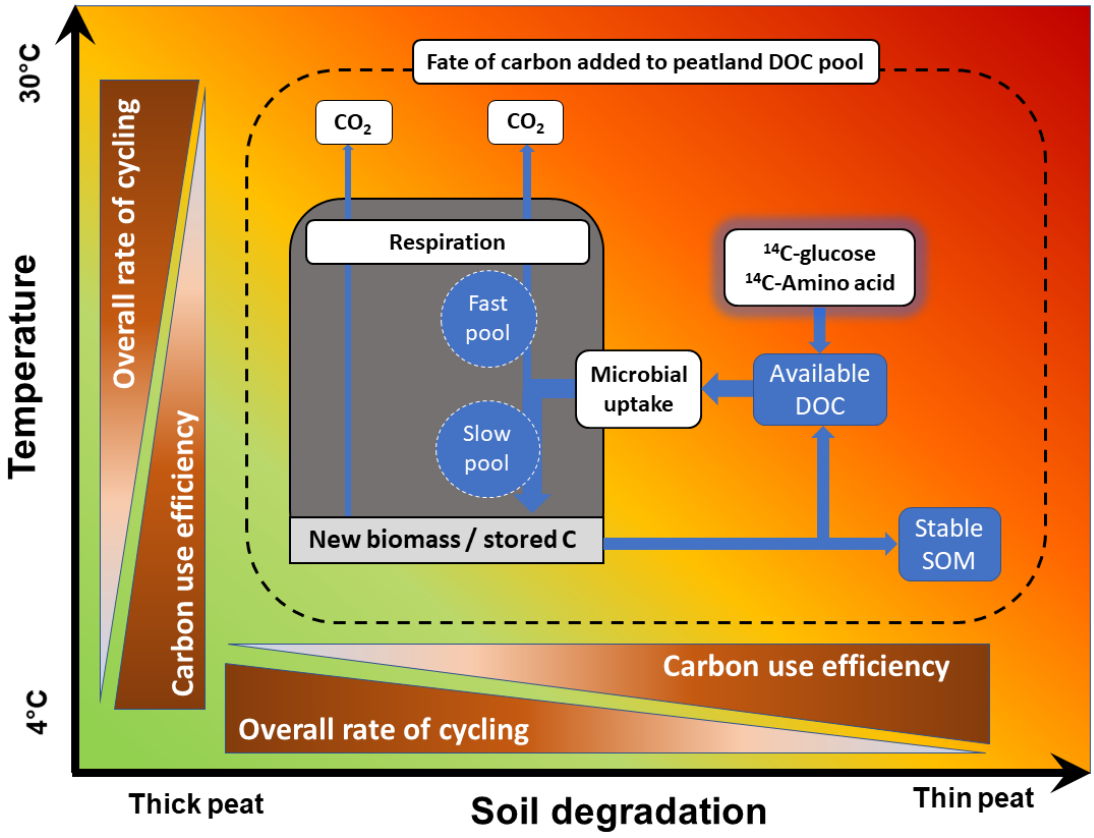
679

680 **Fig. 6**


(a) Glucose (Method 1)
(b) Glucose (Method 2)
(c) Amino acid (Method 1)
(d) Amino acid (Method 2)
Thick peat
Thin peat
Carbon use efficiency
Temperature (°C)
.96
.92
.88
.84
.80
.90
.85
.75
.70
.65
.60
0
10
20
30

681

682 **Fig. 7**


Fate of carbon added to peatland DOC pool
CO_2
CO_2
Respiration
Fast pool
Slow pool
Microbial uptake
^{14}C-glucose
^{14}C-Amino acid
Available DOC
Stable SOM
New biomass / stored C
Overall rate of cycling
Carbon use efficiency
Carbon use efficiency
Overall rate of cycling
Temperature
30°C
4°C
Thick peat
Soil degradation
Thin peat

683

684 **Fig. 8**