



A meta-analysis of the temporal dynamics of priming soil carbon decomposition by fresh carbon inputs across ecosystems



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ABSTRACT

Priming of soil organic matter decomposition by fresh carbon inputs is a key ecological process determining soil carbon (C) and nutrient cycling in terrestrial ecosystems. Although this priming effect (PE) has been studied under various environmental conditions, the conclusions are inconsistent across space and time and the underlying mechanisms unclear. We used a meta-analysis with extensive datasets of CO₂ effluxes from soils with ¹³C or ¹⁴C labelled fresh C inputs and without fresh C inputs under various soil conditions to synthesize and assess the temporal dynamics of the PE. The results indicated that the PE declined in 20 days on average from 67⁺²⁶₋₂₁% (95% confidence interval) immediately following the fresh C inputs to less than 7.6^{+2.0}_{-1.8}% and remained relatively stable thereafter. We also assessed the variability of the temporal dynamics of the PE in the collected datasets and the underlying drivers. The results showed that the magnitude of PE at a specific time (i.e., the instantaneous PE after the fresh C inputs) was significantly and positively correlated with the instantaneous quantity of remaining fresh C. Under the same quantity of remaining fresh C, the PE varied significantly across ecosystems (in the order of grasslands < farmlands < forests < other ecosystems such as lake beds and volcanic soils), but, contrary to our expectation, the PE was independent of the quality of the added fresh C. We found that the PE experienced a faster decrease in soils with higher clay and moisture contents. These results describe the temporal dynamics of PE and the underlying drivers, underpinning the robust predictions of PE dynamics and their impact on soil C and nutrient balances.

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1. Introduction

Soil organic matter (SOM) decomposition can be accelerated or retarded by fresh C inputs – a process known as “the priming effect (PE)” (Cheng et al., 2014; Fontaine et al., 2003; Kuzyakov et al., 2000). Increasingly, studies have demonstrated that the PE plays a significant role in soil carbon (C) and nutrient cycling (Finzi et al., 2015; Fontaine et al., 2004; Keiluweit et al., 2015) and mediates the responses and feedbacks of a series of ecological processes to global change (De Deyn et al., 2008; Dijkstra and Cheng, 2007; Perveen et al., 2014; Phillips et al., 2011; Sulman et al., 2014). On the global scale, for example, Sulman et al. (2014) indicated that the priming of “old” SOM reduced soil C storage in the majority of terrestrial ecosystems, and partially counteracted soil C gains from enhanced ecosystem productivity under elevated CO₂. However,

the significance of the PE in SOM decomposition processes depends on its magnitude, direction and duration, which are soil-specific and influenced by the quality and quantity of new C inputs (Blagodatskaya and Kuzyakov, 2008; Kuzyakov, 2010). Drawing a holistic picture of PE dynamics through time is critical for clarifying the role of the PE in the stabilization and/or destabilization of SOM, particularly at large temporal scales.

The PE dynamics depend on a complex interplay of abiotic and biotic controls such as substrate availability and accessibility, soil physio-chemical properties, and microbial community structure and activity (Blagodatskaya and Kuzyakov, 2008; Fontaine et al., 2003; Kuzyakov, 2010). In the critical review by Kuzyakov et al. (2000), they showed that both positive (i.e., accelerating SOM decomposition) and negative (i.e., retarding SOM decomposition) PEs were common, and positive PEs were reported more frequently. Cheng et al. (2014) comprehensively examined the rhizosphere PE and found that its magnitude varied widely, ranging from an enhancement of 380% to a 50% reduction. Dijkstra et al. (2013) specifically discussed the rhizosphere PE under different soil

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nutrient conditions and postulated that the rhizosphere PE might be more significant in nitrogen-limited than in phosphorus-limited soils. From the perspective of microbial processes, the review by Blagodatskaya and Kuzyakov (2008) suggested that the PE dynamics through time were the consequence of a succession of microbe-substrate relationships, which were modified by substrate and nutrient availability and microbial community structure and activity. Despite these comprehensive reviews, the quantitative and predictive understanding of the PE dynamics and how they are affected by soil and climatic variables across ecosystems and under variable fresh C inputs remain unclear. This uncertainty hinders our understanding of the role of the PE in long term soil C dynamics and our ability to effectively incorporate the PE into soil C models.

Previous analyses of the PE mainly focused on the average PE over fixed time periods and rarely systematically and quantitatively considered the potential general patterns of temporal dynamics of the PE under different environmental conditions. Focusing on the average PE, for example, our recent data assimilation and meta-analysis indicated that on average fresh C inputs stimulated native soil C decomposition by 14.2% (Luo et al., 2015). Another data assimilation by Van Groenigen et al. (2014) demonstrated that overall soil C decomposition accelerated by 16.5% under atmospheric CO₂ enrichment, mainly due to increased fresh C inputs and improved soil moisture for microbial decomposition. However, all these estimates were based on one- or two-pool decomposition models assuming constant decomposition rates. These simple pool-based models cannot capture the fact that the PE may be a consequence of the changes in the distribution of enormous C pools (which are usually represented by one or two pools) and/or microbial C use efficiency under fresh C inputs (Georgiou et al., 2015).

In this study, we conducted an integrative analysis of the extensive datasets from 171 independent experiments consisting of 1695 observations. The datasets cover diverse land use types, soils, climate, and varying fresh C substrates in terms of both quality and quantity. First, a decomposition model driven by time-dependent decay rates was used to derive the decomposition rates of native soil C with and without fresh C inputs (i.e., control vs treatment) through time, and the PE was calculated based on the estimated decomposition rates. Then, meta-analysis and a multilevel regression model were used to assess the PE dynamics and their association with a series of soil properties and the quantity and quality of added C substrates. The objective of this study was to identify the temporal pattern of the PE under various conditions and assess the underlying drivers. Specifically, we addressed three questions: i) what is the magnitude of the PE? ii) how does the PE change with time? and iii) what factors control the magnitude and temporal dynamics of the PE? Based on the results, we further discussed the mechanisms underlying the temporal dynamics of the PE, and suggested future research requirements and directions.

2. Materials and methods

2.1. Data sources

We reused the datasets in a previous study (Luo et al., 2015) and further expanded the datasets by screening new publications that were not included in the original study using the same data collection criterion (Supplementary S1). Briefly, the datasets included the time-course measurements of cumulative CO₂-C effluxes from soil under control (i.e., without fresh C substrate inputs) and treatment (i.e., with ¹³C or ¹⁴C labelled fresh C substrate inputs) of incubation experiments. For a specific study, all other environmental conditions including pre-incubation (i.e., before the input of fresh C substrates) were the same under control and treatment. Based on the isotopic signature of C in CO₂, soil and labelled

substrates, thus, the total CO₂-C efflux can be separated into that derived from native soil C (¹²C) and that from the added substrate (¹³C or ¹⁴C labelled). This partition enabled the calculation of difference in native soil C mineralization under control and treatment, i.e., the priming effect.

A total of 171 individual experimental comparisons (control vs treatment) in 37 studies met our data selection criteria (Luo et al., 2015; Supplementary S1 and S2). All these experiments were conducted under laboratory conditions with controlled soil moisture and temperature. For each individual experiment, we extracted the initial soil and substrate C content, and the cumulative CO₂-C efflux at each time point of the time-course measurements. The corresponding standard deviation (SD) or proxies (e.g., standard error and 95% confidence interval) and sample size were also collected. In many of the studies, SDs were shown as bars in the original figure, and usually masked by the symbols of the corresponding means. By considering that those SDs were very small (masked by the symbols of the means), these SDs were approximately estimated as 2% of the corresponding means. These extracted data were used to estimate the probability distribution function (PDF) for observed C assuming that observations at each time point of the measurements were normally distributed with the extracted mean and SD, i.e., $C \sim (\text{mean}, \text{SD})$. These PDFs represent the data quality at each time point of the measurements in individual studies and were used in the following data assimilation to quantify the uncertainties in the estimation of the PE.

Besides the above C-related data, for each experiment we also recorded the soil clay content (%), the C:N ratios of the soil and added substrate, the soil temperature (°C) and moisture (% water holding capacity), the ecosystem type where experimental soil was sampled, and the substrate type. Ecosystems were categorised into four groups including farmlands (i.e., agricultural lands including croplands and pasture), forests, grasslands (natural grasslands without human management), and others (mainly tundra, volcanic soils and lake beds that receive limited C inputs, and occasionally ecosystem types otherwise unreported in the study). The added substrates were differentiated in two types: simple and complex substrates, according to their polymerised structure. The simple substrates referred to small C molecules and soluble materials such as glucose and fructose. These substrates are generally readily available for microbial utilization. The complex substrates referred to various plant-derived materials and polymerised C molecules such as animal slurry, plant litter and cellulose. These substrates contain polymerised compounds that are generally difficult to decompose and require more energy and nutrient investments of microbes into decomposing enzymes. Based on the C:N ratios of added substrates and soils, the stoichiometric difference (CND) was calculated as their difference. We also calculated the instantaneous mass ratio (M) of added substrate C (i.e., the remaining added substrate C at a specific time during an experiment) to native soil C (i.e., the remaining native C that originally derives from the soil C that exists in the soil before fresh C substrate addition) at each time point of the measurements. These variables were used for the subsequent multilevel regression modelling to address their potential effects on the temporal response of native soil C decomposition to the added fresh C.

2.2. Data assimilation

Soil C decomposition is usually simulated as a first-order decay process:

$$C_t = C_0 \cdot e^{-k \cdot t}, \quad (1)$$

where C_0 is the initial soil C content (mg C g⁻¹ soil), i.e., at the start

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