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Labile carbon retention compensates for CO_2 released by priming in forest soils

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Abstract

Increase of belowground C allocation by plants under global warming or elevated CO_2 may promote decomposition of soil organic carbon (SOC) by priming and strongly affects SOC dynamics. The specific effects by priming of SOC depend on the amount and frequency of C inputs. Most previous priming studies have investigated single C additions, but they are not very representative for litterfall and root exudation in many terrestrial ecosystems. We evaluated effects of ^{13}C-labeled glucose added to soil in three temporal patterns: single, repeated, and continuous on dynamics of CO_2 and priming of SOC decomposition over 6 months. Total and ^{13}C labeled CO_2 were monitored to analyze priming dynamics and net C balance between SOC loss caused by priming and the retention of added glucose-C. Cumulative priming ranged from 1.3 to 5.5 mg C g^{-1} SOC in the subtropical, and from −0.6 to 5.5 mg C g^{-1} SOC in the tropical soils. Single addition induced more priming than repeated and continuous inputs. Therefore, single additions of high substrate amounts may overestimate priming effects over the short term. The amount of added glucose C remaining in soil after 6 months (subtropical: 8.1–11.2 mg C g^{-1} SOC or 41-56% of added glucose; tropical: 8.7–15.0 mg C g^{-1} SOC or 43–75% of glucose) was substantially higher than the net C loss due to SOC decomposition including priming effect. This overcompensation of C losses was highest with continuous inputs and lowest with single inputs. Therefore, raised labile organic C input to soils by higher plant productivity will increase SOC content even though priming accelerates decomposition of native SOC. Consequently, higher continuous input of C belowground by plants under warming or elevated CO_2 can increase C stocks in soil despite accelerated C cycling by priming in soils.

Keywords: ^{13}C, addition frequency, carbon balance, glucose, litter decomposition, priming effect, root exudates, soil organic matter stability, subtropical forest, tropical forest

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Introduction

The global pool of soil organic carbon (SOC) has been estimated to exceed 3300 Pg C (Tarnocai *et al*., 2009; German *et al*., 2011), four times larger than the atmospheric CO_2-C pool and five times greater than the C pool in vegetation. Therefore, even small changes in SOC would have large effects on atmospheric CO_2 and have potential feedbacks to climate (Kirschbaum, 2004; Heimann & Reichstein, 2008), emphasizing the need to understand SOC dynamics. In the past 20 years, an increasing number of studies have shown that inputs of labile organic carbon (LOC) greatly enhance native SOC decomposition (Fontaine *et al*., 2004a, 2007; van Hees *et al*., 2005; Blagodatskaya *et al*., 2007); known as 'priming effects' (Kuzyakov *et al*., 2000). Therefore, priming effects have the potential to change SOC dynamics.

Root exudation and litter decomposition supply LOC to soil microorganisms and are key processes of C cycling in terrestrial ecosystems (Cheng *et al*., 2013). They play important roles in maintaining soil functions and are strongly affected by environmental changes. Numerous studies have observed that both warming and elevated CO_2 can produce more litterfall and root exudates via increasing ecosystem net primary production (NPP, e.g., Pendall *et al*., 2004; Finzi *et al*., 2007; Jackson *et al*., 2009; Wu *et al*., 2011). Increased litter

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decomposition induced by warming has also been demonstrated in a variety of ecosystems (Liski *et al*., 2003). If C stored in soils is released to the atmosphere by SOC priming, there would be a positive feedback on climate. Conversely, if increases of plant-derived C inputs to soils exceed temperature-driven increases in litter decomposition, the feedback would be negative (Davidson & Janssens, 2006). A full understanding of priming effects induced by LOC inputs will be critical to clarify effects of warming and elevated CO_2 on soil C cycling and its feedback to global change (Cheng *et al*., 2013).

Most previous priming experiments focused on single LOC additions, and showed that priming can accelerate decomposition of SOC (Blagodatskaya & Kuzyakov, 2008). However, single additions may not be representative of natural C inputs in terrestrial ecosystems. For example, in forests lacking strong seasonality, root exudates and surface litter are produced throughout the year. Even in strongly seasonal climates, dissolved organic C (DOC) input from root exudation and litter decomposition occurs continuously during the growing season. Root exudation also varies at the spatial scales of microorganisms. As a growing root tip extends through a zone of soil, microorganisms can experience a 'pulse' of exudation. Such variations in time and space could be simulated by repeated additions. Evidence suggests that a small change in the magnitude of priming effects has the potential to outweigh the effects of global change drivers on basal soil organic matter (SOM) decomposition in many ecosystems (Cheng *et al*., 2013). Therefore, to clarify whether single, repeated, and continuous LOC inputs cause different amounts of priming is one of key questions for understanding the significance of priming and its occurrence. If single additions induce more priming than repeated or continuous additions, the former could overestimate priming occurring in natural ecosystems. So far no studies have compared priming effects induced by single, repeated, and continuous inputs in the same experiment, although a few studies have examined priming effects induced by repeated (Hamer & Marschner, 2005; Chigineva *et al*., 2009) or continuous additions of LOC (Kuzyakov *et al*., 2007; Paterson & Sim, 2013).

Priming increases SOC decomposition (e.g., Fontaine *et al*., 2004a, 2007; Sayer *et al*., 2011), but a fraction of the added organics can remain in the soil and compensate for the SOC loss caused by priming, potentially leading to a net C increase in soil (Fontaine *et al*., 2004b; Ohm *et al*., 2007). To understand effects of priming on SOC dynamics, the net balance between primed SOC loss and LOC retention must be known. However, most priming studies have emphasized SOC losses induced by priming and have not reported net SOC balances between primed C and the gain from added LOC (Kuzyakov, 2010). Therefore, despite the overall importance of priming, net effects of LOC inputs on SOC dynamics and stabilization remain unclear.

Tropical and subtropical forests contain more than 20% of the global SOC (Tarnocai *et al*., 2009), and are important sources of CO_2 return to the atmosphere (Raich *et al*., 2002), indicating crucial roles of these forests in the global C cycle (Reich, 2011; Wood *et al*., 2012; Cox *et al*., 2013). Elevated atmospheric CO_2 has increased photosynthesis and productivity of tropical forest (Ziska *et al*., 1991; Lewis *et al*., 2009; Cernusak *et al*., 2013) and understory (Würth *et al*., 1998) species. More than 50 years of data also suggest that elevated atmospheric CO_2 is a driver for increased tree density in South African savannas (Buitenwerf *et al*., 2012). Although some studies suggest that tropical forests are not sensitive to warming, litter production, tree growth, and belowground C allocation all increase significantly with mean annual temperature (Raich *et al*., 2006). This indicates that both warming and elevated CO_2 have potential to increase NPP and litter production, and warming can accelerate litter decomposition in subtropical and tropical forests (Liski *et al*., 2003). Free-air CO_2 enrichment studies have so far been extratropical, and most of them found net SOC increases (Hoosbeek *et al*., 2004; Drigo *et al*., 2008, 2013; Hungate *et al*., 2009; Liu *et al*., 2009; Phillips *et al*., 2009, 2011; Dieleman *et al*., 2010; Drake *et al*., 2011). Modeling by Hickler *et al.* (2008) suggest that tropical forests may be even more sensitive to CO_2 enrichment than temperate ones.

Subtropical and tropical wet forests are dominated by evergreen broad-leaved tree species, and root exudation and litter decomposition can occur throughout the year. Within such forests, there are wide ranges of vegetations, climates, and soils. We chose two very different forests (2.8% SOC in the tropical and 13.8% SOC in the subtropical) to explore priming induced by LOC inputs. Total rhizodeposition in forests has rarely been quantified *in situ*, but available evidence suggests that root exudates can constitute 10% or more of NPP (Chapin *et al*., 2012). According to de Graaff *et al.* (2010), the expected range for root exudation varies from 50 to 1500 μg C g^{-1} soil per day (Trofymow *et al*., 1987; Meharg & Kilham, 1991; Jones & Darrah, 1993; Cheng, 1996). In addition, litter decomposition releases DOC into soils. Elevated CO_2 can increase DOC input to soils, by increasing both root exudation and litter decomposability (Phillips *et al*., 2008, 2009). Accurate evaluations of priming caused by LOC inputs in these forests will improve our understanding of C cycling at low latitudes.

There are large areas of tropical and subtropical forests in southern China (Wu, 1980). Although litter production in our tropical forest is double that in the subtropical (Schaefer *et al*., 2009; Tang *et al*., 2010), litter

decomposes more rapidly in the former (Liu *et al*., 2000; Tang *et al*., 2010). Slower litter decomposition at lower temperatures contributes to fivefold higher SOC content in subtropical soils (Ailaoshan) compared with tropical soils (Xishuangbanna). This tropical forest has 900 g C m^{-2} yr^{-1} of NPP (Tan *et al*., 2010), with 1000 g C m^{-2} yr^{-1} in the subtropical (Tan *et al*., 2011). Assuming that 10% of NPP becomes root exudates (Chapin *et al*., 2012), the current rates are on the order of 100 g C m^{-2} yr^{-1} in these forests.

Although a few studies have examined priming at low latitudes (e.g., Fontaine *et al*., 2004b; Schaefer *et al*., 2009; Sayer *et al*., 2011; Leff *et al*., 2012), many details remain unclear. To clarify whether single vs. more frequent glucose inputs produce different priming effects, we made single (all at the beginning), repeated (once per month), and continuous (once per week) additions. The same total amount of glucose was added to each treatment over the study period. Lower C/N in the tropical than in the subtropical soil suggests faster SOC turnover in the tropical soil (Krull & Skjemstad, 2003; Rumpel & Kögel-Knabner, 2011). We therefore hypothesized that greater SOC priming would occur in the tropical soil. Because microbial responses might persist longer with continuous inputs than after a single addition, we also hypothesized that continuous additions would result in stronger priming than a single addition of the same total amount of glucose. Our first glucose additions differed in amount between treatments, so we could examine the linearity of initial microbial responses. As priming accelerates SOC decomposition (e.g., Fontaine *et al*., 2004a, 2007; Sayer *et al*., 2011), we hypothesized that the net C balances between primed C and retention of added glucose-C could be negative in both forest soils. To test these hypotheses, we conducted 170-day incubations of tropical (Xishuangbanna) and subtropical (Ailaoshan) forest soils.

Materials and methods

Soils

After removing the litter layer, we sampled mineral soil from the top 10 cm in subtropical and tropical forests in July 2009. The subtropical forest was in the Ailao Mountains Nature Reserve (24°32′ N, 101°01′ E, 2476 m asl) in the Yunnan Province of southwestern China. This forest is dominated by the evergreen broad-leaved species *Lithocarpus chintungensis*, *Rhododendron leptothrium*, *Vaccinium duclouxii*, *Lithocarpus xylocarpus*, *Castanopsis wattii*, *Schima noronhae*, *Hartia sinensis*, and *Manglietia insignis* (Li, 1983). Mean annual air temperature is 11 °C and annual precipitation averaged 1950 mm from 1996 to 2006. The monsoon climate causes a wet season from May to October followed by a dry season from November to April (Zhang, 1983). The soil is a loamy Lixisol (World Reference Base for Soil Resources, 2006) or Ustalf Alfisol (by USDA Soil Taxonomy) derived from weakly metamorphosed marine sediments.

The tropical forest site was in the Xishuangbanna Tropical Rainforest Ecosystem Station (21°54′ N, 101°16′ E, 560 m asl) in Menglun, Xishuangbanna, also in Yunnan Province. Annual mean temperature and precipitation are 21.6 °C and 1480 mm. About 85% of the rain falls from May to October. The tree layer is dominated by *Pometia tomentosa*, *Gironniera subaequalis*, *Chisocheton siamensis*, *Barringtonia macrostachya*, and *Pseuderanthemum latifolium*. The soil is a Ferrasol (World Reference Base for Soil Resources, 2006) or Oxisols (by USDA Soil Taxonomy) derived from marine sandstone (Table 1).

Experimental design

Thirty grams of air-dried, 2-mm-sieved, root-picked soil were added to 250-ml Schott bottles, and adjusted to 60% of the water-holding capacity (WHC). All soils were pre-incubated at 20 °C for 7 days. Thereafter, water or ^{13}C-uniformly-labeled glucose (5.97 atom% ^{13}C) solution was added evenly dropwise to the soil surface using a pipette to obtain uniform distribution. These additions raised soils to 70% of WHC and they were maintained at this level throughout the experiment. One gram of $CaCl_2$ was added to small cups placed in the incubation bottles to absorb water vapor and to prevent soil moisture increases from subsequent water additions. The $CaCl_2$ was replaced weekly to maintain its water-absorptive capacity.

Assuming that 10% of NPP becomes root exudates (Chapin *et al*., 2012), the current rates are on the order of 100 g C m^{-2} yr^{-1} in these forests. In addition to root exudation, litter decomposition also can release LOC into soils. Decomposing litter can release 3% of its C as DOC (Don & Kalbitz, 2005), which would correspond to some 10 g C m^{-2} yr^{-1} in these forests. Allison *et al*. (2010) used an annual DOC flux of 44 g C m^{-2} to the top 1 cm of soil surface in their model. Elevated CO_2 also can increase LOC input to soils through increasing root exudates and litter decomposition (Phillips *et al*., 2009). Hoosbeek & Scarascia-Mugnozza

Table 1 Properties of the surface 10 cm mineral soils in a subtropical forest at Ailaoshan and in a tropical forest at Xishuangbanna in Yunnan Province, China. Means ± 1 SE, $n = 4$

Soil	Organic carbon (% dry wt.)	Total nitrogen (% dry wt.)	Microbial biomass carbon (mg g^{-1} dw soil)	C/N	WHC (%)
Subtropical forest	13.84 ± 0.20	0.88 ± 0.01	2.50 ± 0.20	15.64 ± 0.13	95.1 ± 0.2
Tropical forest	2.78 ± 0.01	0.28 ± 0.00	0.52 ± 0.10	9.98 ± 0.02	57.5 ± 3.5

(2009) summarized several FACE studies (typically doubling CO_2) as increasing SOC by 50 g C m^{-2} yr^{-1} or more (mostly from increased litterfall). Phillips *et al.* (2011) estimated total root exudation in a pine forest as 10 g C m^{-2} yr^{-1}, and we speculate that doubled CO_2 could increase exudation by a similar amount. Based on these soils' %SOC, bulk density, 10 cm soil depth, and the glucose-C added (g^{-1} SOC) in this experiment; our additions correspond to 110 and 280 g C m^{-2} yr^{-1} at the field scale to the tropical and subtropical soils. Our glucose-C additions were thus of the magnitude expected in these soils for current annual root exudation (de Graaff *et al.*, 2010) and DOC from litter decomposition. These additions were also comparable to microbial biomass-C (MBC), and so could change microbial activity but not be sufficient to induce obvious microbial growth (Blagodatskaya & Kuzyakov, 2008). To maintain comparability in these two different soils, total glucose-C additions were equal to 2% of the SOC in each soil (Table 1).

Single-addition treatments received all the glucose-C at the start of the experiment (after one week of pre-incubation) and all subsequent weekly additions were water only. Repeated addition treatments received 1/6 of the total glucose-C at monthly intervals with the intervening weekly additions being water only. Continuous-addition treatments received 1/24 of the total glucose-C each week. Controls received water-only additions each week. Each treatment had four replicates. The first glucose additions to each soil treatment varied in amount between treatments, but on an SOC-specific basis they were the same in corresponding treatments for both soils. This allowed us to examine whether different glucose additions saturated microbial utilization.

All incubations were conducted at 20 °C. Five milliliters of 1 M NaOH were placed in small cups in each incubation bottle to trap CO_2 and were replaced at the end of each week. CO_2 samples were trapped from each incubation bottle and analyzed for CO_2 and $\delta^{13}C$.

CO_2 analysis

To measure CO_2 absorbed in NaOH, 4 ml of 0.5 M $SrCl_2$ was added to precipitate carbonate. Unreacted NaOH was titrated with 0.2 M HCl against the phenolphthalein endpoint (Zibilske, 1994). Precipitated $SrCO_3$ was centrifuged three times at 1200 *g* for 10 min followed each time by rinsing with degassed water. The $SrCO_3$ was then dried at 105 °C and weighed into tin capsules to analyze for total C and $^{13}C/^{12}C$ ratios by continuous flow gas isotope ratio mass spectrometry (MAT253; Finnigan MAT, Bremen, Germany), coupled by ConFlo III device (Finnigan MAT) to a elemental analyzer (EA 1112; CE Instruments, Milan, Italy).

Microbial biomass and dissolved organic carbon

After the incubations, MBC was measured by chloroform fumigation/extraction (modified after Vance *et al.*, 1987). Briefly, 5 g fresh soil was extracted with 20 ml of 0.05 M K_2SO_4. An additional 5 g soil was fumigated with ethanol-free chloroform for 24 h, and then was extracted again in the same manner. Total organic C concentrations in the K_2SO_4 extracts were measured with a Dimatec-100 TOC/TIC analyzer (Dimatec Analysentechnik GmbH, Essen, Germany). Total organic C concentrations in the K_2SO_4 extracts from nonfumigated soils were defined as DOC. Aliquots of the K_2SO_4 extracts were pipetted directly into tin capsules and dried at 60 °C to measure $\delta^{13}C$ in the microbial biomass by mass spectrometry (Brant *et al.*, 2006).

Calculations

Total CO_2-C in trapped CO_2 was analyzed weekly and their values were reported on a specific basis (i.e. per unit of SOC). For each soil and treatment, CO_2 fluxes from the four replicates of were summed through the experiment, and cumulative mean values and standard deviations (SDs) were calculated for each week. Flux-weighted δ values were based on weekly values and CO_2 fluxes.

The end-member mixing model used to calculate fractions of CO_2-C derived from SOC (C_{SOC}) and from added glucose ($C_{glucose}$) was from Phillips & Gregg (2001) and Phillips *et al.* (2005), http://www.epa.gov/wed/pages/models.htm. This model allows variability from mass-spectrometric measurements to be combined with that from CO_2 flux measurements.

Based on the fractions of glucose-derived CO_2 and their SDs obtained from the model by Phillips & Gregg (2001), primed C was calculated as follows:

$$\text{Primed C} = C_{total} - C_{glucose} - C_{water\ only}$$

where C_{total} is total C-CO_2 from the glucose-treated soil, $C_{glucose}$ is C-CO_2 derived from added glucose, and $C_{water\ only}$ is total C-CO_2 from the soil adding only water.

Glucose release (%) was $C_{glucose}$ divided by total glucose added, and net C balance was calculated as the difference between primed C and retention of added glucose-C.

Standard deviations of cumulative CO_2 fluxes, glucose release (%), priming, and net C balances were calculated according to the following equations described by Ku (1966).

$$\sigma_{x+y} = \sqrt{(\sigma_x)^2 + (\sigma_y)^2}$$

where σ_{x+y} is SD of the combined flux and σ_x and σ_y are SDs of the individual fluxes.

$$\sigma_{xy} = \overline{x} * \overline{y} * \sqrt{\frac{(\sigma_x)^2}{\overline{x}^2} + \frac{(\sigma_y)^2}{\overline{y}^2}}$$

where σ_{xy} is SD of the combined flux, σ_x and σ_y are SDs of the CO_2 flux and SOC fractions, and $\overline{x}$ and $\overline{y}$ are their respective mean values.

At the end of the incubations, MBC content was calculated as the difference between the total C in fumigated and nonfumigated soils, divided by a k_{EC} factor of 0.45 (Wu *et al.*, 1993). The $\delta^{13}C$ of DOC was measured from the K_2SO_4 extracts from nonfumigated soils. The $\delta^{13}C$ of the microbial biomass was calculated as the difference of ^{13}C between fumigated and nonfumigated samples divided by the difference of the C amount between fumigated and nonfumigated samples (Blagodatskaya *et al.*, 2011). With these $\delta^{13}C$ values

of MBC and DOC, the Phillips & Gregg (2001) end-member mixing model was also used to estimate the fraction of added glucose incorporated to the DOC and MBC pools.

Statistics

Tukey's HSD was used to test the effects of the pattern of glucose addition on primed SOC, retained glucose, and net C balances among treatments and between soils. Repeated measures ANOVAs (Pallant, 2007) over time were performed with SPSS 21.0 (SPSS Inc., Chicago, IL, USA) to evaluate the effects of soil type and the pattern of glucose addition on CO_2 fluxe rates. Standardized major axis regressions were used to test for differences in the CO_2 slopes and intercepts against substrate additions to the subtropical and tropical forest soils using R 3.0.1 with the SMATR package (Falster *et al.*, 2006; Warton *et al.*, 2006; R Development Core Team, 2011). All differences were tested for significance at $P = 0.05$.

Results

CO_2 efflux responses to glucose additions

Throughout incubations of the water-only controls, specific CO_2 efflux rates from the tropical soil (169 ± 8 μg C g^{-1} SOC d^{-1}) were significantly higher than from the subtropical soil (94 ± 4 μg C g^{-1} SOC d^{-1}; Fig. 1a,b). The CO_2 effluxes depended on glucose input patterns (Fig. 1a,b) with increases after each glucose addition. Repeated-measures ANOVA indicated that soil type and glucose addition patterns significantly affected CO_2 efflux rates (Table 2).

Table 2 Results of repeated-measures ANOVA over time to evaluate effects of soil type and the frequency of LOC addition on CO_2 fluxe rates. Bold numbers indicate significant differences at $P < 0.05$

Source of variation	df	MS	*F*	*P*
Between subjects				
Intercept	1.00	22946752	9136.34	**0.000**
Soil type	1.00	869964	346.38	**0.000**
Adding frequency	3.00	469036	62.25	**0.000**
Soil type × Adding frequency	3.00	8193	1.09	0.373
Error	24.00	60278		
Within subjects				
Time	6.94	3451797	75.71	**0.000**
Time × Soil type	6.94	338534	7.43	**0.000**
Time × Adding frequency	20.82	7358948	53.80	**0.000**
Time × Soil type × Adding frequency	20.82	1105378	8.08	**0.000**
Errors	166.56	1094247		

Glucose release as CO_2

Expressed as percent of the amount added, release of glucose CO_2 differed among treatments (Fig. 1c,d; Table S1, Tukey's HSD test, $P < 0.05$). In the tropical soil, continuous additions released less glucose than repeated additions during the incubation, but finally converged with the single additions ($28.8 \pm 0.7\%$). More glucose-CO_2 was respired from the repeated addition ($43.1 \pm 0.02\%$) to the tropical soil than from the other two treatments at the end of incubations (Fig. 1c, Table S1). In the subtropical soil, the pattern of glucose respiration was similar to that in the tropical soil, but their final fractions were significantly different among the three treatments (repeated $41.9 \pm 0.9\%$ > continuous $37.5 \pm 1.4\%$ > single $32.2 \pm 1.0\%$; Fig. 1d; Table S1). By the end of the incubations, single and continuous additions to the subtropical soil increased glucose-CO_2 release by 12% and 35% compared with the tropical soil. Compared with the tropical soil, repeated additions to the subtropical soil decreased by 3% glucose-CO_2 loss (tropical vs. subtropical: $43.1 \pm 0.02\%$ vs. $41.1 \pm 0.9\%$, $P < 0.05$; Fig. 1c,d; Table S1).

Dynamics of cumulative priming effects

Soil type and glucose-addition patterns significantly affected priming intensity and dynamics (Fig. 1, Table S2, Tukey's HSD test, $P < 0.05$). In the tropical soil, cumulative priming caused by single addition was positive and significantly greater than with repeated and continuous additions. The repeated and continuous additions produced similar priming and the values fluctuated around zero throughout the incubations (Fig. 1e; Table S2). In the subtropical soil, single additions also caused more priming than repeated and continuous additions throughout the incubations. However, the dynamics of priming were distinctly different between soils. Single addition quickly reached maximal priming in the tropical soil, with only minor changes later. In the subtropical soil, the priming induced by single addition increased gradually in the first 2 months and then remained unchanged. Compared with the invariant priming caused by repeated and continuous additions in the tropical soil, the priming induced by these addition patterns increased with time in the subtropical (Fig. 1e,f; Table S2). On an SOC-specific basis, priming induced by single addition was significantly higher in the tropical soil than in the subtropical in the first 3 months, but they were similar by the end of incubation. Finally, there were no significant differences in priming induced by repeated and continuous additions to these soils (Fig. 1e,f; Table S2).

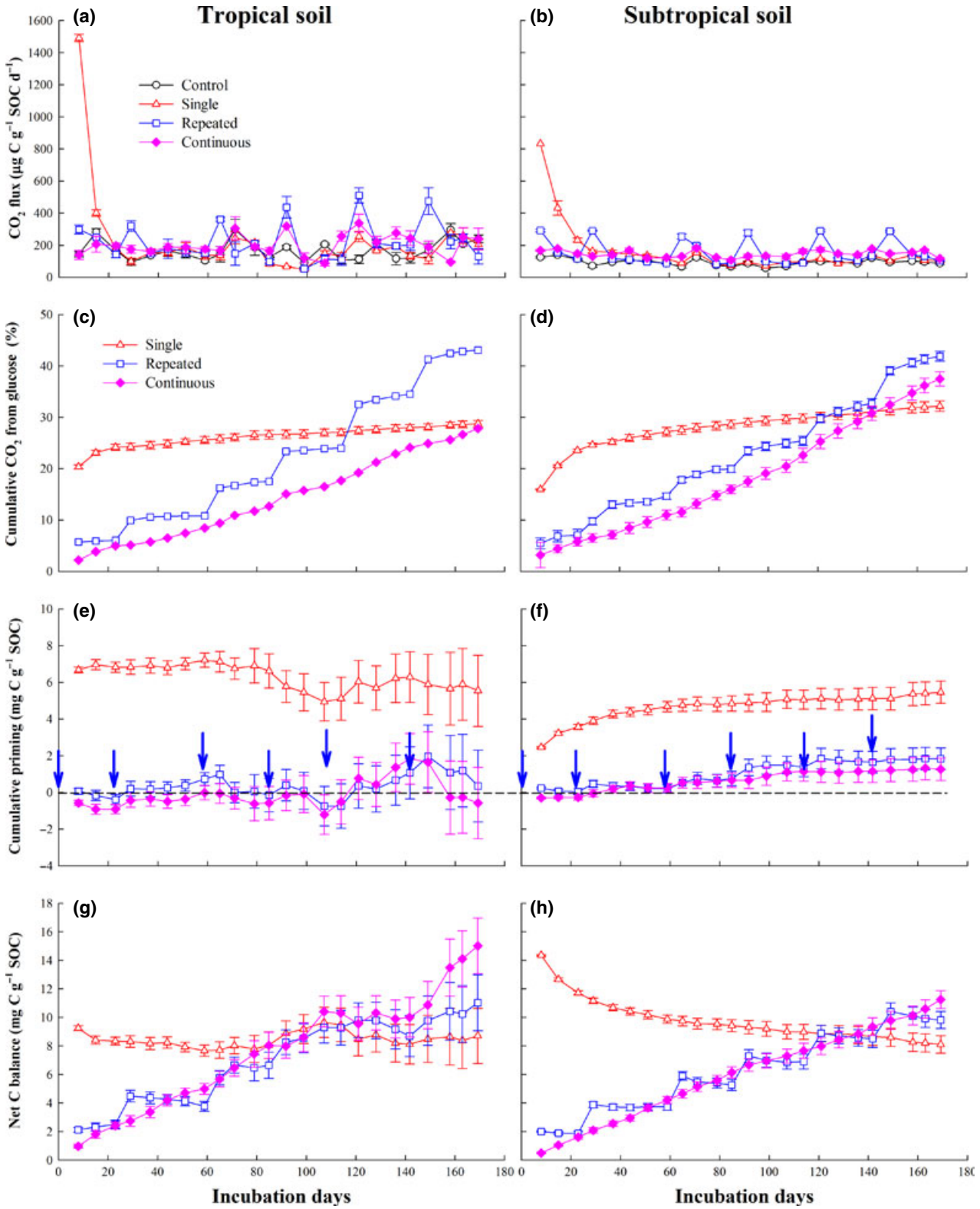

Fig. 1 Incubation results for tropical (left) and subtropical (right) soils. Panels (a) and (b) show weekly total CO_2 fluxes in each treatment and soil. Panels (c) and (d) show the cumulative fraction of added glucose released as CO_2. Panels (e) and (f) show the cumulative net priming of SOC. Panels (g) and (h) show the net C balance between SOC priming and retention of added glucose. Color lines represent different treatments, i.e. black lines with empty circles in (a,b) indicate water-only, while red lines with triangles, blue lines with crossed squares, and pink lines with filled diamonds in (a-h) indicate single, repeated and continuous glucose additions to soils respectively. (c,d) indicate cumulative fraction of glucose released as CO_2, (e,f) indicate cumulative fluxes of SOC priming, and (g,h) indicate cumulative (positive) net effects of glucose additions on net soil C balances. Blue arrows in (e,f) indicate times of glucose additions to repeated treatments.

Net C balance of primed SOC and net retention of added glucose

The C retained from the glucose (not released as CO_2) exceeded the amount of primed SOC throughout the 170-day incubation period. Thus, net-C balances in both soils and all addition treatments were positive (Fig. 1g,h; Table S3; Tukey's HSD test, $P < 0.05$). Single additions to both soils initially caused significantly higher net-C increases than repeated and continuous additions. Positive net-C increase from single additions to tropical soil was constant, but it decreased through time in the subtropical soil (Fig. 1g,h; Table S3). At the end of the incubations, net-C increase was higher in continuous than single in the tropical soil (Fig. 1g). In the subtropical soil, net-C increases caused by single addition were significantly lower than in the other two addition patterns (Fig. 1h; Table S3). Net-C increases caused by continuous addition in the tropical soil were significantly higher than those caused by all three treatments in the subtropical soil (Fig. 1g,h; Table S3).

Responses of total CO_2 flux and primed C to added glucose

The first glucose additions to each soil varied in amount, but the amount was the same on an SOC-specific basis for the same treatment in both soils. Therefore, the correlation between initial CO_2 effluxes and glucose additions reflected microbial utilization for added glucose. The tropical-soil response was much larger (slopes of tropical vs. subtropical: 0.554 vs. 0.277; $P < 0.0001$; Fig. 2). Both soils responded linearly to glucose inputs ($R^2 = 0.99$; Fig. 2), indicating that microbial responses were not saturated even at the highest addition levels. The initial primed C of the tropical soil was probably higher (slopes of tropical vs. subtropical: 0.387 vs. 0.139; $P < 0.05$; Fig. 2). Since continuous and repeated glucose addition levels were much lower and closer to each other, the relatively close correlations presented here largely relied on the highest glucose additions. More intermediate values would make the correlation observed more convincing.

Microbial biomass, dissolved organic C and incorporation of glucose-C into microbial biomass

At the end of incubations, a significant decrease in DOC was observed only in repeated and continuous additions to the tropical soil, while there was no significant difference between single addition and the control treatment (Tukey's HSD test, $P < 0.05$, Fig. 3a). There were no treatment differences in the subtropical soil. Control, single, and repeated additions had higher MBC in subtropical than tropical soils (Fig. 3b). Continuous addition had higher MBC than other treatments in tropical soil, but there were no treatment differences in the subtropical soil (Tukey's HSD, $P < 0.05$, Fig. 3b).

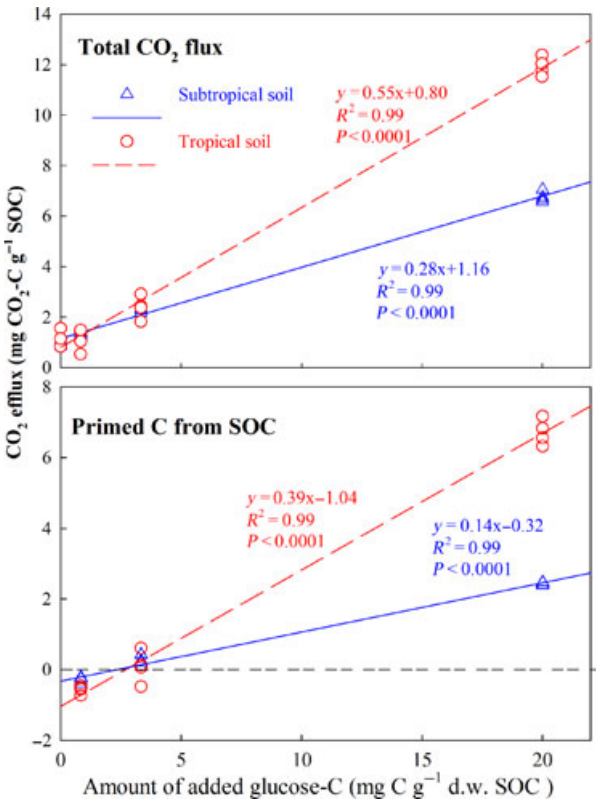

Fig. 2 Responses of total CO_2 flux (top) and primed C (bottom) to the amount of added glucose in tropical and subtropical soils. Red long dash lines and empty circles indicate the tropical soil while blue solid lines and triangles represent the subtropical soil. There were 4 replicates for each treatment.

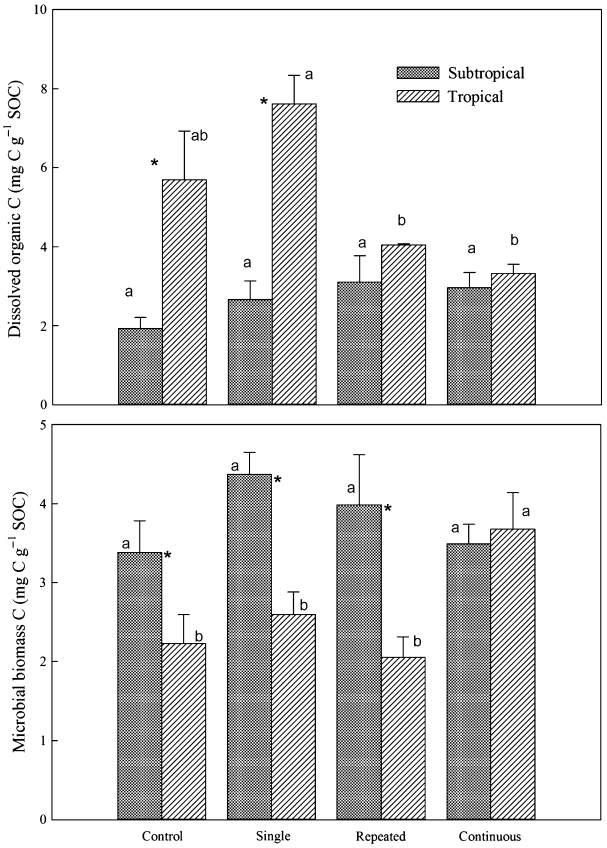

Fig. 3 Concentrations of dissolved organic C and microbial biomass in subtropical soil and tropical soils at the end of a 170-day incubation period. Bars show standard errors of the means (n = 4). Different letters above columns indicate significant difference among treatments for each soil at $P < 0.05$ level. The asterisk above columns indicates significant difference in microbial biomass C between subtropical and tropical soils at $P < 0.05$ level.

In both soils, the amount of primed SOC released as CO_2 was negatively correlated with glucose incorporation into microbial biomass (R^2 = 0.63, $P < 0.001$, Fig. 4), indicating that higher priming was accompanied by faster microbial turnover. Even though this relationship was similar for both soils, tropical soil was more variable in microbial glucose incorporation (range from 0.63 to 1.85% for tropical and from 0.76 to 1.37% for subtropical, Fig. 4).

Discussion

Rhizodeposition and decomposing litter DOC fluxes compared with experimental glucose additions

The glucose additions in this incubation study correspond to approximately 200 g C m^{-2} yr^{-1} to the soil surface. Rhizodeposition could represent

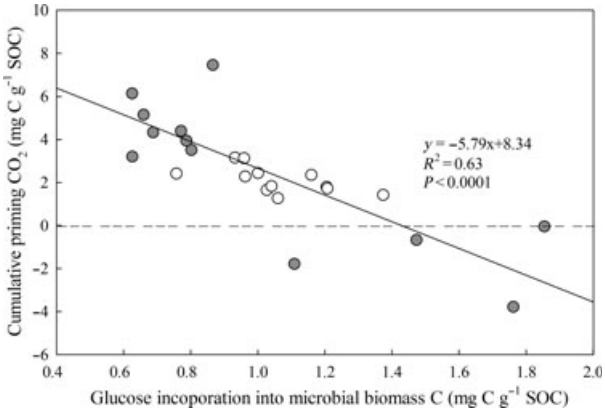

Fig. 4 Correlations between cumulative SOC priming and glucose incorporated and remaining in microbial biomass after 170-day incubation of subtropical and tropical soils. Open circles indicate the subtropical, and filled circles indicate the tropical soils.

100 g C m^{-2} yr^{-1}, DOC from litter decomposition 10 g C m^{-2} yr^{-1}, and future CO_2 doubling could increase total DOC fluxes by 50 g C m^{-2} yr^{-1} (see Introduction and Methods sections). None of those estimates are directly applicable to the forests we studied, but they suggest that we are exploring an appropriate range of LOC additions (de Graaff *et al.*, 2010).

Dependence of priming effects on C-addition patterns

To the best of our knowledge, this is the first time that priming effects induced by different addition patterns (i.e. single, repeated, and continuous additions) with the same total amounts have been compared in soils. We demonstrate that addition patterns can stimulate different priming of SOM decomposition, which strongly rely on initial addition amount, soil type, and the timing since glucose was added (Fig. 1e,f). The results of the initial glucose additions to both soils clearly showed that the amount of C added is an important driver for priming (Fig. 2). However, throughout the experiment, single additions caused more priming than repeated and continuous additions in both soils, while continuous and repeated additions produced similar priming (Fig. 1e,f). These results indicate that single glucose additions cannot represent SOC priming resulting from repeated or continuous glucose inputs. Therefore, our hypothesis that continuous glucose additions would induce more SOC priming than single additions was not supported.

The differences among addition patterns could be ascribed to different microbial activities, because the activation of microorganisms from no-growth or starvation states to active states (Morita, 1990; Blagodatskaya & Kuzyakov, 2008) by easily available organics can be

the main reason for accelerated SOM mineralization (Kuzyakov *et al*., 2000; Hamer & Marschner, 2005; Kuzyakov, 2010). Most soil microorganisms are energy limited and oscillate between dormant and active physiological states (Morita, 1990; Stenström *et al*., 2001). A fraction of microorganisms are activated when LOC arrives in soils (Stenström *et al*., 2001). Microbial growth and enzyme production are accompanied by increased microbial demand for nutrients. Subsequently, microorganisms scavenge N from SOM and cause priming (Kuzyakov *et al*., 2002; Fontaine *et al*., 2004a; Cheng, 2009; Dijkstra *et al*., 2013; Paterson & Sim, 2013). This is apparent in the subtropical soil but only for single additions in the tropical soil.

Although previous studies have demonstrated that microbial biomass can be activated by trace amounts of available organics and produce positive priming (De Nobili *et al*., 2001; Mondini *et al*., 2006), small continuous glucose additions were not enough to activate microorganisms and trigger positive priming in this tropical soil, despite increased microbial biomass compared with the control (Fig. 3). Even repeated glucose additions caused little priming. In contrast, small glucose additions to the subtropical soil triggered positive priming after the first month, and priming increased similarly as with repeated additions. This may result from alleviating microbial C or energy limitation, thus leading to increased microbial activities and nutrient demand (Cheng & Kuzyakov, 2005). These results indicate that the occurrence of positive priming requires the amount of added LOC to reach some threshold, but this threshold differs between soils (Fig. 1e,f). Several differences could contribute to this. First, we suggest that different physiological states of microorganisms in tropical and subtropical soils could be responsible for their activation by inputs of organics because inherent physiological states are strongly related to history (Stenström *et al*., 2001). Compared with subtropical, the tropical SOC could be highly processed by microorganisms. Low MBC to SOC ratios from the controlled treatment of the tropical soil reflect high fraction of recalcitrant OC (Moscatelli *et al*., 2005). Therefore, microorganisms could require more energy to decompose tropical SOC. Second, the availability of substrates in these soils (Fig. 3, top), including pools of available C and nutrients, could affect the direction and magnitude of priming induced by addition patterns. Numerous studies have demonstrated that microbial growth and growth states strongly depend on the size and quality of soil-available resources (Stenström *et al*., 2001; Blagodatskaya & Kuzyakov, 2008).

Soils with higher C : N ratios generally exhibit stronger priming than those with low C:N ratios due to lack of available N (Zhang *et al*., 2013), but our results did not support this pattern. In our study, both soils produced similar priming effects under corresponding treatments by the end of incubations (Fig. 1e,f), and that single additions induced stronger priming for the first 3 months in the tropical soil having a lower C:N ratio (Table 1). We suggest vegetation, climate, microbial communities and soil properties other than C:N could be more important for the occurrence of priming. Therefore, our hypothesis that greater SOC priming would occur in the tropical soil than in the subtropical soil was only partly supported by our results.

Priming induced by a single glucose addition reached a maximum more rapidly in the tropical soils (Fig. 1e), suggesting more rapid microbial response to added glucose in the tropical soil (Paterson & Sim, 2013). A previous study also suggested that tropical soil C is very sensitive to changes in C inputs (Leff *et al*., 2012). However, the underlying mechanisms should be investigated for a better understanding of SOC decomposition and turnover in forest soils.

Net soil C balance between SOC priming and net glucose retention

We observed that priming increased decomposition of SOC in both forest soils (Fig. 1e,f). However, the effects of LOC inputs on SOC dynamics should be evaluated in the context of net C balance. In the present study, we excluded CO_2 fluxes from the water-only treatments in calculating net C balances. These balances were always positive and initially (shortly after addition) highest with large glucose additions (Fig. 1g,h). High net-C accumulations in both soils with continuous glucose additions suggest that LOC inputs such as root exudation may increase SOC as observed by free-air CO_2 enrichments (Hoosbeek *et al*., 2004; Liu *et al*., 2009), even with soil C cycling accelerated by rhizosphere priming (Kuzyakov *et al*., 2007; Cheng, 2009; Zhu & Cheng, 2011; Cheng *et al*., 2013). Therefore, our hypothesis that the net C balances between primed C and the gain from added glucose could be negative in both forest soils was not supported.

To explore relationships between the amount of added glucose and the net SOC balance between primed C and the gain from added glucose, we compared our results with those of 13 previous studies (Fig. 5). Including the retention of added LOC, most of the studies showed net C increases in soil despite SOC priming (Fig. 5, top) and in only a very few studies priming was accompanied by a net decrease in SOC (Fig. 5, bottom). Some studies concluded that priming leads to SOC losses, but net SOC balance was usually positive when the remaining LOC was accounted for. Net soil C increases have been demonstrated in

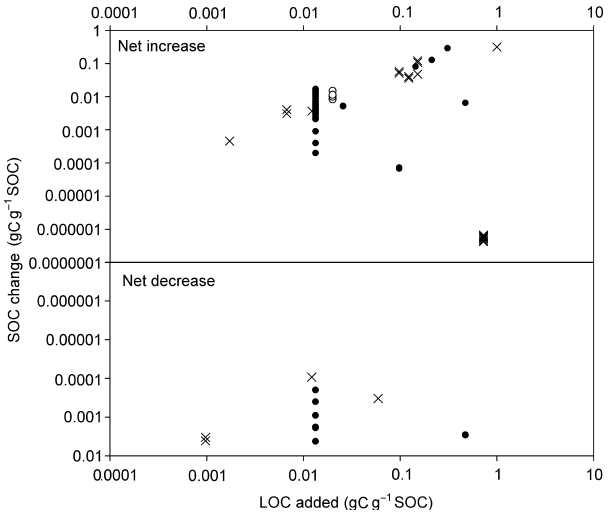

Fig. 5 Net soil C balance under priming by additions of glucose and other labile organic carbon (LOC) from this and previous studies. Open circles represent our incubations of tropical and subtropical forest soils, filled circles represent data presented by Fontaine *et al.*, 2004a,b; Hamer & Marschner, 2005; Ohm *et al.*, 2007;. The X-symbols represent our calculations of soil-C balance from Wu *et al.*, 1993; Bell *et al.*, 2003; Brant *et al.*, 2006; Blagodatskaya *et al.*, 2007; Fontaine *et al.*, 2007; Hoyle *et al.*, 2008; Nottingham *et al.*, 2009; Guenet *et al.*, 2010; Garcia-Pausas & Paterson, 2011, based on our calculations from data presented by those authors. Positive net C balances are on the top panel and negative on the bottom.

other studies, e.g., free-air CO_2 enrichment, in which ^{13}C-depleted CO_2 was added to small forest stands, and net soil C balances were examined. Most of these studies (Hoosbeek *et al.*, 2004; Liu *et al.*, 2009) found net SOC increases, while some observed a neutral balance (Jastrow *et al.*, 2005; van Kessel *et al.*, 2006) or net SOC decreases (Hoosbeek & Scarascia-Mugnozza, 2009). Similarly, Gattinger *et al.* (2012) reviewed studies on reduced-tillage agriculture and found that SOC increased, even though increased plant litter may have primed SOC losses.

Thus, several lines of evidence support our conclusion that net SOC often increases in response to C inputs, but particular local conditions may also affect C balances. Despite accelerated turnover by priming, increased C input contributes to C sequestration in the soil (Phillips *et al.*, 2011; Cheng *et al.*, 2013). Priming studies should consider net C-balances between primed C and the gain from added LOC and accelerated mineralization of native SOM is only a part of the C budget. It has also been suggested that priming can act on recalcitrant SOC (Fontaine *et al.*, 2007; Blagodatskaya *et al.*, 2011). If retained C from added LOC is less recalcitrant than primed C, then long-term effects on C sequestration remain uncertain. Therefore, further studies should investigate the fate of added organics and sources of the primed C.

In summary, we found that single additions of glucose overestimate priming effects in these subtropical and tropical soils and thus do not adequately reflect natural ecosystem C inputs. Continuous C inputs resulted in a greater C increase in the soil than single additions, further emphasizing the importance of LOC addition patterns. Those patterns aside, responses of these very different soils to glucose additions were remarkably similar in terms of glucose release, priming, and net-C balance. From this experiment and previous studies, we present evidence that LOC additions may generally increase net C balances in soils. Accurate evaluation of the direction and intensity of priming must consider the observation period, dynamics of C utilization, and induced CO_2 losses, as well as the net C balance and other soil properties. Understanding and modeling effects of global change such as warming and elevated CO_2 on soil-C cycles need to be linked to plant production of LOC and its effects on microbial activity (Cheng *et al.*, 2013).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Results of Tukey's HSD test on cumulative glucose CO_2 (as % of added glucose), cumulative priming effect and net carbon balance among different treatments and those between two forest soils, which were shown in Fig. 1.

Table S1. Results of Tukey's HSD test on cumulative glucose CO_2 (as% of added glucose) among different treatments and those between two forest soils.

Table S2. Results of Tukey's HSD test on cumulative priming effect among different treatments and those between two forest soils.

Table S3. Results of Tukey's HSD test on net carbon balance among different treatments and those between two forest soils.