



Mycelium- and root-derived C inputs differ in their impacts on soil organic C pools and decomposition in forests

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ABSTRACT

While multiple lines of evidence suggests that root carbon (C) can significantly impact the soil organic C (SOC) pool and subsequent C cycles via rhizosphere priming effects, the relative magnitude of the effects that root- and fungal-derived C inputs have in driving the priming of SOC decomposition are currently unknown. In this study, we used ingrowth cores and stable C isotope analyses to quantify root- and mycelium-derived C sequestered in soil labile and recalcitrant C pools and their relative contributions to the decomposition of native SOC in a spruce-fir-dominated coniferous forest on the eastern Tibetan Plateau, China. The results showed that new C sequestered in the soil labile C pool was primarily (77%) from mycelium-derived C, while 60% of the root-derived C sequestered in the soil was incorporated into the recalcitrant pool. Furthermore, although the total native SOC pool was not significantly influenced by new C derived from both roots and mycelia, mycelium-derived C induced a remarkably greater negative priming effect (−12.0%) on the native labile C pool than did root-derived C (−5.8%); in contrast, mycelium-derived C induced a greater positive priming effect (13.8%) than root-derived C (7.1%) on the native recalcitrant C pool. Collectively, our findings suggest that mycelium-derived C make a greater contribution to the newly sequestered C in the soil labile C pool than root-derived C, thereby inducing a remarkably greater positive priming effect on the decomposition of native soil recalcitrant C. Therefore, mycelium-derived C inputs may play a dominant role in soil C dynamics and long-term C storage, at least in alpine forest ecosystems where ectomycorrhizal mutualisms dominate.

1. Introduction

The supply of fresh plant-derived carbon (C) into the soil matrix can accelerate or retard the decomposition of soil organic matter (SOM) – a phenomenon known as ‘the priming effect’ (Fontaine et al., 2004, 2007; Blagodatskaya and Kuzyakov, 2008). It is increasingly recognized that the priming effect plays a critical role in mediating soil C and nutrient cycling and has important implications for ecological feedbacks to global change (Drake et al., 2011; Phillips et al., 2011; Keiluweit et al., 2015). For example, a recent meta-analysis has indicated that fresh C input stimulated native soil organic C (SOC) decomposition by 14% on average (Luo et al., 2015). Root C input is one of the most important ways that plant-derived C is added to the soil, mainly through root exudation and the turnover of fine roots (Pendall et al., 2004), and can represent on average between 11% and 17% of net fixed C in plants (Jones et al., 2009). C inputs derived from root exudation and

rhizodeposition can serve as an important energy source for the microbial production of extracellular enzymes that breakdown SOM (i.e., the rhizosphere priming effect) (Dijkstra et al., 2013; Cheng et al., 2014).

In addition to the well-established rhizosphere priming effect on SOC decomposition induced by C secretion from roots (hereafter, root-derived C), plant roots can also input C compounds into soil microsites through provisioning C to the mycelia of symbiotic mycorrhizal fungi (hereafter, mycelium-derived C), consequently generating a ‘hyphosphere priming effect’ (Talbot and Treseder, 2010; Averill and Finzi, 2013; Meier et al., 2015). The extramatrical mycelia (EMM) produced by mycorrhizal fungi provide soil nutrients to their host plants, which, in return, allocate a large portion of C assimilated via photosynthesis to the fungal partner (Smith and Read, 2008; Orwin et al., 2011). Apart from the well-recognized importance of EMM for nutrient uptake by the plant, EMM are known to be a significant sink for plant-derived C, and

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play a key role in C cycling processes (Terrer et al., 2016). Field and laboratory studies estimate that approximately 20%, and sometimes up to 50%, of assimilates can be allocated to EMM of mycorrhizal fungi (Simard et al., 2003; Hobbie and Hobbie, 2008). Similar to root-derived C inputs, C derived from EMM can be incorporated into SOC pools either through the excretion of a range of C-containing compounds into the soil or through the turnover of decaying EMM (Johansson et al., 2009; Cairney, 2012; Phillips et al., 2012). EMM are thus recognized as a crucial conduit for C flow into the soil beyond the rhizosphere (Erland et al., 1991; Wallander et al., 2011). Due to different chemical properties and turnover rates of mycelia and fine roots, mycelium-derived C likely induces priming effects in ways distinct from root-derived C (Högberg and Högberg, 2002; Cairney, 2012). Consequently, the relative proportions of root-versus mycelium-derived C inputs can have profound consequences on soil C pools and ecosystem C cycling.

While there is ample evidence of priming effects induced by root C inputs in forests, existing models often treat roots and EMM as a single organ (i.e., mycorrhiza) (Wallander et al., 2013), meaning that priming effects generated by fine roots and EMM are seldom distinguished. Given the potential differences in the intrinsic traits between root- and mycelium-derived C (Averill and Finzi, 2013; Meier et al., 2015), it is necessary to quantify the relative contributions of root- and mycelium-derived C on the process of SOC decomposition. This will help understand how the potential mechanisms involved in the associations within root systems regulate soil microbial processes in forest ecosystems, and is fundamental to predicting the effects of plants on terrestrial C cycling under various environmental changes.

The chemical components of root C are diverse, ranging from labile and low-molecular-weight organic compounds (e.g., sugars, amino acids, and carboxylic acids) to insoluble and recalcitrant macromolecules (e.g., lignin and cellulose) (Machinet et al., 2011; Paterson et al., 2011; Thomas et al., 2014; Baptist et al., 2015). These chemically distinct root C will be transferred into corresponding SOC pools with the same chemical and physical characteristics, and continually impact the proportion of SOC fractions (Rovira and Vallejo, 2002). SOC can be chemically divided into labile and recalcitrant pools (Belay-Tedla et al., 2009). Given that the two C pools are characterized by different mobility and turnover rates (Rovira and Vallejo, 2002; Xu et al., 2015), the ecological consequences of priming effects induced by root C inputs on the decomposition of the labile and recalcitrant SOC fractions may be substantially different (Belay-Tedla et al., 2009; Guenet et al., 2010). However, most of the previous studies on priming effects are limited mainly to the decomposition of the total SOC pool (Fontaine et al., 2004; Hamer and Marschner, 2005; Dijkstra and Cheng, 2007; Vestergard et al., 2016), and few studies have attempted to investigate the priming effect on the decomposition of different SOC fractions (i.e., labile and recalcitrant C pools) (Yin et al., 2016). The paucity of information on the changes in labile and recalcitrant fractions of SOC pool may cause misjudgment of the magnitude and direction of the priming effect because the determination of total SOC does not permit detection and prediction of small changes in soil C dynamics (Belay-Tedla et al., 2009). Therefore, fractionating SOC into labile and recalcitrant pools and determining their respective feedback to the priming effect induced by root C inputs could be helpful for better understanding soil C dynamics under environmental changes.

In this study, we conducted an experiment using ingrowth cores to partition the growth of fine roots and EMM in an alpine coniferous forest on the eastern Tibetan Plateau. This area is a natural forest (NF) dominated by spruce (*Picea asperata* Mast.) and fir (*Abies faxoniana*). The alpine coniferous forests in this region are dominated by ectomycorrhizal (ECM) fungi (Song et al., 2006), one of the most ecologically important types of mycorrhizae (Courty et al., 2010; Laliberté, 2017). The SOC chemical fractionation technique was coupled with the natural abundance of stable C isotopes technique to examine changes in soil labile and recalcitrant C stocks following root C inputs. The purposes of the present investigation were to (1) quantify the relative contributions

of root- and mycelium-derived C sequestration in soil labile and recalcitrant C pools; and (2) further evaluate the magnitude and direction of root- and mycelium-derived C on the decomposition of different fractions of native SOC. Given that fungal biomass is generally more labile relative to most plant tissues present in forest soils (Drigo et al., 2012; Fernandez and Koide, 2012), we hypothesized that new C sequestration in the soil labile C pool would primarily be from mycelium-derived C, which would further induce a greater positive priming effect on native recalcitrant SOC decomposition.

2. Materials and methods

2.1. Study sites

This research was conducted in a spruce-fir-dominated NF (c. 200 years old) located in the Miyaluo Experimental Forest on the eastern Tibetan Plateau in Lixian County, Sichuan Province, China (31° 35'N, 102° 35'E, and 3150 m a.s.l.). The understory of the NF is dominated by moss, woody trees (e.g., *Acer mono*, *Lonicera* spp., and *Betula albo-sinensis*) and grasses (e.g., *Anemone rivularis* and *Carex capilliformis*). The mean annual temperature is 8.9 °C with a maximum monthly mean air temperature of 12.6 °C in July and a minimum of −8 °C in January. Annual precipitation ranges from 600 to 1100 mm. The soils are classified as Cambic Umbrisols according to the IUSS Working Group (2007). The basic soil properties in the upper surface (0–15 cm) were determined in July 2015 (Zhang et al., 2017) and are as follows: sand 61.0 ± 4.5%, silt 31.7 ± 1.5%, clay 7.3 ± 0.9%, organic C 80.36 ± 15.85 g kg^{−1}, total N 4.97 ± 0.79 g kg^{−1}, and pH 5.64 ± 0.7.

2.2. Experimental design and sampling

The experimental device (ingrowth core) was modified from the apparatus of Booth (2004) and Phillips et al. (2012). Briefly, cylinders were fabricated from sections of PVC pipe (15 cm length, 5 cm internal diameter, and ~6 cm external diameter) from which large windows of the PVC wall (~80% of the surface area) were removed. The wall and bottom of the cylinders were wrapped tightly in a mesh of three different pore sizes. The 1 μm pore size was designed to inhibit the ingrowth of fine roots and fungal hyphae ('mycelia exclusion'), but allow the flow of water, whereas the 48 and 1000 μm pore sizes would also permit the penetration of mycelia ('mycelia only') and fine roots ('root accessible'), respectively.

In September 2014, four plots separated by more than 50 m were delineated at the forest site. Each plot measured 5 m × 5 m and contained three different ingrowth cores, for a total of 12 cores. The three adjacent ingrowth cores were spaced 50 cm apart. The soil placed in the ingrowth cores was a composite of soil from the NF and a spruce (*P. asperata*) plantation which was later planted following the harvest of most spruce-fir-dominated NFs. Soils from both forest sites were collected from the mineral soil horizon (approximately 20–30 cm) with a 5-cm diameter soil sampler. According to the local Forestry Bureau, maize was cultivated on the cleared area of the NFs before the spruce plantation was planted, leaving the soil in the plantation a high ¹³C signature relative to that in the NF. Soils were passed through a 1-mm sieve prior to filling each core. Any visible living plant material or rock was manually removed from the samples. The basic chemical properties of the pre-ingrowth transplant soil were as follows: organic C 20.14 g kg^{−1}, total N 1.24 g kg^{−1}, and δ¹³C −21.7‰. Each ingrowth core was filled with 240 g transplanted soil and carefully inserted into a hole dug into the upper mineral horizon where most roots and mycorrhizal hyphae proliferate (Baath et al., 2004; Parent and Vilgalys, 2007). A small volume of transplanted soil was placed into the gaps between the cores and bulk soil when necessary. In addition, we physically removed aboveground understory vegetation by cutting stems at 10 cm above the ground and transferring the cut vegetation outside of

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