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

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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 $\mu g\,C\,g^{-1}\,week^{-1}$) 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 $\mu g\,C\,g^{-1}\,week^{-1}$), 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.

## 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

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(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 $\mu g\ g^{-1}$ | pH | | day/T | Type | Weekly $\mu g\ C\ g^{-1}$ | Total $\mu g\ C\ g^{-1}$ | PE[b] $\mu g\ C\ g^{-1}$ |
| 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 ($\mu g\ C\ g^{-1}$ 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.