Effects of Exogenous Carbon Input on Key Processes of the Carbon Cycle in Terrestrial Ecosystems and Their Microbiological Driving Mechanisms: Postprint

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Abstract

Changes in soil carbon source availability induced by exogenous carbon input not only directly influence microbial participation in carbon cycling processes of terrestrial ecosystems, but also constrain microbial demand for other nutrient elements. Against the backdrop of global change characterized by continuously increasing atmospheric nitrogen deposition, significant alterations in ecosystem nitrogen nutrient conditions have emerged in some regions, even leading to excessive accumulation of reactive nitrogen in soils, which consequently enhances microbial demand for carbon sources. Artificial regulation of carbon source availability to ameliorate microbial carbon limitation holds extremely significant implications for scientifically enhancing the carbon sequestration capacity of terrestrial ecosystems. This review synthesizes relevant research findings from domestic and international studies concerning the effects of exogenous carbon input on soil carbon emissions, litter decomposition, and soil carbon pools, as well as the primary microbial mechanisms involved, aiming to provide references for scientifically and effectively enhancing ecosystem carbon sink potential under future scenarios of continuously increasing nitrogen deposition.

Full Text

Preamble

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Effects of External Carbon Input on Key Processes of Carbon Cycle in Terrestrial Ecosystems and Its Microbial Driving Mechanism

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Abstract

External carbon input to soil influences the availability of carbon substrates and microbial carbon cycling, as well as microbial utilization of other nutritional elements in terrestrial ecosystems. With globally increasing nitrogen deposition, the nitrogen content of soils in some regions has changed significantly and now exceeds microbial demand, leading to increased need for available carbon. Therefore, artificial regulation of available carbon sources might be essential for relieving microbial carbon limitation and improving carbon sequestration capacity of terrestrial ecosystems. This paper reviews previous studies concerning the influences of external carbon input on soil carbon emission, litter decomposition, soil carbon pools, and the functional microbial mechanisms in these processes. This work will provide a reference for improving the carbon sink capacity of terrestrial ecosystems under future scenarios of continuous nitrogen deposition increase.

Keywords: available carbon source; carbon cycle; microbial mechanism

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1. Effects of External Carbon Input on Terrestrial Ecosystem Carbon Cycle

Soil microorganisms are the drivers and regulators of key soil carbon cycling processes. In addition to directly causing increases in microbial biomass and activity, external carbon input can improve soil microenvironments by altering soil physical and chemical properties such as bulk density and soil texture, enhancing water retention, and increasing the supply of other nutrient elements required by plants. These changes indirectly affect microbial life activities and their participation in carbon cycling processes such as soil organic matter mineralization and litter decomposition.

1.1 Effects of External Carbon Input on Soil Carbon Emissions

Soil respiration represents the primary pathway for soil carbon loss to the atmosphere. Studies have shown that increased carbon input exerts a priming effect on soil respiration. Reported research results indicate that adding simple carbon compounds such as glucose, cellulose, and sucrose, as well as complex compounds including organic manure, straw, and litter, all significantly increase soil respiration rates. Moreover, soil respiration rates gradually increase with the amount of carbon input. Compared with complex carbon compounds, simple carbon compounds are more readily utilized by microorganisms, resulting in more rapid increases in soil respiration.

Nottingham et al. comprehensively evaluated and compared the differential effects of sucrose and leaf litter as carbon sources on forest soil respiration, concluding that due to differences in substrate utilization ease, soil respiration rates in sucrose-amended treatments were significantly higher than those with leaf litter addition. The duration of effects also varies among different carbon sources: simple carbon compounds influence soil respiration rates for relatively short periods (2–70 days), while litter and straw contain not only simple compounds but also complex carbon compounds that provide sustainable carbon sources for decomposers, resulting in longer-lasting priming effects on soil respiration.

Chemidlin-Prévost-Bouré et al. found that in a French deciduous forest ecosystem, the priming effect of litter addition on soil respiration could last for an entire year, with annual average soil respiration rates increasing by 31% compared to the control. Regarding the effects of addition frequency with equal carbon input amounts, Duong et al. examined the impacts of different wheat straw addition frequencies on soil respiration in the understory of arid regions in southern Australia. When equal amounts of straw were added in 2, 4, or 8 applications versus a single addition, cumulative CO_2 release increased by 57%, 82%, and 98%, respectively. Some studies have also shown that increased addition frequency of oxalic acid and catechol as external carbon sources leads to increased soil CO_2 emissions. One explanation suggests that soils contain considerable amounts of easily mineralizable organic carbon, and multiple or frequent carbon additions continuously accelerate the consumption of this pool. Another interpretation holds that because different microorganisms have varying abilities to decompose soil organic carbon, frequent carbon addition leads to rapid growth of microorganisms that can decompose these substrates or causes shifts in soil microbial community structure, thereby increasing soil respiration.

Seasonal variation in the effects of external carbon input on soil respiration has been documented. Studies by Wang Bingwen et al. in winter wheat fields with corn straw addition, Wang Jinsong et al. in pine plantations, Wang Guangjun et al. in Chinese fir plantations, and Crow et al. in forests at the Andrews Experimental Forest in the USA all demonstrated that the influence of increased carbon input on soil respiration shows obvious seasonal patterns. Differences in soil respiration rates between treatments with added carbon and controls are greater during peak growing seasons than during non-growing seasons. However, in forest ecosystems, some studies have shown that the significance of differences in soil respiration flux between double litter addition treatments and controls is not affected by seasonal changes, likely due to variations in forest plant types and litter species used in experiments.

Regarding effects on environmental factors related to soil respiration, research indicates that adding plant stems and leaves as litter to the soil surface blocks heat exchange between soil and atmosphere, thereby reducing the impact of external environmental changes on soil respiration. Wang Guangjun et al. found that in Chinese fir plantations, double litter addition treatments lowered soil temperature in the surface layer and reduced the temperature sensitivity coefficient (Q_{10}) of soil respiration compared to controls, consistent with findings from studies on pine plantations in China, coniferous forests in the USA, and deciduous forests in France. Some studies have also found that double litter addition treatments significantly increased soil moisture compared to controls. Since soil moisture regulates root and microbial physiological processes as well as the diffusion of microbial substrates and oxygen, increased carbon input can directly or indirectly affect soil respiration intensity through its influence on soil moisture.

In summary, increased carbon input directly and indirectly affects soil respiration, and the duration of priming effects varies depending on carbon source type and addition method. Although numerous studies have examined the priming effects of carbon input on soil respiration, controversy remains regarding whether short-term or long-term carbon addition increases terrestrial ecosystem carbon emissions. Further exploration of the underlying mechanisms of external carbon effects on soil respiration is necessary to better support theoretical frameworks for carbon emission reduction and carbon sequestration in terrestrial ecosystems.

2. Effects of External Carbon Input on Litter Decomposition

Litter plays a crucial role in maintaining soil nutrient pools, regulating ecosystem energy flow and nutrient cycling, and influencing primary productivity. Its quantity and decomposition rate also affect soil organic matter formation and changes in plant nutrient demand and soil carbon emissions. Since litter decomposition rate is constrained by microbial activity, carbon input regulation of microbial activity inevitably influences litter decomposition.

Studies have shown that the effects of increased carbon input on litter decomposition rates can be positive, negative, or neutral. These varied responses partly result from competition for nutrients between microbial groups that primarily utilize easily decomposable organic carbon (r-strategists) and those that decompose complex structural organic carbon (K-strategists). In boreal coniferous forests, the mineral soil layer and litter contain large amounts of lignin and humic acid that are not easily utilized by microorganisms, with K-strategist microbial communities dominating. When labile carbon sources are added externally, the activity and decomposition capacity of K-strategists for litter can be suppressed or weakened.

Chigineva et al. studied the response of litter decomposition rate to carbon addition in a Moscow spruce forest, finding that sugar treatment altered fungal communities and significantly reduced litter decomposition rate. Kuzyskov et al. also found that in fertilized grasslands with high nutrient content, the addition of labile carbon sources like glucose promoted rapid increases in microbial activity and competitive ability for nutrients, thereby accelerating litter decomposition. The different responses to external carbon input depend on the availability of the carbon source and the content of other nutrient elements it contains. Sayer et al. found that double litter treatment increased microbially available nutrients, thus accelerating decomposition.

Litter decomposition is an important pathway for carbon exchange between plant and soil carbon pools and largely determines soil microbial community composition. Its decomposition rate not only affects carbon transfer from litter to soil but also influences soil carbon input rates. When increased carbon input promotes litter decomposition, it inevitably affects soil carbon storage. However, whether this ultimately increases soil carbon stocks remains uncertain and requires comprehensive analysis combined with responses of original soil organic carbon mineralization and decomposition. Strengthening research on these processes and their microbial mechanisms is crucial for scientifically evaluating and predicting changes in terrestrial ecosystem carbon sequestration capacity under future global change scenarios.

3. Effects of External Carbon Input on Soil Carbon Pools

Soil carbon pools represent the largest carbon storage reservoir in terrestrial ecosystems but are also a major source of atmospheric CO_2. The relationship between carbon input and soil organic carbon is critical to ecosystem carbon balance. Regarding the effects of carbon input quality, plant stem and leaf carbon sources promote mineralization of soil organic carbon. Under laboratory incubation conditions, carbon addition increases mineralization rates of original soil organic carbon and decreases total organic carbon content. Fontaine et al. examined the effects of cellulose addition on grassland soil total carbon content, finding that when ^{13}C-labeled cellulose was added to soil, organic carbon decomposition accelerated, releasing large amounts of CO_2 derived from unlabeled carbon sources, and total soil organic carbon content decreased by 1.3%.

Nottingham et al. conducted laboratory simulations using sucrose, corn straw fragments, and corn leaves as carbon inputs, obtaining consistent results on the effects of different carbon sources on soil organic carbon. The reductions in organic carbon following addition of corn straw fragments and corn leaves accounted for 3.3% and 0.9% of total organic carbon, respectively. However, other studies have shown that under field conditions, adding plant stem and leaf carbon sources such as corn straw and millet straw increases soil organic carbon content, particularly in the surface layer. Tian Shenzhong et al. examined the effects of straw return on soil organic carbon in wheat fields, finding that soil organic carbon content was higher in straw-amended soils than in non-amended soils during different wheat growth stages, with the most significant increase in the 0–10 cm layer.

The different effects among experiments are attributed to laboratory incubations isolating soils from normal external carbon input, causing the carbon source consumed by microbial activity to come entirely from soil organic carbon. Regarding the effects of equal carbon input amounts at different addition frequencies, Qiao et al. examined how different glucose addition frequencies affect tropical and subtropical forest soil organic carbon. Under equal glucose input conditions, small frequent additions reduced the priming effect compared to single large additions while maintaining microbial demand for labile carbon sources, preventing excessive carbon input from being completely respired by microorganisms and thus facilitating accumulation of added carbon in soil. Tenua et al. compared the effects of applying organic manure twice annually (spring and autumn) versus a single spring application. Three years of observations showed that CO_2 emissions from the twice-yearly treatment were significantly lower than from the single-application treatment. Under conditions of equal carbon source amounts, small frequent additions not only benefit accumulation of added carbon in soil but can also compensate for carbon lost through priming effects.

Active organic carbon is extremely sensitive to environmental changes and can reflect subtle soil changes before total organic carbon shows variation, serving as an early warning indicator for soil carbon pool dynamics and representing organic carbon that is more readily utilized by microorganisms. Whether simple carbon compounds like glucose or complex compounds such as straw and litter, carbon input directly or indirectly increases soil active organic carbon content. In agroecosystems, straw return significantly increases active organic carbon in the 0–20 cm soil layer and increases the proportion of active organic carbon to total organic carbon. In forest ecosystems, studies by Nadelhoffer et al. and Hamer et al. found that double litter treatments significantly increased soil dissolved organic carbon (DOC) content compared to controls.

From existing research, due to differences in experimental environmental conditions and the inherent availability of different carbon sources, the effects of carbon source availability on soil organic carbon content vary. Under natural conditions, carbon input from straw and organic manure can increase soil organic carbon content, but addition amounts should be appropriate to avoid offsetting carbon sequestration benefits. Small frequent additions represent an ideal approach for increasing soil organic carbon content.

4. Effects of External Carbon Input on Soil Microbial Characteristics

Carbon source availability is a primary environmental factor directly limiting soil microbial activity and biomass changes. External carbon input not only directly affects soil carbon source availability but also indirectly influences microbial quantity and community structure by altering soil environment and physical structure.

Regarding effects on microbial biomass, after adding simple carbon compounds like glucose and cellulose, soil microbial biomass and activity generally increase. Part of the increased CO_2 emissions comes from mineralization of original soil organic carbon, while another portion derives from decomposition of added carbon sources. Fontaine et al. used incubation methods to explore responses of grassland soil organic matter decomposition to glucose addition in three different management systems, finding that significant increases in soil microbial biomass caused obvious changes in soil organic matter decomposition rates. Using substrate-induced respiration methods to measure soil microbial biomass, Nottingham et al. found that when glucose input amounts were high, glucose-induced acceleration of soil organic matter decomposition was directly and positively correlated with changes in soil microbial activity.

Due to differences in the availability of complex carbon sources like plant straw and organic manure, their effects on soil microbial biomass also differ. Yan et al. found that long-term straw or manure addition significantly increased microbial biomass in Jiangsu paddy soils. Li et al. studied the effects of litter on coniferous and secondary forests in northeastern Puerto Rico, also finding important influences of litter on soil microbial quantity and activity. Rinnan et al. examined forest ecosystem litter addition experiments, showing that while total microbial biomass did not change significantly with litter addition, the proportion of Gram-positive bacteria increased. Sirra-Pietikäinen et al. studied responses of Finnish coniferous forest soil microorganisms to organic manure, finding changes in bacterial community composition but no significant changes in total microbial biomass or bacterial biomass.

The different responses of soil microbial biomass to external carbon input are partly due to different microbial communities having different carbon utilization capacities, leading to increases or decreases in specific community numbers after carbon input. Another reason is that the availability of added carbon sources may be lower than that of original soil organic matter, resulting in no obvious changes in microbial biomass. Kuzyskov et al. examined the effects of glucose and plant residues on organic matter mineralization in two grassland soils in southwestern England, finding that the availability of external carbon to microorganisms determines microbial responses to carbon input. Under equal carbon input conditions, glucose decomposition rates were higher than plant residue decomposition rates.

Besides simple, easily decomposable carbon compounds, litter in the early decomposition stage contains high amounts of cellulose and other easily decomposable carbon compounds. Small frequent addition methods can continuously maintain high levels of available carbon sources for soil microorganisms, promoting increases in microbial biomass and activity. Wang Yikun et al. studied agroforestry ecosystems, finding that under equal litter addition conditions, small frequent addition treatments resulted in higher microbial biomass than single addition treatments, with higher net organic carbon mineralization cumulative amounts because different microbial communities have different carbon source metabolic capacities.

Regarding effects on microbial community composition: Kathleen et al. used carbon labeling techniques to study glucose effects on permanent grassland soil microorganisms, finding that fungal community numbers differed significantly between early and late stages after glucose addition, while bacterial community numbers remained stable. The fungal-to-bacterial ratio increased significantly, indicating that fungal communities have stronger metabolic capacity for low-molecular-weight carbon compounds than bacterial communities. Reischke et al. studied the effects of different glucose addition amounts on soil bacteria and fungi, finding that when glucose addition was below 4 mg C per gram of soil, bacterial biomass increased, but when input exceeded 10 mg per gram of soil, fungal biomass increased at a rate significantly exceeding that of bacterial biomass. This demonstrates that when external carbon enters soil, the quantity and activity of microorganisms capable of utilizing that carbon change, potentially altering microbial community structure.

Falchini et al. studied the effects of glucose, oxalic acid, and glutamic acid addition on Italian grassland microorganisms, finding that bacteria specialized in decomposing oxalic acid and glutamic acid increased in number and that bacterial community composition changed. Hamer et al. found in forest ecosystems that double litter treatments altered soil bacterial community structure, and these changes affected soil respiration. Brant et al. comprehensively analyzed microbial community changes in the Andrews Experimental Forest, concluding that different microbial metabolic capacities for glucose, oxalic acid, and phenol in litter were the main reasons for the significant increase in fungal-to-bacterial ratios under double litter treatments. Chemidlin-Prévost-Bouré et al. found that in simulations with equal carbon amounts but different input methods, small frequent additions promoted increases in specialized decomposer microbial numbers, leading to changes in soil microbial community composition.

Some studies have found that straw addition significantly altered microbial community composition, with different addition frequencies (2 times vs. 4 times) producing different community structures. Hamer et al.' s simulation of different oxalic acid and catechol inputs on forest microbial communities also supported this conclusion. However, other research found that double litter addition had no effect on forest soil microbial community structure, possibly because the availability of added carbon was lower than that of native carbon sources, resulting in slow microbial metabolism and relatively slow growth of microbial communities that decompose recalcitrant carbon, making community changes less obvious.

Changes in microbial community composition induced by external carbon input inevitably affect microbial participation in soil respiration, litter decomposition, and other carbon cycling processes. Creamer et al. concluded from incubation studies of Australian woodland soils that increased soil respiration from litter addition was mainly caused by changes in microbial community composition with different carbon decomposition capacities. Based on the above research, the availability of input carbon sources and microbial selectivity in carbon utilization affect the direction and magnitude of microbial quantity and community composition responses to changes in carbon availability. The effects of different carbon source types at the same research site, and the same carbon source in different regions or ecosystems with different background microbial compositions, show considerable variation, adding complexity to research in this area.

Outlook

Carbon source availability is not only crucial for microbial life activities and key terrestrial ecosystem carbon cycling processes but also plays an important regulatory role in ecosystem nutrient element cycles like nitrogen. Changes in soil carbon availability induced by external carbon input inevitably affect these ecosystem processes. Although some reports exist on external carbon effects on terrestrial ecosystem carbon cycling, the mechanisms of action on soil respiration priming, litter decomposition, and other carbon cycling processes remain unclear. The residence time of carbon sources in soil and their effects on microbially available substrates and other nutrient cycling processes require further exploration. Under global multi-factor coupled change scenarios, how carbon availability changes affect ecosystem carbon cycling processes represents an urgent scientific question.

Given current research status, future studies should focus on:

1. **In-depth exploration of mechanisms**: Investigate the primary mechanisms of external carbon input in microbially mediated ecosystem carbon cycling processes, and examine contributions to ecosystem net primary productivity and responses of microbial community structure and functional characteristics. Although some studies exist on soil respiration priming effects, uncertainty remains regarding whether increased CO_2 emissions mainly come from added carbon or native soil organic carbon decomposition, creating a bottleneck for understanding how microorganisms utilize and allocate input carbon and its mechanisms in ecosystem carbon cycling. Meanwhile, research on external carbon effects on net primary productivity is relatively scarce, preventing scientific assessment of contributions to ecosystem carbon source-sink dynamics.

2. **Long-term studies under global change**: Conduct long-term experiments on how carbon availability regulates ecosystem nutrient element

dynamic cycling balance under global change scenarios. Carbon availability changes affect microbial carbon demand balance, thereby regulating other nutrient cycling processes. Continuous global nitrogen deposition increases have led to accumulation of reactive nitrogen in soils and changes in microbial substrate quality, inevitably disrupting microbial carbon demand balance. Future research should combine ecological stoichiometry and microbiology theory with field control experiments and laboratory incubations to systematically monitor microbial dynamic responses to carbon availability changes. This will provide theoretical references and data support for scientifically reasonable artificial regulation of carbon availability under global change scenarios.

3. **Optimization of carbon input strategies**: Explore appropriate carbon source types and input thresholds. When input carbon meets microbial carbon demand, excess external carbon will be consumed through microbial heterotrophic respiration. Excessive carbon input not only increases soil carbon emissions but also fails to achieve long-term improvement of soil carbon availability. Exploring scientifically sound input methods and quantities for different carbon sources, especially highly labile carbon sources, is scientifically and practically important for effectively avoiding increased greenhouse gas emissions that offset positive carbon sequestration effects.

References:

[1] Research Progress on Carbon Cycling in Terrestrial Ecosystems, 2001, 20(5): 564-575. [2] German DP, Chacon SS, Allison SD. Substrate concentration and enzyme allocation can affect rates of microbial decomposition. Ecology, 2011, 92(7): 1471-1480. [3] Kirkby CA, Richardson AE, Wade LJ, Batten GD, Blanchard C, Kirkegaard JA. Carbon-nutrient stoichiometry to increase soil carbon sequestration. Soil Biology and Biochemistry, 2013, 60: 77-86. [4] Rinnan R, Bååth E. Differential utilization of carbon substrates by bacteria and fungi in tundra soil. Applied and Environmental Microbiology, 2009, 75(11): 3611-3620. [5] Van Hees PAW, Jones DL, Finlay R, Godbold DL, Lundström US. The carbon we do not see—the impact of low molecular weight compounds on carbon dynamics and respiration in forest soils: a review. Soil Biology and Biochemistry, 2005, 37(1): 1-13. [6] Hamer U, Marschner B. Priming effects in soils after combined and repeated substrate additions. Geoderma, 2005, 128(1/2): 38-51. [7] Ilstedt U, Singh S. Nitrogen and phosphorus limitations of microbial respiration in a tropical phosphorus-fixing acrisol (ultisol) compared with organic compost. Soil Biology and Biochemistry, 2005, 37(7): 1407-1410. [8] Oyedele DJ, Schjønning P, Sibbesen E, Debosz K. Aggregation and organic matter fractions of three Nigerian soils as affected by soil disturbance and incorporation of plant material. Soil and Tillage Research, 1999, 50(2): 105-114. [9] Demoling F, Figueroa D, Bååth E. Comparison of factors limiting bacterial growth in different soils. Soil Biology and Biochemistry, 2007, 39(10): 2485-2495. [10] Reischke

S, Roussk J, Bååth E. The effects of glucose loading rates on bacterial and fungal growth in soil. Soil Biology and Biochemistry, 2014, 70: 88-95. [11] Daufresne T, Loreau M. Ecological stoichiometry, primary producer-decomposer interactions, and ecosystem persistence. Ecology, 2001, 82(11): 3069-3082. [12] Sirulnik AG, Allen EB, Meixner T, Allen MF. Impacts of anthropogenic N additions on nitrogen mineralization from plant litter in exotic annual grasslands. Soil Biology and Biochemistry, 2007, 39(1): 24-32. [13] Herbert DA, Williams M, Rastetter EB. A model analysis of N and P limitation on carbon accumulation in Amazonian secondary forest after alternate land-use abandonment. Biogeochemistry, 2003, 65(1): 121-150. [14] Hessen DO, Ågren GI, Anderson TR, Elser JJ, De Ruiter PC. Carbon sequestration in ecosystems: the role of stoichiometry. Ecology, 2004, 85(5): 1179-1192. [15] Ecological Stoichiometric Characteristics of Carbon, Nitrogen, and Phosphorus Elements in Ecosystems, 2008, 28(8): 3937-3947. [16] Effects of Nitrogen Deposition on Forest Soil Organic Matter and Litter Decomposition and Their Microbial Mechanisms, 2013, 33(5): 1337-1346. [17] Vitousek PM, Aber JD, Howarth RW, Likens GE, Matson PA, Schindler DW, Schlesinger WH, Tilman DG. Human alteration of the global nitrogen cycle: sources and consequences. Ecological Applications, 1997, 7(3): 737-750. [18] Emmett BA. Nitrogen saturation of terrestrial ecosystems: some recent findings and their implications for our conceptual framework. Water, Air, & Soil Pollution: Focus, 2007, 7(1/3): 99-109. [19] Aber J, McDowell W, Nadelhoffer K, Magill A, Bernston G, Kamakea M, McNulty S, Currie W, Rustad L, Fernandez I. Nitrogen saturation in temperate forest ecosystems. BioScience, 1998, 48(11): 921-934. [20] Magill AH, Aber JD, Bernston GM, McDowell WH, Nadelhoffer KJ, Melillo JM, Steudler P. Long-term nitrogen additions and nitrogen saturation in two temperate forests. Ecosystems, 2000, 3(3): 238-253. [21] Kopáček J, Cosby BJ, Evans CD, Hruška J, Moldan F, Oulehle F, Šantrůčková H, Tahovská K, Wright RF. Nitrogen, organic carbon and sulphur cycling in terrestrial ecosystems: linking nitrogen saturation to carbon limitation of soil microbial processes. Biogeochemistry, 2013, 115(1/3): 33-51. [22] Fontaine S, Bardoux G, Abbadie L, Mariotti A. Carbon input to soil may decrease soil carbon content. Ecology Letters, 2004, 7(4): 314-320. [23] Nottingham AT, Griffiths H, Chamberlain PM, Stott AW, Tanner EVJ. Soil priming by sugar and leaf-litter substrates: a link to microbial groups. Applied Soil Ecology, 2009, 42(3): 183-190. [24] Duong TTT, Baumann K, Marschner P. Frequent addition of wheat straw residues to soil enhances carbon mineralization rate. Soil Biology and Biochemistry, 2009, 41(7): 1475-1482. [25] Effects of Straw Return on Soil Organic Carbon Content and Soil Carbon Mineralization in the Arid Region of Southern Ningxia, 2011, 30(12): 2518-2525. [26] Effects of Straw Return on Soil Active Organic Carbon and Enzyme Activity in Dryland Wheat Fields of Southern Ningxia, 2011, 30(3): 522-528. [27] Li YY, Dong SK, Wen L, Wang XX, Wu Y. Soil carbon and nitrogen pools and their relationship to plant and soil dynamics of degraded and artificially restored grasslands of the Qinghai-Tibetan Plateau. Geoderma, 2014, 213: 178-184. [28] Stavast LJ, Baker TT, Ulery AL, Flynn RP, Wood MK, Cram DS. New Mexico blue grama rangeland response to dairy manure application. Rangeland Ecology & Management, 2005, 58(4): 423-429. [29] Effects of Continuous Multi-Year Straw Return on Physical and Chemical Properties and Microbial Biomass of Corn Tillage Layer Soil, 2011, 25(5): 81-85. [30] Jeffrey S, Verheijen FGA, Van Der Velde M, Bastos AC. A quantitative review of the effects of biochar application to soils on crop productivity using meta-analysis. Agriculture, Ecosystems & Environment, 2011, 144(1): 175-187. [31] Wheat in Dryland Farmland Under Conservation Tillage Conditions, Guangdi LI, Kwong Yin CHAN, Water Dynamics of Wheat-Soybean Double-Crop Rotation System and, 2006, 26(4): 1176-1185. [32] Effects of Reduced/No-Tillage and Straw Return on Extreme Soil Moisture and Winter Wheat Yield, 2010, 26(1): 41-46. [33] Effects of Straw Return and Nitrogen Fertilizer Management on Rice Nutrient Uptake, 2007, 23(7): 191-195. [34] Raich JW, Schlesinger WH. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. Tellus B, 1992, 44(2): 81-99. [35] Kuzyakov Y, Friedel JK, Stahr K. Review of mechanisms and quantification of priming effects. Soil Biology and Biochemistry, 2000, 32(11-12): 1485-1498. [36] Kuzyakov Y, Bol R. Sources and mechanisms of priming effect induced in two grassland soils amended with slurry and sugar. Soil Biology and Biochemistry, 2006, 38(4): 747-758. [37] Liang LL, Eberwein JR, Allsman LA, Grantz DA, Jenerette GD. Regulation of CO_2 and N_2O fluxes by coupled carbon and nitrogen availability. Environmental Research Letters, 2015, 10(3): 034008. [38] Tenua M, Mkhabela M, Tremorin D, Coppi L, Phipps G, Flaten D, Ominski K. Nitrous oxide and methane emission from a coarse-textured grassland soil receiving hog slurry. Agriculture, Ecosystems & Environment, 2010, 138(1/2): 35-43. [39] Effects on Soil Organic Carbon Sequestration, 2011, 30(11): 2362-2367. [40] Short-Term Effects of Altered Litter Input on Soil Respiration in Chinese Fir Plantations, 2009, 33(4): 739-747. [41] Paterson E, Sim A. Soil-specific response functions of organic matter mineralization to the availability of labile carbon. Global Change Biology, 2013, 19(5): 1562-1571. [42] Chemidlin-Prévost-Bouré N, Soudani K, Damesin C, Berveiller D, Lata JC, Dufresne E. Increase in aboveground fresh litter quantity over-stimulates soil respiration in a temperate deciduous forest. Applied Soil Ecology, 2010, 46(1): 26-34. [43] Sulzman EW, Brant JB, Bowden RD, Lajtha K. Contribution of aboveground litter, belowground litter, and rhizosphere respiration to total soil CO_2 efflux in an old-growth coniferous forest. Biogeochemistry, 2005, 73(1): 231-256. [44] Killham K. Soil Ecology. Cambridge, UK: Cambridge University Press, 1994: 89-106. [45] Stemmer M, Watzinger A, Blochberger K, Haberhauer G, Gerzabek MH. Linking dynamics of soil microbial phospholipid fatty acids to carbon mineralization in a 13C natural abundance experiment: impact of heavy metals and acid rain. Soil Biology & Biochemistry, 2007, 39(12): 3177-3186. [46] Paterson E, Osler G, Dawson LA, Gebbing T, Sim A, Ord B. Labile and recalcitrant plant fractions are utilised by distinct microbial communities in soil: independent of the presence of roots and mycorrhizal fungi. Soil Biology and Biochemistry, 2008, 40(5): 1103-1113. [47] Cahyani VR, Watanabe A, Matsuya K, Asakawa S, Kimura M. Succession of microbiota estimated by phospholipid fatty acid analysis and changes in organic constituents during the composting process of rice straw. Soil Science and Plant Nutrition, 2002, 48(5):

735-743. [48] Rantalainen ML, Kontiola L, Haimi J, Fritze H, Setälä H. Influence of resource quality on the composition of soil decomposer community in fragmented and continuous habitat. Soil Biology and Biochemistry, 2004, 36(12): 1983-1996. [49] Effects of Different Corn Straw Return Methods on Soil Respiration in Winter Wheat Fields, 2013, 24(5): 1374-1380. [50] Effects of Carbon Source Input on Soil Respiration in Chinese Pine Plantations, 2012, 32(9): 2768-2777. [51] Crow SE, Lajtha K, Bowden RD, Yano Y, Brant JB, Caldwell BA, Sulzman EW. Increased coniferous needle inputs accelerate decomposition of soil carbon in an old-growth forest. Forest Ecology and Management, 2009, 258(10): 2224-2232. [52] Effects of Litter Removal and Addition on Soil Respiration in Liquidambar formosana and Cinnamomum camphora Forests, 2009, 29(2): 643-652. [53] Prescott CE. Do rates of litter decomposition tell us anything we really need to know? Forest Ecology and Management, 2005, 220(1/3): 66-74. [54] Wan SQ, Norby RJ, Ledford J, Weltzin JF. Responses of soil respiration to elevated CO_2, air warming, and changing soil water availability in a model old-field grassland. Global Change Biology, 2007, 13(11): 2411-2424. [55] Sayer EJ, Tanner EVJ, Lacey AL. Effects of litter manipulation on early-stage decomposition and meso-arthropod abundance in a tropical moist forest. Forest Ecology and Management, 2006, 229(1/3): 285-293. [56] Kuzyakov Y, Hill PW, Jones DL. Root exudate components change litter decomposition in a simulated rhizosphere depending on temperature. Plant and Soil, 2007, 290(1/2): 293-305. [57] Chigineva NI, Aleksandrova AV, Tiunov AV. The addition of labile carbon alters litter fungal communities and decreases litter decomposition rates. Applied Soil Ecology, 2009, 42(3): 264-270. [58] Wu J, Brookes PC, Jenkinson DS. Formation and destruction of microbial biomass during the decomposition of glucose and ryegrass in soil. Soil Biology and Biochemistry, 1993, 25(10): 1435-1441. [59] Swift MJ, Heal OW, Anderson JM. Decomposition in Terrestrial Ecosystems. California, USA: University of California Press, 1979: 131-156. [60] Fontaine S, Mariotti A, Abbadie L. The priming effect of organic matter: a question of microbial competition? Soil Biology and Biochemistry, 2003, 35(6): 837-843. [61] Hobbie SE. Contrasting effects of substrate and fertilizer nitrogen on the early stages of litter decomposition. Ecosystems, 2005, 8(6): 644-656. [62] Research Progress on Carbon Cycling in Grassland Ecosystems, 2005, 13(S1): 67-73. [63] Effects of Full-Amount Corn Straw Return for Different Durations on Corn Growth and Soil Physical-Chemical Properties, 2012, 20(3): 291-296. [64] Effects of Different Tillage Methods and Straw Return on Soil Organic Carbon Content in Wheat Fields, 2010, 21(2): 373-378. [65] Qiao N, Schaefer D, Blagodatskaya E, Zou XM, Xu XL, Kuzyakov Y. Labile carbon retention compensates for CO_2 released by priming in forest soils. Global Change Biology, 2014, 20(6): 1943-1954. [66] Mclauchlan KK, Hobbie SE. Comparison of labile soil organic matter fractionation techniques. Soil Science Society of America Journal, 2004, 68(5): 1616-1625. [67] Characterization of Soil Active Organic Carbon and Its Ecological Effects, 1999, 18(3): 32-38. [68] Karlen DL, Rosek MJ, Gardner JC, Allan DL, Alms MJ, Bezdicek DF, Flock M, Huggins DR, Miller BS, Staben ML. Conservation reserve program effects on soil quality indicators. Journal of Soil and Water Conservation, 1999, 54(1):

439-444. [69] Jenkinson DS, Rayner JH. The turnover of soil organic matter in some of the Rothamsted classical experiments. Soil Science, 1977, 123(5): 298-305. [70] Dominant Influencing Factors of Soil Organic Carbon and Research Progress, 2005, 20(1): 99-105. [71] Fractionation and Determination Methods of Soil Active Organic Carbon, 2012, 28(5): 18-22. [72] Yan DZ, Wang DJ, Yang LZ. Long-term effect of chemical fertilizer, straw, and manure on labile organic matter fractions in a paddy soil. Biology and Fertility of Soils, 2007, 44(1): 93-101. [73] Nadelhoffer KJ, Boone RD, Bowden RD, Canary JD, Kaye J, Micks P, Ricca A, Aitkenhead JA, Lajtha K, McDowell WH. The DIRT experiment: litter and root influences on forest soil organic matter stocks and function. In: Foster DR, Aber JD, eds. Forests in Time: The Environmental Consequences of 1000 Years of Change in New England. New Haven: Yale University Press, 2004: 300-315. [74] Brant JB, Sulzman EW, Myrold DD. Microbial community utilization of added carbon substrates in response to long-term carbon input manipulation. Soil Biology and Biochemistry, 2006, 38(8): 2219-2232. [75] Tyler G. Effects of litter treatments on the sporophore production of beech forest macrofungi. Mycological Research, 1991, 95(9): 1137-1139. [76] Li YQ, Xu M, Sun OJ, Cui WC. Effects of root and litter exclusion on soil CO_2 efflux and microbial biomass in wet tropical forests. Soil Biology and Biochemistry, 2004, 36(12): 2111-2114. [77] Rinnan R, Michelsen A, Jonasson S. Effects of litter addition and warming on soil carbon, nutrient pools and microbial communities in a subarctic heath ecosystem. Applied Soil Ecology, 2008, 39(3): 271-281. [78] Sirra-Pietikäinen A, Haimi J, Kanninen A, Pietikäinen J, Fritze H. Responses of decomposer community to root-isolation and addition of slash. Soil Biology and Biochemistry, 2001, 33(14): 1993-2004. [79] Effects of Litter Addition on Soil Organic Carbon Mineralization and Soil Microbial Biomass in Agroforestry Systems, 2012, 32(22): 7239-7246. [80] Lemanski K, Scheu S. Incorporation of 13C-labeled glucose into soil microorganisms of grassland: effects of fertilizer addition and plant functional group composition. Soil Biology and Biochemistry, 2014, 69: 38-45. [81] Falchini L, Naumova N, Kuikman PJ, Bloem J, Nannipieri P. CO_2 evolution and denaturing gradient gel electrophoresis profiles of bacterial communities in soil following addition of low molecular weight substrates to simulate root exudation. Soil Biology and Biochemistry, 2003, 35(6): 775-782. [82] Chemidlin-Prevost-Bouré N, Maron PA, Ranjard L, Nowak V, Dufrene E, Damesin C, Soudani K, Lata JC. Seasonal dynamics of the bacterial community in forest soils under different quantities of leaf litter. Applied Soil Ecology, 2011, 47(1): 14-23. [83] Creamer CA, De Menezes AB, Krull ES, Sanderman J, Newton-Walters R, Farrell M. Microbial community structure mediates response of soil C decomposition to litter addition and warming. Soil Biology and Biochemistry, 2015, 80: 175-188.

Note: Figure translations are in progress. See original paper for figures.