Labile carbon input determines the direction and magnitude of the priming effect

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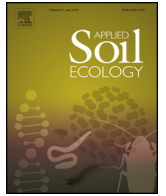Some of the authors of this publication are also working on these related projects:

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Labile carbon input determines the direction and magnitude of the priming effect

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Xiao-Jun Allen Liu[a,b,*], Jingran Sun[a], Rebecca L. Mau[a], Brianna K. Finley[a,b], Zacchaeus G. Compson[a,c], Natasja van Gestel[a,d], Jamie R. Brown[a], Egbert Schwartz[a,b], Paul Dijkstra[a,b], Bruce A. Hungate[a,b]

[a] Center for Ecosystem Science and Society (Ecoss), Northern Arizona University, Flagstaff, AZ 86011, USA
[b] Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011, USA
[c] Canadian Rivers Institute, University of New Brunswick, Fredericton, NB E3 B 5A3, Canada
[d] South Central Climate Science Center, Texas Tech University, Lubbock, TX 79409, USA

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ABSTRACT

Labile carbon (C) input to soil can accelerate or slow the decomposition of soil organic matter, a phenomenon called priming. However, priming is difficult to predict, making its relationship with C input elusive. To assess this relationship, we added ^{13}C-glucose at five levels (8 to 1606 μg C g^{-1} week^{-1}) to the soil from four different ecosystems for seven weeks. We observed a positive linear relationship between C input and priming in all soils: priming increased from negative or no priming at low C input to strong positive priming at high C input. However, the sensitivity of priming to C input varied among soils and between ways of expressing C input, and decreased with elevation. Positive substrate thresholds were detected in three soils (56 to 242 μg C g^{-1} week^{-1}), suggesting the minimum C input required to trigger positive priming. Carbon input expressed as a fraction of microbial biomass explained 16.5% less variation in priming than did C input expressed as a fraction of dry soil mass, indicating that priming is not strongly related to the size of the soil microbial biomass. We conclude that priming increases with the rate of labile C input, once that rate exceeds a threshold, but the magnitude of increase varies among soils. Further research on mechanisms causing the variation of priming sensitivity to increasing labile C input might help promote a quantitative understanding of how such phenomenon impacts soil C cycling, offering the potential to improve earth system models.

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1. Introduction

Soil holds the largest amount of carbon (C) in terrestrial ecosystems and has the potential to mitigate climate change (Paustian et al., 2016). Under climate change, plant growth and C input (e.g., plant litter, roots, root exudates) to soils are predicted to increase. This increase of C input can accelerate the decomposition of soil organic matter (SOM), a phenomenon called the priming effect or positive priming (Chen et al., 2014; Kuzyakov et al., 2000). Alternatively, increased C input can suppress SOM decomposition and induce negative priming (Blagodatskaya et al., 2014; Qiao et al., 2014). Therefore, the direction and magnitude of priming in response to C input remain uncertain and might depend on interactions between C input and priming that we still do not understand.

The quantity of C input to soil impacts the direction and magnitude of priming. A positive linear relationship between C input and priming has been reported in some studies (Chowdhury et al., 2014; Tian et al., 2015; Wu et al., 1993); however, the opposite relationship between C input and priming has been also observed. For instance, glucose additions induced strong priming at low C input and weak priming at high C input (Qiao et al., 2014). Hence, the relationship between C input and priming remains elusive.

In addition, the relationship between C input and priming might be affected by the size of microbial biomass present in the soil. Blagodatskaya and Kuzyakov (2008) suggested that C input to soil affects microbial biomass C (MBC), and thus that C input needs to be expressed as a fraction of soil MBC. They observed more priming at low C input and less priming at high C input, when C input was expressed relative to soil MBC. This contrasts with most studies where C input is expressed relative to dry soil mass

(Fontaine et al., 2003; Guenet et al., 2012; Hu et al., 2014). This raises the question, which way of expressing C input is a better predictor of priming?

Besides C input, soil type and other characteristics also affect priming (Table 1). For instance, greater priming was observed in low nutrient soils compared to high nutrient soils (Dimassi et al., 2014). By contrast, similar magnitudes of priming were detected in soils with different nutrients (Qiao et al., 2014). Soils with higher soil C and C:N ratio exhibited higher priming in some soils (Blagodatskaya et al., 2014; Conde et al., 2005) but lower priming in others (Dimassi et al., 2014; Qiao et al., 2014). Furthermore, soils with higher MBC showed less priming compared to soils with lower MBC (Wang et al., 2015), yet similar magnitudes of priming were detected in soils with different soil MBC (Murphy et al., 2015).

These inconsistent results suggest the necessity to test the relationship between C input and priming, especially with multiple levels of C input in different soils.

We assessed priming effect in four different soils with repeated additions of glucose to tackle the following questions: (1) Does priming increase with C input across the four soils? (2) Are substrate thresholds (minimum C input) required to elicit positive priming? (3) Is C input expressed relative to soil MBC a better predictor of priming than C input expressed relative to dry soil? To address these questions, we conducted a seven-week laboratory incubation by adding five different amounts of ^{13}C-glucose weekly to the four soils. We evaluated these results in the context of data from other published studies about the priming effect (Table 1).

Table 1
Published data on priming effect in response to labile C additions using isotope tracers[a].

Citation	Soil					Land use	Study	Substrate			Total
	Type	C %	C:N	MBC µg g^{-1}	pH		day/T	Type	Weekly µg C g^{-1}	Total µg C g^{-1}	PE[b] µg C g^{-1}
Blagodatskaya et al. (2007)	Loam	5.0	14.5	609	7.4	Cropland	14/22	^{14}C-glucose	24.4	48.7	110
									2435	4870	0
Blagodatskaya et al. (2011)	Loam	2.4	12.0		5.1	Grassland	54/22	^{14}C-glucose	13.0	100	860
									130	1000	500
	Loam	2.1	10.0		5.1	Grassland	54/22	^{14}C-glucose	13.0	100	−150
									130	1000	355
Blagodatskaya et al. (2014)	Loam	2.4	12.0		5.1	Grassland	103/22	^{14}C-glucose	27.2	400	110
	Loam	2.1	10.0		5.1	Grassland	103/22		27.2	400	60
Chowdhury et al. (2014)	Clay	3.1	15.7	301	6.7	Cropland	7/22	^{14}C-malic acid	100	100	77
									1000	1000	410
	Clay	2.7	17.5	248	6.7	Cropland	7/22	^{14}C-malic acid	100	100	60
									1000	1000	359
Conde et al. (2005)	Clay	5.3	7.9		10	Forest	28/22	^{14}C-glucose	250	1000	700
	Sand	3.9	3.4		10	Forest	28/22		250	1000	400
Falchini et al. (2003)	Loam	1.7	9.8		7.9	Grassland	7/25	^{14}C-glucose	182	182	60
								^{14}C-oxalic acid	182	182	385
								^{14}C-glutamic acid	182	182	65
Hopkins et al. (2014)	Loam	15.0				Forest	30/5	^{13}C-sucrose	16.3	70	350
							30/15		16.3	70	400
							30/25		16.3	70	290
Qiao et al. (2014)	Loam	2.8	10	520		Forest	170/20	^{13}C-glucose	23.1	560	1260
	Loam	13.8	15.6	2500		Forest	170/20		114	2770	840
	Loam	2.8	10	520		Forest	170/20		23.1	560[c]	189
	Loam	13.8	15.6	2500		Forest	170/20		114	2770[c]	231
	Loam	2.8	10	520		Forest	170/20		23.1	560[d]	−105
	Loam	13.8	15.6	2500		Forest	170/20		114	2770[d]	147
Tian et al. (2015)	Loam	1.2	9.2	204	6.0	Cropland	49/22	^{14}C-glucose[e]	2.9	20.4	70
									29.1	204	149
									2.9	20.4	−52
									29.1	204	140
									2.9	20.4	−22
									29.1	204	25
Wang et al. (2015)	Organic	15.0	16.6	1410	5.3	Forest	53/25	^{13}C-WSC[f]	4.2	32	24
									8.5	64	20
									21.1	160	33
									42.3	320	78
									84.5	640	115
									211	1600	103
	Mineral	1.5	12.9	90	5.1	Forest	53/25	^{13}C-WSC	2.1	16	5
									4.2	32	19
									10.6	80	14
									21.1	160	20
									42.3	320	19
									106	800	27

[a] MBC = microbial biomass C; Day/T = incubation days and temperature; all substrates were added once at the beginning of experiments, except the last four treatments in Qiao et al. (2014).
[b] PE = priming effect (µg C g^{-1} dry soil).
[c] Substrate added monthly.
[d] Substrate added weekly.
[e] Labile C applied to three soil aggregate sizes: >2 mm, 2–0.25 mm, and < 0.25 mm.
[f] WSC = water-soluble C.

Table 2
Soil properties of four ecosystems along the elevation gradient in Flagstaff, Arizona, USA[a].

Ecosystems	Elevation (m)	MAP (mm)	MAT (°C)	Soil C (%)	Soil N (%)	C:N ratio	MBC ($\mu g\,g^{-1}$)	MBC/SOC (%)	pH
Cool desert grassland	1760	229	13.6	1.82	0.14	12.6	424	2.3	6.9
Piñon-juniper woodland	2020	381	11.4	1.56	0.14	11.4	287	1.8	6.2
Ponderosa pine forest	2340	660	10.8	1.83	0.10	17.5	183	1.0	5.8
Mixed conifer forest	2620	787	6.7	4.44	0.35	12.8	372	0.8	6.3

[a] MAP and MAT are mean annual precipitation and temperature; MBC and MBN are soil microbial biomass C and N; FC represents water field capacity.

2. Materials and methods

2.1. Field sites and soil sampling

The four ecosystems were located along an elevation gradient in northern Arizona: cool desert grassland (35.58 N, −111.57 W), piñon-juniper woodland (35.50 N, −111.62 W), ponderosa pine forest (35.42 N, −111.67 W), and mixed conifer forest (35.35 N, −111.73 W). Soils from these ecosystems, which differ in soil C, N, microbial biomass, vegetation, climate, and other factors (Table 2), provide an excellent platform for comparing priming across a wide range of soil physiochemical characteristics.

In October 2013, soil samples (0 – 10 cm from surface, no organic layer was observed) were taken from the field, sieved (2 mm), and stored at 4 °C before incubation. For each replicate sample, the soil (equivalent to 20.0 g oven-dry soil at 105 °C for 72 h) was weighed into specimen cups (125 ml) and pre-incubated in mason jars (473 ml; n = 4 for all treatments) at 22 (±1) °C in the dark for one week, with soil moisture adjusted to 70% field capacity.

2.2. Laboratory incubation

Each soil received five levels of glucose per week for seven weeks. Specifically, soil samples received a weekly 200 μl of uniformly labeled ^{13}C-glucose solution per jar (δ^{13}C = 1159‰; Cambridge Isotope Laboratories, Andover, Massachusetts, USA) at concentrations adjusted to glucose treatments (Table 3) or the same amount of deionized water (controls).

We selected five levels of C input for each soil, based on the size of the soil MBC, which is thought to regulate the priming effect (Blagodatskaya and Kuzyakov, 2008). We used previous measurements of soil MBC (unpublished) in these soils to select levels of C input. We also measured MBC in the soil samples used in the laboratory incubation described here (see Section 2.3 below), in order to express C input as a precise percentage of the MBC in the soils used for the incubations. Soils used for this study differed in MBC from past measurements, resulting in some inconsistencies in the precise percentages of the MBC among soils (Table 3). We also expressed C input as absolute amounts (μg glucose-C g^{-1} dry soil week^{-1}), and we use both metrics to explore the relationship between C input and the priming effect.

2.3. Sample analysis

Gas samples were taken to measure CO_2 concentration and $\delta^{13}CO_2$. Briefly, we took headspace gas from incubation jars three times per week with 10- and 60- ml syringes. Then gas samples were analyzed with a LI-Cor 6262 (LI-Cor Biosciences Inc. Lincoln, Nebraska, USA) for CO_2 concentration and a Picarro G2201 (Picarro Inc., Sunnyvale, California, USA) for $\delta^{13}CO_2$.

Soil samples at the beginning of experiment were processed for soil C, δ^{13}C, and MBC. First, the soil was ground into fine powder and analyzed for total C and δ^{13}C with a Carlo Erba NC2100 elemental analyzer configured to a Delta V isotope ratio mass spectrometer (Thermo Fisher Scientific, West Palm Beach, Florida, USA). Then, soil MBC was analyzed with the chloroform-fumigation extraction (Joergensen et al., 1990; Vance et al., 1987): 10 g of fumigated (five days) or unfumigated soil was extracted with 25 ml K_2SO_4 solution (0.05 M) with a soil solution ratio of 1:2.5 (Qiao et al., 2014; Tian et al., 2015), shaken for one hour, and purified with filter papers (Whatman #3). Filtrate solution was then oven-dried at 60 °C for four days to obtain a constant weight, and salt extracts were ground and analyzed for total C and δ^{13}C. An extraction efficiency of 0.45 was used to calculate soil MBC (Vance et al., 1987).

2.4. Data analysis

Mass balance was used to separate SOM-derived CO_2 from glucose-derived CO_2 (Eq. (1)), and priming was the difference of SOM-derived CO_2 between glucose-amended and control samples (Eq. (2)):

$$C_{SOM-glucose} = C_{total}(\delta_{total} - \delta_{glucose})/(\delta_{SOM-control} - \delta_{glucose}) \tag{1}$$

$$Priming = C_{SOM-glucose} - C_{SOM-control} \tag{2}$$

where $C_{SOM-control}$ is CO_2-C (mg g^{-1}) from the control, $C_{SOM-glucose}$ and C_{total} are CO_2-C (mg g^{-1}) derived from SOM and glucose in glucose-amended samples, δ_{total} and $\delta_{glucose}$ are δ^{13}C of CO_2 from glucose-amended samples and glucose solution (1159‰), and $\delta_{SOM-control}$ is the δ^{13}C of CO_2 from control samples.

Bootstrapping was used to test sensitivity of priming to C input (slopes) and substrate thresholds (x-intercepts) for each soil.
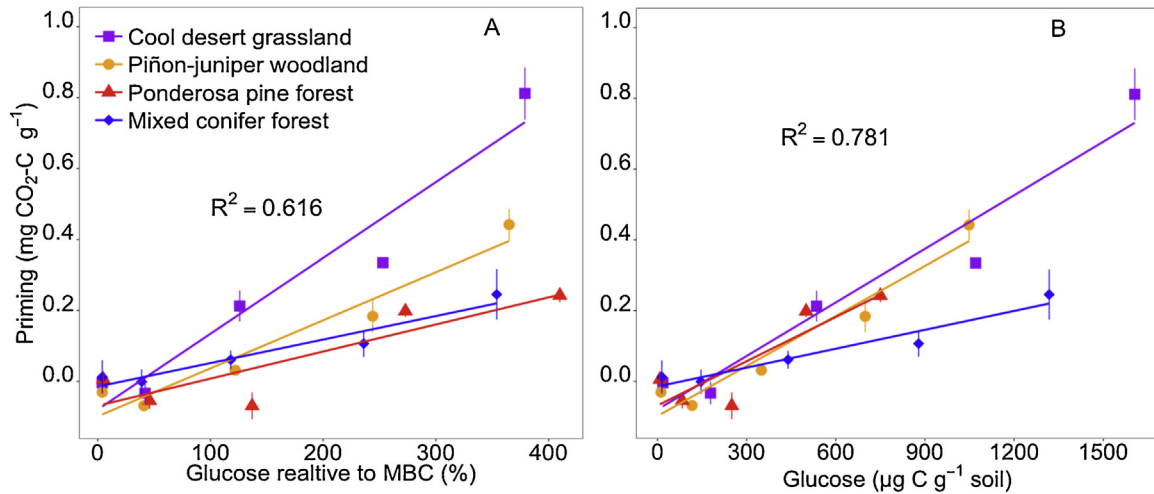
Table 3
Carbon (^{13}C-glucose) input relative to initial soil microbial biomass C (MBC%; μg C μg MBC-C^{-1} × 100%) or relative to dry soil (GDS; μg C g dry soil^{-1}) for four ecosystems[a].

Treatment No.	Cool desert grassland		Piñon-juniper woodland		Ponderosa pine forest		Mixed conifer forest	
	MBC%	GDS	MBC%	GDS	MBC%	GDS	MBC%	GDS
1	0	0	0	0	0	0	0	0
2	4	18	4	12	5	8	4	15
3	42	178	41	116	46	83	39	150
4	126	535	122	349	137	250	118	439
5	253	1071	244	699	273	500	236	879
6	379	1606	365	1048	410	750	354	1318

[a] %MBC stands for glucose addition as a fraction (percentage) of soil microbial biomass C; GDS indicates the glucose addition as a fraction of dry soil mass (absolute amount of glucose added as μg C g^{-1} soil).

Fig. 1. Seven-week cumulative priming (mg CO_2-C g^{-1}) with weekly ^{13}C-glucose additions expressed relative to soil microbial biomass (μg C μg C$^{-1} \times 100\%$) (A) or relative to dry soil (μg C g soil^{-1}) (B). r^2 values were calculated from linear regression analysis across the four ecosystems.

Slopes and substrate thresholds of each soil were inferred to be present for each soil if their bootstrapped 95% confidence intervals (CIs) did not overlap zero, and were considered different between soils if 95% CIs did not overlap with each other. Linear models were used with C input expressed relative to soil MBC or with C input expressed relative to dry soil as an explanatory variable to compute r^2 values. Bootstrapping and statistical analyses were conducted in R (version 3.3.0 with packages *stats, nlme, ggplot2, plyr*); R Core Team, 2016).

3. Results

3.1. Carbon input and priming

We detected a positive linear relationship between C input and priming in all of the four soils (Figs. 1, S1, and S2). Low C input induced slightly negative or no priming, whereas high C input stimulated strong positive priming. We found no evidence for a non-linear relationship between C input and priming: the r^2 values for the linear models ($r^2 = 0.78$ for dry soil, 0.62 for MBC) were consistently higher than r^2 values for non-linear models ($r^2 = 0.42$ for dry soil and 0.37 for MBC). Thus, there was no evidence that the

higher amounts of substrate addition caused a saturating response of priming.

The sensitivity of priming to C input varied among soils and between ways of expressing C input (Fig. 2). For C input expressed relative to MBC (Fig. 1A), priming in the cool desert grassland was most sensitive to C input (slope = 2.14), followed by the piñon-juniper woodland, ponderosa pine forest, and mixed conifer forest (Fig. 2). For C input expressed relative to dry soil (Fig. 1B), however, sensitivity of priming was similar in the cool desert grassland, piñon-juniper woodland, and ponderosa pine forest (mean slope = 0.47), whereas priming was least sensitive to C input in the mixed conifer forest (Fig. 2). In general, priming sensitivity was greater and was more variable when C input was expressed relative to MBC compared to C input expressed relative to dry soil. Regardless of the way of expressing priming, the sensitivity of priming to C input declined with elevation.

3.2. Substrate thresholds and priming

Substrate thresholds (minimum C input required to stimulate positive priming) were detected in three of the four soils, regardless of the way of expressing C input (Table 4). The cool desert grassland, piñon-juniper woodland, and ponderosa pine forest exhibited positive substrate thresholds, with 95% CIs of each soil that did not overlap zero. Although the mean value of the threshold in the mixed conifer forest was lower than those observed in the other soils, the 95% CIs were wide, overlapped zero, and overlapped the CIs found for the other soils.

3.3. Predictors of priming

Carbon input expressed relative to soil MBC was a poorer predictor of priming compared to C input expressed relative to dry soil (Fig. 1). Across the four soils, substrate C input expressed as a fraction of dry soil mass explained 16.5% more variation in priming than did C input expressed as a percentage of soil MBC.

4. Discussion

4.1. Relationship between C input and priming

We observed a positive linear relationship between C input and priming in all soils, where low C input induced negative or no priming and high C input induced strong positive priming (Figs. 1,
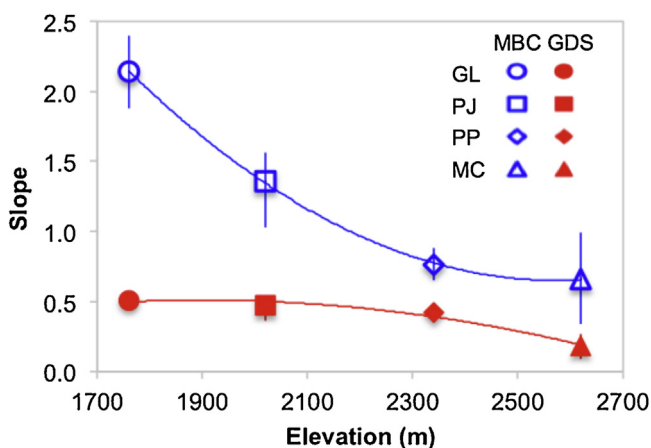

Fig. 2. Relationships between slopes and elevation in four soils (GL = grassland; PJ = Piñon-juniper; PP = Ponderosa pine; MC = Mixed conifer) for C input expressed relative to soil microbial biomass C (MBC; μg C μg C$^{-1} \times 100\%$; y = −0.000002*x^2− 0.0116*x + 15.556; $r^2 = 0.9996$) or relative to dry soil (GDS; μg C g soil^{-1}; y = −0.0000006*x^2 + 0.0023*x − 1.7008; $r^2 = 0.9683$). Bars are 95% confidence intervals.

Table 4
Substrate thresholds (x-intercepts) and 95% confidence intervals (CIs) between priming (μg C g dry soil^{-1}) and C input relative to soil microbial biomass C (MBC%; μg C μg C^{-1} × 100%) or relative to dry soil (GDS; μg C g dry soil^{-1}) in four ecosystems. Thresholds were inferred to be present for each soil if CIs did not overlap with zero, and were considered different between soils if CIs did not overlap with each other[a].

| Ecosystems | Glucose additions (MBC%) | | | Glucose additions (GDS) | | |
df	x-intercept	Lower CI	Upper CI	x-intercept	Lower CI	Upper CI
Grassland	36	25	52	153	111	220
Piñon-juniper	73	63	83	209	181	228
Ponderosa pine	81	31	132	149	57	242
Mixed conifer	4.8	−194	156	18	−722	581

[a] %MBC stands for glucose addition as a percentage of soil microbial biomass C; GDS indicates the absolute amount of glucose added as μg C g^{-1} dry soil week^{-1}.

S1, and S2). Others have also observed this positive linear relationship between C input and priming (Chowdhury et al., 2014; Tian et al., 2015). Negative priming at low C input might be caused by preferential substrate utilization, where soil microbes switch to utilize added labile C instead of native soil C, as the former is a low-cost energy source (Cheng, 1999; Rainey and Travisano, 1998). The absence of priming at low C input could be insufficient energy input that failed to stimulate microbial growth and activity (Fig. S3) (Blagodatskaya and Kuzyakov, 2008). The transition to positive priming at higher C input might be initiated by microbial N mining, where soil microbes consume added labile C as an energy source to decompose SOM and acquire N (Craine et al., 2007; Dijkstra et al., 2013; Fontaine et al., 2011; Moorhead and Sinsabaugh, 2006). Thus, the positive linear relationship between C input and priming might be attributed to the shift of microbial energy-limitation at low C input to nutrient-limitation at high C input (Figs. S2 and S3) (Blagodatskaya et al., 2011; Tian et al., 2015).

Our data suggest that a linear relationship between C input and priming is better than a non-linear relationship, given the higher r^2 values for the linear models. In some cases, priming seems to saturate in response to increasing amounts of recalcitrant substrate input (i.e., wheat straw, plant litter) such that a non-linear model provides a better fit (Guenet et al., 2010; Xiao et al., 2015). The discrepancy between linear and nonlinear relationships suggests that addition of different substrates, such as recalcitrant (e.g, crop residues, plant litter) versus labile C (e.g., glucose, root exudates), might affect the relationships between C input and the priming effect (Guenet et al., 2010).

4.2. Substrate thresholds and priming

We observed positive substrate thresholds for priming in three of the four soils, irrespective of the way of expressing C input (Table 4). The shift from negative to positive priming with increased C input has been reported by prior studies (Blagodatskaya et al., 2011; Qiao et al., 2014; Tian et al., 2015). However, no substrate thresholds were detected in the mixed conifer forest soil, where priming was the least sensitive to C input, with its slope two times smaller compared to slopes of the other soils (Fig. 2). The mixed conifer had relatively high SOC and soil N but smaller microbial biomass compared to other soils (Table 2; smallest MBC/SOC ratio), indicating that microbes in the mixed conifer were less prone to nutrient limitation, perhaps causing weaker – and more variable – priming compared to the other soils. Our results suggest that minimum quantities of C input (56 to 242 μg C g^{-1} week^{-1}) were required to stimulate positive priming in the three soils.

The rates of C addition we used were well within the range of those used in past soil priming incubations (Table 1), but were likely higher than naturally occurring rates of C input to soil. For example, if root turnover and exudation constitute 20 – 40% of photosynthetically fixed C (Hütsch et al., 2002; Lynch and Whipps, 1990), in the four ecosystems studied here, this would amount to C flux rates of as much as 67 μg C g^{-1} soil week^{-1} or 3500 μg C g^{-1} soil yr^{-1} (gross ecosystem production as reported in Wu et al. (2011), scaled to a soil mass basis for the top 10 cm of soil using bulk density data from Blankinship et al. (2010). Rather than simulating actual C fluxes in nature, the rates of C input we selected were designed to explore a broad range of relationships among the priming effect, amounts of C input, and the size of the soil microbial biomass.

4.3. A better predictor of priming

Carbon input expressed relative to dry soil mass explained more variation in priming than did C input expressed relative to soil MBC, suggesting that microbial biomass was a weaker predictor of priming (Fig. 1). Although C input expressed relative to MBC was proposed as an alternative that might better explain priming (Blagodatskaya and Kuzyakov, 2008), this supposition has never been tested directly. Our study confirmed that C input expressed as a fraction of dry soil mass can be a better and more stable predictor of priming than is C input as a fraction of soil MBC (Figs. 1 and 2). That soil MBC is a poorer predictor of priming might be owing to variable rates of microbial growth, enzyme synthesis, and turnover among different soils and over time (Moorhead et al., 2013; Xu et al., 2014).

Despite being a weaker predictor, C input expressed relative to MBC also showed a positive linear relationship with priming in all of the four soils. Priming increased linearly with C input from 3% to 410% of soil MBC, showing no indication of decline as C input increased thereafter. Similar priming responses to C input relative to soil MBC have been reported by earlier studies (Table 1). For example, increasing C input from 10% to 370% of soil MBC increased priming by up to six-fold (Chowdhury et al., 2014; Tian et al., 2015). Further, increasing C input from 2% to 113% of MBC stimulated priming in an organic soil layer, and C input from 18% to 900% of MBC stimulated priming in the underlying mineral soil layer as well; in both cases the stimulation was large, on average, a five-fold increase in priming with the higher C addition amounts (Wang et al., 2015). In general, our findings suggest a positive linear relationship that increasing C input to soils can enhance priming and accelerate SOM decomposition.

Based on a review of the literature, however, priming was proposed to increase with C input up to only 15% of MBC; after that, priming was proposed to decrease and become negative priming from 15% to 600% of MBC (Blagodatskaya and Kuzyakov, 2008). Results reported here and a synthesis of literature data (Table 1) do not support this idea and suggest that the inference from this review paper could be misleading for several reasons: (1) the review collected data from only 10 papers, two of which (De Nobili et al., 2001; Mondini et al., 2006) did not use C isotope tracers

(^{13}C or ^{14}C) to distinguish substrate-derived CO_2 from SOM-derived CO_2, making it impracticable to calculate the real priming effect (see Eqs. (1) and (2)); (2) data used in this review paper were from different soils, substrate types, and incubation times under variable environmental factors that can be more important drivers of the priming effect than C input; and (3) the conceptual model put forward in this review paper is not supported by the evidence that has accrued thus far (Blagodatskaya et al., 2011; Chowdhury et al., 2014; Qiao et al., 2014; Tian et al., 2015; Wang et al., 2015) (Fig. 1).

4.4. Substrate addition patterns and type

We used multiple C additions rather than a single addition to more accurately resemble the dynamics of labile C input in the field (Hamer and Marschner, 2005; Qiao et al., 2014). With multiple substrate additions to different soils, we were able to explore the relationship between C input and priming across multiple ecosystems over time. However, single versus multiple additions might influence priming differently. For the same amount of total added labile C, a single addition caused a larger priming effect compared to multiple additions (Qiao et al., 2014). The larger priming with a single substrate addition could occur if high C input triggered microbial growth and enzyme production; the weak priming with repeated labile C input, especially when the C input of each addition is very low, might occur because the energy provided by the substrate is insufficient to support microbial growth (Qiao et al., 2014). However, if the C input of each repeated addition is high, exceeding the required thresholds to elicit priming (as we showed here, Table 4), multiple substrate additions probably will increase activity and enzyme synthesis of SOM-feeding microbes (whist suppressing labile substrate-feeding microbes) (Fontaine et al., 2003), stimulating stronger priming responses than a single substrate addition.

We used a labile C source (^{13}C-glucose) as a model substrate to explore priming, as has been done by many prior priming studies (Table 1). Because of the lack of N in our experiment, the priming effect we observed may have been higher compared to experiments where N-containing substrates are added. For example, adding N along with low and high C (48.7 and 4870 μg C g^{-1}; C:N ratio = 10) reduced priming by about 50 and 80 μg C g^{-1} compared to the priming induced by C input alone (Blagodatskaya et al., 2007). Thus, for fresh organic matter (e.g., litter, leaves, roots, root exudates) that contains additional N, the priming effect might be reduced. This decreased priming with fresh organic matter input, along with the soil physiochemical properties, microbial communities, and surrounding environment factors (e.g., moisture, temperature), should be considered and accounted to improve the soil C models and enhance our capacity to predict soil responses to climate change (Schmidt et al., 2011).

5. Conclusions

Our findings suggest a positive linear relationship between C input and priming: negative or no priming at low C input and strong positive priming at high C input. However, the sensitivity of priming in response to C input differed among soils, declining with elevation (Fig. 2), a pattern that may reflect effects of climate, primary production, soil organic matter content, or other ecosystem properties that vary systematically with elevation. Three soils showed positive substrate thresholds for priming, indicating minimum quantities of C input required to stimulate positive priming (56 – 242 μg C g^{-1} week^{-1}). Furthermore, C input expressed as a fraction of microbial biomass explained less variation in priming than did the C input as a fraction of dry soil mass, suggesting that the size of soil microbial biomass was not

strongly related to priming. In general, our results indicate that the labile C input to soils enhances the priming effect, but the magnitude of the enhancement varies among ecosystems. Future research focused on the mechanisms causing variation in the sensitivity of priming to increasing C input would help develop a quantitative understanding of how this enigmatic phenomenon influences soil organic matter decomposition, lending the possibility to create better soil C models.

Appendix A. Supplementary data

Supplementary data associated with this article can be found online at http://dx.doi.org/10.1016/j.apsoil.2016.10.002.

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