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Variability of aboveground litter inputs alters soil physicochemical and biological processes: a meta-analysis of litterfall-manipulation experiments

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Abstract

Global change has been shown to greatly alter the amount of aboveground litter inputs to soil, which could cause substantial cascading effects on belowground biogeochemical cyling. Although having been studied extensively, there is uncertainty about how changes in aboveground litter inputs affect soil carbon and nutrient turnover and transformation. Here, we conducted a comprehensive compilation of 68 studies on litter addition or removal experiments, and used meta-analysis to assess the responses of soil physicochemical properties and carbon and nutrient cycling under changed aboveground litter inputs. Our results suggested that litter addition or removal could significantly alter soil temperature and moisture, but not soil pH. Litter inputs were more crucial in buffering soil temperature and moisture fluctuations in grassland than in forest. Soil respiration, soil microbial biomass carbon and total carbon in the mineral soil increased with increasing litter inputs, suggesting that soil acted as a net carbon sink although carbon loss and transformation increased with increasing litter inputs. Total nitrogen and the C : N ratio in the mineral soil increased with increased litter inputs. However, there was no correlation between litter inputs and extractable inorganic nitrogen in the mineral soil. Compared to other ecosystems, tropical and subtropical forests are more sensitive to variation in litter inputs. Increased or decreased litter inputs altered the turnover and accumulation of soil carbon and nutrient in tropical and subtropical forests more substantially over a shorter time period compared to other ecosystems. Overall, our study suggested that, although the magnitude of responses differed greatly among ecosystems, increased litter inputs generally accelerated the decomposition and accumulation of carbon and nutrients in soil, and decreased litter inputs reduced them.

1 Introduction

Aboveground litterfall is one of the most important components of carbon and nutrient cycling, and regulates soil microclimate by forming a buffering interface between the soil surface and the atmosphere (Sayer, 2006). Terrestrial ecosystems are undergoing simultaneous changes in climate and biogeochemical cycles, and those changes could affect plant net primary production (NPP) positively or negatively. Changes such as elevated CO_2 (King et al., 2005), nitrogen deposition (Xia and Wan, 2008), elevated temperature (Raich et al., 2006) were found to increase plant productivity, whereas elevated O_3 (Liu et al., 2005), drought (Zhao and Running, 2010) and acid deposition (Irving and Miller, 1981) generally decreased it. Those changes in primary production could alter both the quality and quantity of aboveground litter inputs to soil (Liu et al., 2005), and therefore physical, chemical and biological properties of the litter layer. In addition, extreme events, the frequencies of which may increase in the future, could also lead to a dramatic change in litter layer, such as a large increase in aboveground litter inputs after hurricane events (Ostertag et al., 2003), or rapid loss of litter layer after wild fire (Wardle et al., 2003).

As one of the most important carbon and nutrient fluxes to soil, changes in aboveground litter inputs could lead to cascading effects on belowground biogeochemical processes. Although changes in aboveground litter inputs have been observed in numerous global change manipulation experiments in multiple ecosystems, most of those studies found that total soil carbon (C) content was generally unchanged (Baer and Blair, 2008; Talhelm et al., 2009, but see Fornara and Tilman, 2012). For example, in the Aspen Free Air CO_2 Enrichment Experiment, elevated CO_2 increased aboveground litter inputs by 25 to 60 %, and elevated O_3 reduced it by 13 to 24 % (King et al., 2005). However, total soil C was not altered by either CO_2 or O_3 fumigation even after 11 yr of experimental treatments (Talhelm et al., 2009). In a tallgrass prairie restoration at Kansas, USA, eight years of N enrichment increased aboveground NPP (ANPP) by ∼ 48 %, but the high aboveground litter inputs did not cause significant changes in soil

C storage (Baer and Blair, 2008). Several mechanisms have been proposed to explain why soil C showed small changes even when aboveground litter inputs were greatly altered. One possible explanation is that soil C may be altered by litter inputs, but the changes are too small to be detected in the large and heterogeneous soil C pool (Hungate et al., 1996). The change in priming effect strength is another possible reason. High litter inputs could cause greater priming effects and the increase in new C from litter may be offset by the decomposition of older soil C (Sayer et al., 2011). Soil carbon saturation is also a plausible theory to explain the lack of changes in soil C content in response to varying levels of litter inputs. The theory states that the capacity of soil to stabilize organic C has an upper limit, which is determined by soil physical, chemical and biochemical characteristics (Six et al., 2002a).

An emerging view suggests that the majority of organic C in soil is derived from rhizodeposition, and aboveground litter inputs have a limited influence on soil C storage (Schmidt et al., 2011). The lack of changes in total soil C brings up a debate whether alteration in aboveground litter production caused by global change will lead to a meaningful change in the long term soil C storage. Quantification of the contribution of aboveground litter to soil C sequestration and nutrient cycling is therefore needed to assess the roles of aboveground litter in belowground processes.

A large number of litter manipulation experiments including litter addition and litter removal started as early as 1850s (Sayer, 2006). The information we draw from the rich research history of litter manipulation experiments could help us better understand how aboveground litter inputs affect belowground processes, and therefore the mechanisms regulating the potential of soil to sequester additional C. Belowground processes, such as soil respiration, microbial activity, and soil C formation are simultaneously influenced by litter inputs and these processes intrinsically interact with each other (Chapin et al., 2011). To quantitatively assess the consequences of aboveground litter inputs on soil physical, chemical and biochemical processes, we conducted a meta-analysis on litter manipulation experiments from multiple terrestrial ecosystems. The changes in litter productivity are often accompanied by changes in litter biochemistry, and the two interact with each other in biogeochemical processes (Liu et al., 2009a). However, because of data limitation on changes in litter biochemistry, this study focused on how changes in litter productivity affect belowground C and nutrient cycling.

2 Methods

2.1 Data selection

A comprehensive literature search, covering relevant peer reviewed articles and dissertations from 1950 to 2012, was conducted using the databases of Web of Science® and ProQuest. We also cross-checked the references of the relevant articles to identify other potential book chapters and peer reviewed reports. Only data from field litter manipulation experiments were included in our dataset. Studies were excluded if they were conducted in a controlled laboratory setting (e.g. Liu et al., 2009a) or the additional carbon was supplied as synthetic organic chemicals such as glucose (e.g. Park and Matzner, 2006) or cellulose (e.g. Fontaine et al., 2004). When data from multiple years were given in the literature, we only selected data from the last year. Litter-manipulation experimental sites were from multiple climatic zones, including arctic, boreal, temperate and (sub-)tropical regions (Supplement). Here, (sub-)tropical includes both tropical and sub-tropical regions.

Four categories of data related to belowground biotic and abiotic processes were extracted from the literatures on field litter-manipulation experiments: (1) soil surface physical and chemical properties, including soil temperature, soil moisture and soil pH; (2) microbial responses, including microbial biomass carbon (MBC) and microbial biomass nitrogen (MBN); (3) C fluxes and pools, including soil respiration, total carbon (C) and dissolved organic carbon (DOC); (4) nutrient fluxes and pools, including total nitrogen (N), C : N ratios (C : N), dissolved organic nitrogen (DON), extractable inorganic nitrogen (EIN), and extractable phosphorus (P). All variables, except soil respiration, were grouped by sampling depth as litter layer or mineral soil. In our dataset, litter layer data were all from studies conducted in boreal forest or temperate forest, including “forest floor” (Fisk and Fahey, 2001), “O horizon” (Nadelhoffer et al., 2004), “O layer” (Fröberg et al., 2005), “epihumus subhorizon” (Dzwonko and Gawronski, 2002), “humus horizon” (Dzwonko and Gawronski, 2002). Mineral soil in our dataset is defined as soil below the litter layer, or top soil from ecosystems such as grassland and (sub-)tropical forest. The sample depth of mineral soil ranged from 1 to 40 cm. When measurements were conducted in different mineral soil depths, we only used the data reported for the first depth (e.g. Tian et al., 2010). When data were graphically presented, we extracted the numerical values by digitizing the figures using Engauge Digitizer (Free Software Foundation, Inc., Boston, MA, USA).

2.2 Meta analysis

The data were analyzed using meta-analysis described by Hedges et al. (1999). The effect size of litter manipulation treatment for each individual observation was estimated by the natural log of response ratio (RR): $\ln \mathrm{RR} = \ln(\overline{X_t}/\overline{X_c})$, where $\overline{X_c}$ is the control mean, $\overline{X_t}$ is the treatment mean. The average response ratio (RR) was calculated using the mixed model of the meta-analytical software, METAWIN (Sinauer Associates, Inc. Sunderland, MA, USA). The variance of mean effect size was calculated using resampling techniques (Adams et al., 1997). If the lower bound of the 95 % CI of RR was larger than 1, then the response was significantly positive at $P < 0.05$. If the upper bound of the 95 % CI of RR was smaller than 1, then the response was significantly negative at $P < 0.05$. Total heterogeneity (Q_T) was partitioned into within-group (Q_W) and between-group (Q_B) heterogeneities. According to Hedges et al. (1999), a significant Q_B indicates that the response ratios differ among groups. Means of the groups were considered significantly different if their 95 % CI did not overlap.

2.3 Regression analysis

Most studies included in our dataset reported the amounts of litter added or removed. Data from both litter removal and litter addition experiments were grouped for each parameter, with negative values representing litter removal and positive values representing litter addition. The correlation between the response ratios of a biogeochemical parameter (RR) and the amounts of litter manipulation was determined by linear regression. All regression analyses were conducted with SAS software (SAS Institution Inc., Cary, NC).

3 Results

In total, 473 observations were collected from 68 publications, including ecosystems such as boreal forest (3 publications), temperate forest (23 publications), (sub-)tropical forest (16 publications), grassland (22 publications) and shrubland (4 publications; Supplement). Across all studies, the mean annual air temperature ranged from −4.2 to 27 °C, mean annual precipitation ranged from 315 to 5000 mm, and the experiments ranged in duration from half a year to 20 yr. Additional site characteristics are given in the Supplement.

3.1 Physical and chemical properties in the litter layer and mineral soil

Litter removal increased the temperature of the mineral soil by an average of 5 % across all ecosystems and litter addition decreased it by an average of 4 % (Table 1). When looking at different ecosystems, litter removal reduced the temperature of the mineral soil in (sub-)tropical forest, but increased it in temperate forest and grassland (Table 1). Litter addition induced a larger decrease in the temperature of the mineral soil in grassland than in temperate forest (Table 1).

Across all studies, litter removal decreased soil moisture in the mineral soil by an average of 10 % (Table 1). In contrast to litter removal, litter addition had no significant effect on soil moisture in the mineral soil (Table 1). However, when data were divided into ecosystem types, litter addition increased moisture in the mineral soil in grassland by an average of 13 % but had no significant effect in forests (Table 1).

Litter removal had no significant effect on soil pH in the litter layer or the mineral soil (Table 1). Overall, litter addition increased soil pH in the litter layer by an average of 2 %, but had no significant effect on pH in the mineral soil (Table 1).

3.2 Microbial responses

Litter removal decreased MBC in the litter layer and litter addition showed no significant effect (Table 2). Overall, litter removal reduced MBC in the mineral soil by an average of 39 %, with the mineral soil in (sub-)tropical forest showing a significantly greater decrease than in other ecosystems (Table 2). Litter addition increased MBC in the mineral soil by an average of 26 % (Table 2), with grassland showing a greater increase than the other ecosystems.

Litter removal reduced MBN in the mineral soil by an average of 18 % and litter addition significantly increased MBN in the mineral soil by an average of 46 % (Table 2). When data were divided into different ecosystems, MBN in the mineral soil in grassland showed a greater increase than in forest ecosystems (Table 2).

3.3 C cycling

Soil respiration rates decreased by an average of 37 % across all studies under litter removal and increased by an average of 37 % under litter addition (Table 2). The response ratio of soil respiration was positively correlated with the amounts of litter added or removed (Fig. 1a, $R^2 = 0.71$, $P < 0.01$) and with the response ratio of MBC (Fig. S3, $R^2 = 0.66$, $P < 0.01$).

All DOC data were from temperate forest. Litter removal reduced DOC concentrations in the litter layer by an average of 22 %, whereas the response of DOC concentrations in the mineral soil was not significant (Table 2). Litter addition increased DOC concentrations in the litter layer by an average of 67 %, but had no significant effect on DOC concentrations in the mineral soil (Table 2).

Litter removal decreased total C in the litter layer, whereas litter addition increased it (Table 2). However, the low number of published values of total C in the litter layer limited the statistical power of this analysis. Litter removal decreased total C in the mineral soil by an average of 12 % (Table 2). When data were divided into different ecosystems, litter removal induced a greater decrease in total C of the mineral soil in (sub-)tropical forest than that in temperate forest and grassland. Overall, litter addition increased total C in the mineral soil by an average of 15 %. When data were divided into different ecosystems, litter addition resulted in the largest increase in total C in the mineral soil in (sub-)tropical forest, but had no significant effect in grassland (Table 2). The effects of litter manipulation on C in the mineral soil also varied with soil depth. When data were divided into different sample depths, only the top 5 cm of the mineral soil showed significant response to litter manipulation, with litter addition increasing total C by 28 % and litter removal reducing it by 11 % (Table S1).

3.4 Nutrient cycling

The C : N ratio of the litter layer did not change under litter removal, but showed a significant increase under litter addition (Table 3). The C : N ratio of the mineral soil significantly decreased by an average of 6 % under litter removal, but did not change under litter addition (Table 3).

Litter removal reduced total N in the litter layer, but litter addition had no significant effect (Table 3). However, the low number of published values of total N in the litter layer limited the statistical power of this analysis. Overall, litter removal reduced total N in the mineral soil by an average of 14 %. When data were divided into different ecosystems, litter removal induced greater reductions in total N of the mineral soil in temperate and (sub-)tropical forests than that in grassland. Litter addition had no significant impact on total N in the mineral soil (Table 3).

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For both the litter layer and the mineral soil, the responses of DON to litter removal were not significant (Table 3). Litter addition increased DON in the litter layer by an average of 74 % but had no significant effect on DON in the mineral soil (Table 3).

Across all studies, EIN in the litter layer was significantly increased by an average of 103 % under litter removal whereas, EIN in the mineral soil was significantly decreased by an average of 28 % under litter removal (Table 3). Litter addition had no significant effect on EIN in the litter layer, but decreased it in the mineral soil (Table 3).

Across all studies, neither litter removal nor litter addition had significant effects on extractable P in the mineral soil (Table 3). When data were divided into different ecosystems, litter removal significantly decreased extractable P in the mineral soil in (sub-)tropical forest (Table 3).

3.5 The effects of litter manipulation levels on belowground processes

Regression analysis of the response ratio of the biogeochemical parameters (RR) and the amounts of litter inputs suggested that soil respiration, MBC in the mineral soil, total C in the litter layer and mineral soil, total N in the mineral soil, DOC in the litter layer, C : N ratio in the mineral soil, and DON in the litter layer all showed a positive linear relationship with litter inputs, whereas soil temperature and EIN in the litter layer showed a negative relationship with litter inputs (Fig. 1, Fig. S2). The regression models for each of the individual parameters are given in Table S3 and Fig. S2.

4 Discussion

Global change has been shown to significantly alter plant productivity, which leads to increased or decreased aboveground litter inputs to soil. These changes are expected to alter soil C stocks and nutrient supply. Yet to our surprise, only a few litter manipulation experiments have examined how variation in litter inputs affected belowground processes (e.g. Liu et al., 2009a; Sayer et al., 2011). A systematic synthesis of litter manipulation experiments is therefore important for better understanding the responses of belowground processes to varying inputs of aboveground litter under global change. Here we used meta-analysis to summarize the results of litter manipulation experiments conducted in different ecosystems, and examined how aboveground litter addition and removal affected soil physical and chemical properties, microbial activity, and carbon and nutrient cycling.

4.1 Physical and chemical properties in the litter layer and mineral soil

The litter layer acts as a protective interface between atmosphere and soil by regulating soil physicochemical conditions such as soil temperature, moisture and pH (Sayer, 2006). Results of our study suggested that the temperature of the mineral soil decreased with increasing litter inputs, whereas the water content of the mineral soil decreased under litter removal but did not respond to litter addition. The importance of aboveground litter in maintaining a stable soil microclimate differed among ecosystems. Litter inputs were more crucial in buffering mineral soil temperature and moisture fluctuations in grassland than in forest (Table 1). Forest canopies can intercept solar heat and precipitation by the large surface area of branches and foliage (Lowman and Schowalter, 2012), whereas the vegetation in grassland has a much shorter and simpler structure, and has limited capacity to intercept solar radiation and precipitation compared to the forest canopy. Grassland therefore relies more on surface litter to maintain a favorable soil environment (Amatangelo et al., 2008).

Litter inputs may change soil pH via changing the release of organic acids or the supply of exchangeable base cations during the processes of litter decomposition, and the direction of the change mainly depends on litter type and initial soil pH (Sayer, 2006). Overall, we found that litter manipulation had a small impact on soil pH. However, the non-significant response of soil pH under litter addition may be due to the opposite responses between forest and grassland. Litter addition tended to increase the soil pH of forest ecosystems, but decreased it in grassland, although the low number of published values limits confidence in the reported results (Table 1).

4.2 Microbial responses

It is generally accepted that microbes are C-limited and fresh litter can increase soil microbial biomass and activity. We found that litter addition significantly increased MBC in the mineral soil for all ecosystems (Table 2). Litter removal caused a general decrease in MBC and MBN in both the litter layer and the mineral soil. However, when divided into different ecosystems, only (sub-)tropical forest showed a significant reduction in MBC in the mineral soil under litter removal. One possible explanation for this is that microbes are more reliant on carbon supply from fresh litter in (sub-)tropical forest than in other ecosystems. The mean residence time (MRT) of surface litter in tropical forest is 0.25 to 1 yr, which is much shorter than the 4–16 yr MRT in temperate forest (Olson, 1963) and there is little or no build-up of an organic forest floor in lowland tropical forests (Wieder and Wright, 1995). Litter removal therefore induced a greater decline in microbial activities in (sub-)tropical forest because microbes did not have access to organic C from the forest floor as they did in temperate forest. The decrease in soil extractable P under litter removal (Table 3) is another possible cause. Microbial utilization of soil organic carbon is generally P limited in tropical forest (Cleveland et al., 2002). Litter removal decreased aboveground C supply for microbial growth, and simultaneously decreased soil extractable P in (sub-)tropical forest (Table 3), which may limit microbial decomposition of old soil organic carbon.

Microbial biomass is the living microbial component of the soil, and can be used as a bio-indicator for evaluating soil organic matter turnover rates (Wardle, 1992). We found that the response ratio of MBC was positively correlated with the response ratio of soil respiration, explaining 66 % of the variance in changes in soil respiration (Fig. S3). Although litter manipulation could also affect root respiration by altering root biomass (Sayer and Tanner, 2010), the high correlation between the responses of MBC and soil respiration suggest that the changes in soil respiration under litter manipulation are largely controlled by CO_2 efflux from heterotrophic respiration during litter decomposition.

4.3 C cycling

4.3.1 DOC

The DOC data included in our study all came from temperate forest. Our results suggested that although DOC of the litter layer in temperate forest responded substantially to litter manipulation, DOC of the mineral soil was insensitive to litter manipulation. This may be because DOC was quickly mineralized by soil microbial communities (Kalbitz et al., 2003) or absorbed by the soil mineral matrix associated with soil organic matter (Kaiser and Guggenberger, 2000). Increasing fresh litter inputs could cause priming effects and lead to an increase in DOC flux from decomposing old soil C (Kalbitz et al., 2007). However, our analysis cannot distinguish whether the increase of DOC in the litter layer was a result of fresh litter inputs or the decomposition of old organic C in forest floor due to the priming effect.

4.3.2 Total C

The processes and mechanisms underlying the influence of fresh litter inputs on soil C dynamics are complex, involving the balance between C input and output and the turnover among different C pools (Kuzyakov, 2011). Fresh litter inputs increase C and the energy supply to soil microbes, and can often cause priming effects. Several experiments have found that priming effects derived from fresh litter inputs had substantially accelerated soil organic matter turnover (Sulzman et al., 2005; Sayer et al., 2007, 2011), which leads to the speculation that soil C storage may be decreased under elevated litter inputs (Kuzyakov, 2010). However, the increase in new organic C may compensate for the release of older soil organic carbon (Talhelm et al., 2009; Hofmockel et al., 2011; Kuzyakov, 2011; Leff et al., 2012). We were unable to assess the strength of priming effects from our data but our results indicated that, although the response diminished with soil depth (Table S1), total C in the top mineral soil increased with increased litter inputs (Fig. 1c). This suggests that the soil acts as a net C sink,

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even though additional litter inputs will stimulate C loss via respiration and leaching as indicated by higher soil respiration rate and higher DOC concentrations in the litter layer.

Our results also suggested that soil C storage in different ecosystems responded differently to litter manipulation (Table 2). (Sub-)tropical forest was more responsive to changes in litter production than other ecosystems. Compared to other ecosystems, total C in the mineral soil in (sub-)tropical forest showed a greater reduction under litter removal and a greater increment under litter addition. Field experiments in (sub-)tropical forests also suggested that soil C showed a more rapid response to litter manipulation than other ecosystem: soil C concentrations were significantly increased by 31 % after only two years of litter addition in a tropical forest (Leff et al., 2012), while there was often no detectable change in soil C in temperate forest or grassland even after 5 to 11 yr of elevated litter inputs (Nadelhoffer et al., 2004; Baer and Blair, 2008; Talhelm et al., 2009). Three possible explanations for the notable responses of soil C in (sub-)tropical forest to litter manipulation are: (1) Litter manipulation experiments conducted in temperate or boreal biomes generally lasted from 2 to 8 yr (Fisk and Fahey, 2001; Fröberg et al., 2005; Sulzman et al., 2005), which was often shorter than the mean residence time of the litter (4–16 yr) in those ecosystems (Olson, 1963). A large proportion of the litter inputs therefore remains on the soil surface throughout the experiments in these ecosystems. However, in (sub-)tropical forest, most carbon from fresh litter is rapidly mineralized and respired or transferred to the mineral soil. (2) The mean residence time of soil aggregate C in tropical forest is shorter than that in temperate forest (Six et al., 2002b), and new C inputs can be integrated into soil aggregates more rapidly. (3) The tropical soils contain high clay content and easily combine leached litter-derived C into soil aggregates (Six et al., 2002a). Soil C concentration was therefore more likely to respond to altered litter inputs during the experimental period in (sub-)tropical forest (Leff et al., 2012).

In contrast to forest ecosystems, soil C in grassland showed no significant responses to either litter addition or litter removal. A growing number of studies have shown that solar radiation, especially ultraviolet radiation, can be a dominant driver controlling litter decomposition in arid and semiarid regions (Austin and Vivanco, 2006; Brandt et al., 2007). For example, in a semi-arid steppe, Austin and Vivanco (2006) found that around 60 % of C lost from aboveground litter was due to photochemical mineralization. The lack of response of total C in the mineral soil in grassland could be a consequence of the photodegradation of plant litter, which results in a large proportion of litter-derived C being lost directly to the atmosphere without entering the soil.

We would expect that total C changes in the mineral soil will become more pronounced with increased experimental duration. However, there were no significant differences in the responses of soil C pools to either litter addition or litter removal among studies with different experimental duration (Table S2). This lack of effect of experimental duration on soil C was probably due to the high variation in litter mineralization rates among biomes, as discussed above, making it difficult to detect an effect of experimental duration when comparing studies across ecosystems.

4.4 Nutrient cycling

Litter is an important carrier of nutrients from plants to soil, and the litter layer is critical for ecosystem nutrient retention. How soil nutrient fluxes and pools change under altered litter inputs could greatly affect soil fertility under global change. Our results suggested that total N and C : N ratios in the mineral soil increased with increased litter inputs. However, there was no correlation between EIN in the mineral soil and litter inputs. The lack of overall response of EIN to litter manipulation was mostly due to the opposite responses of EIN in (sub-)tropical forest and temperate forest. EIN in the mineral soil showed a positive correlation with litter inputs in (sub-)tropical forest, but a negative relation in temperate forest (Table 3). This may be because in (sub-)tropical forest, where litter decomposition is fast (Zhang et al., 2008), the N from the litter was quickly mineralized, and hence EIN increased with litter inputs. However, litter decomposition is much slower in temperate than in (sub-)tropical forest (Zhang et al., 2008), increased litter inputs could therefore increase the strength of immobilization and decrease EIN in the mineral soil.

Plant growth in tropical forest is generally P-limited, and litter is the dominant P source to soil (Cleveland et al., 2011). It is therefore not surprised to find that litter removal significantly reduced soil extractable P in the mineral soil in (sub-)tropical forest (Table 3). However, soil extractable P of the mineral soil did not increase under litter addition in (sub-)tropical forest. This can be due to that litter-derived P could be quickly absorbed by plant roots before entering the mineral soil (Stark and Jordan, 1978; Herrera et al., 1978; Attiwill and Adams, 1993), thus soil extractable P would not increase under litter addition. For example, Sayer and Tanner (2010) found that, after a 5-yr litter manipulation study, litter-derived P inputs significantly doubled under litter addition, but extractable P in the mineral soil did not change relative to the controls.

5 Conclusions

Global change not only alters the amount of aboveground litter inputs to soil, but also other factors regulating soil C cycling, such as litter chemistry, rhizodeposition and microbial activity (Liu et al., 2009a,b; Phillips et al., 2011). It is very difficult to separate the contribution of aboveground litter inputs to soil C and nutrient cycling from other drivers because the processes interact in complex ways. Litter manipulation experiments therefore provide valuable information to estimate the effects of litter production on soil organic C formation (Sayer et al., 2011). Our meta-analysis of litter manipulation experiments indicated that the changes in total C of the mineral soil and soil respiration showed a positive linear correlation with aboveground litter inputs, suggesting that soil acts as a C sink even though the C turnover rate is accelerated under increasing litter inputs. In contrast to the significant responses revealed in our meta-analysis, most individual litter manipulation experiments observed changes in total soil C, but those changes were often statistically non-significant (Xiao et al., 2007; Crow et al., 2009). In addition to the high spatial heterogeneity and slow formation of soil organic C, the failure to detect the changes in total soil C could be because changes in aboveground litter production caused by global change are much smaller than the litter manipulation levels in our dataset, which were often one to two times the ambient litter production (Supplement). It is reasonable to conjecture that an increase/decrease in aboveground litter will lead to increase/decrease in soil C storage if given enough time.

Our meta-analysis also suggested that the impact of changes in litter inputs upon belowground processes differed among ecosystems. Compared to boreal and temperate forests, (sub-)tropical forest was more sensitive to variation in litter inputs. Increases or decreases in litter inputs could therefore alter the turnover and accumulation of soil C and nutrient in (sub-)tropical forest more substantially in a shorter time period (Leff et al., 2012). The critical role of tropical forests in regulating atmospheric CO_2 has been widely recognized. However, much attention has focused on the vegetation C rather than tropical forest soil. A number of studies demonstrated that global change has stimulated ANPP in tropical forests over recent decades (Lewis et al., 2009; Pan et al., 2011). Although soil C accumulation may be lower than expected because of C release by priming effects (Sayer et al., 2011), we expect that tropical forest soils will act as a C sink alongside the increased ANPP under global change (Table 2). However, the current lack of long-term monitoring of tropical soil C dynamics makes it difficult to determine the sink strength of tropical forest soil for C.

Litter manipulation not only directly alters C and nutrient cycling by providing substrates to soil microbes, it also indirectly changes C cycling by modifying soil physiochemical conditions (Sayer, 2006), which is especially important in grassland (Wang et al., 2011). Although litter addition showed small impacts on soil C storage in grassland, our analysis suggested that aboveground litter inputs play a critical role in maintaining favourable soil conditions by buffering soil temperature and moisture. For example, a litter manipulation study in a typical steppe found that litter removal led to warmer and drier soil conditions and thus lower ANPP, whereas litter addition brought about the opposite results (Wang et al., 2011).

The changes in litter production caused by environmental change could lead to cascading effects on soil physicochemical properties, and C and nutrient cycling. Except for a few parameters, such as DIN in temperate and tropical forests, the directions of the responses were similar among terrestrial ecosystems for the investigated parameters, but the response magnitudes varied greatly. Overall, our study suggests that increases in litter inputs generally accelerated the rates of belowground biogeochemical responses and transformations, and decreases in litter inputs reduced them.

Supplementary material related to this article is available online at: http://www.biogeosciences-discuss.net/10/5245/2013/ bgd-10-5245-2013-supplement.zip.

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Table 1. Effects of litter removal and litter addition on soil physicochemical properties of different ecosystems.

			Litter removal			Litter addition		
Response variable	Soil layer	Group	RR	95 % CI	*n*	RR	95 % CI	*n*
Soil temperature	Mineral soil	All	**1.05**	**1.01–1.09**	17	**0.96**	**0.91–0.99**	8
		Temperate forest	**1.01^{a}**	**1.00–1.02**	2	0.99^{a}	0.97–1.01	3
		(Sub-)tropical forest	**0.99^{b}**	**0.98–1.00**	7	–	–	–
		Grassland	**1.11^{c}**	**1.05–1.19**	7	**0.92^{b}**	**0.86–0.97**	4
Soil moisture	Mineral soil	All	**0.90**	**0.83–0.95**	32	1.04	0.99–1.09	32
		Temperate forest	**0.86^{a}**	**0.70–0.98**	8	0.96^{a}	0.90–1.03	12
		(Sub-)tropical forest	**0.94^{a}**	**0.89–0.99**	15	1.03^{ab}	0.97–1.09	3
		Grassland	**0.82^{a}**	**0.66–0.95**	6	**1.13^{b}**	**1.06–1.20**	11
		Shrubland	0.99^{a}	0.86–1.15	2	1.05^{ab}	0.92–1.21	6
Soil pH	Litter layer	All	1.00	0.97–1.03	9	**1.02**	**1.01–1.02**	**2**
		Boreal forest	1.00^{a}	0.96–1.05	6	–	–	–
		Temperate forest	**1.01^{a}**	**1.00–1.01**	**3**	**1.02**	**1.01–1.02**	**2**
	Mineral soil	All	1.00	0.98–1.03	11	1.04	0.99–1.09	7
		Temperate forest	**0.94^{a}**	**0.91–0.98**	2	**1.10^{a}**	**1.08–1.12**	2
		(Sub-)tropical forest	1.02^{b}	0.99–1.03	8	**1.07^{a}**	**1.01–1.15**	2
		Grassland	–	–	–	**0.98^{b}**	**0.97–0.99**	3

Notes: RR, the mean response ratio; 95 % CI, 95 % confident intervals; *n*, no. observations; "–", no data. Significant differences between groups are denoted by lowercase superscript letters.

Table 2. Effects of litter removal and litter addition on soil carbon cycling parameters of different ecosystems. The notation is the same as Table 1.

			Litter removal			Litter addition		
Response variable	Soil layer	Group	RR	95 % CI	*n*	RR	95 % CI	*n*
MBC	Litter layer	All	**0.77**	**0.54–0.96**	3	1.29	0.99–1.68	2
		Temperate forest	**0.68**	**0.54–0.88**	2	1.29	0.99–1.68	2
	Mineral soil	All	**0.61**	**0.48–0.76**	17	**1.26**	**1.17–1.36**	23
		Temperate forest	0.71^{a}	0.36–1.07	4	**1.18**^{ab}	**1.02–1.35**	2
		(Sub-)tropical forest	**0.51**^{a}	**0.39–0.66**	10	**1.08**^{a}	**1.03–1.14**	2
		Grassland	0.86^{a}	0.64–1.01	3	**1.34**^{b}	**1.22–1.49**	15
		Shrubland	–	–	–	**1.12**^{a}	**1.05–1.17**	4
MBN	Mineral soil	All	**0.82**	**0.74–0.91**	4	**1.46**	**1.21–1.77**	10
		(Sub-)tropical forest	**0.82**	**0.75–0.89**	2	1.07^{a}	0.98–1.17	2
		Grassland	–	–	–	**1.82**^{b}	**1.57–2.11**	6
		Shrubland	–	–	–	1.03^{a}	0.96–1.11	2
Soil respiration		All	**0.63**	**0.54–0.72**	23	**1.37**	**1.27–1.47**	22
		Temperate forest	**0.63**^{a}	**0.49–0.77**	11	**1.38**^{a}	**1.22–1.57**	7
		(Sub-)tropical forest	**0.62**^{a}	**0.49–0.77**	9	**1.45**^{a}	**1.23–1.74**	3
		Grassland	**0.68**^{a}	**0.53–0.91**	3	**1.35**^{a}	**1.21–1.48**	12
DOC	Litter layer	Temperate forest	**0.78**	**0.67–0.87**	7	**1.67**	**1.43–1.98**	14
	Mineral soil	All	0.75	0.58–1.02	6	1.03	0.73–1.41	9
		Temperate forest	0.81	0.59–1.09	5	0.98	0.69–1.40	8
Total C	Litter layer	Temperate forest	**0.95**	**0.94–0.96**	2	**1.09**	**1.04–1.17**	3
	Mineral soil	All	**0.88**	**0.82–0.95**	22	**1.15**	**1.07–1.23**	26
		Temperate forest	0.91^{ab}	0.78–1.06	8	**1.16**^{a}	**1.04–1.30**	15
		(Sub-)tropical forest	**0.77**^{a}	**0.72–0.84**	6	**1.38**^{b}	**1.31–1.49**	3
		Grassland	0.94^{b}	0.86–1.06	8	1.03^{a}	0.99–1.10	6
		Shrubland	–	–	–	**1.03**^{a}	**1.01–1.05**	2

Table 3. Effects of litter removal and litter addition on soil nutrient cycling parameters of different ecosystems. The notation is the same as Table 1.

			Litter removal			Litter addition		
Response variable	Soil layer	Group	RR	95 % CI	*n*	RR	95 % CI	*n*
C : N	Litter layer	All	0.99	0.94–1.03	9	**1.24**	**1.04–1.66**	4
		Boreal forest	0.98^{a}	0.91–1.05	6	–	–	–
		Temperate forest	0.99^{a}	0.98–1.01	3	**1.24**	**1.04–1.66**	4
	Mineral soil	All	**0.94**	**0.90–0.98**	9	1.03	0.99–1.07	17
		Temperate forest	0.94^{a}	0.89–1.00	6	1.02^{bc}	0.97–1.07	11
		(Sub-)tropical forest	**0.94^{a}**	**0.93–0.96**	2	**1.14^{a}**	**1.10–1.18**	2
		Grassland	–	–	–	0.99^{b}	0.97–1.01	2
		Shrubland	–	–	–	**1.06^{c}**	**1.03–1.09**	2
Total N	Litter layer	Temperate forest	**0.92**	**0.91–0.92**	2	0.84	0.62–1.02	3
	Mineral soil	All	**0.86**	**0.80–0.93**	16	1.07	0.99–1.15	23
		Temperate forest	**0.85^{ab}**	**0.75–0.94**	8	1.08^{a}	0.97–1.21	14
		(Sub-)tropical forest	**0.80^{a}**	**0.79–0.81**	4	**1.24^{b}**	**1.23–1.26**	2
		Grassland	0.94^{b}	0.85–1.16	4	1.07^{a}	0.99–1.18	3
		Shrubland	–	–	–	0.93^{a}	0.83–1.02	4
DON	Litter layer	Temperate forest	1.08	0.88–1.24	4	**1.74**	**1.54–1.99**	4
	Mineral soil	All	1.00	0.79–1.25	6	1.19	0.90–1.52	13
		Temperate forest	1.00	0.79–1.25	6	1.20^{a}	0.88–1.61	11
		Shrubland	–	–	–	1.16^{a}	0.92–1.47	2
EIN	Litter layer	Temperate forest	**2.03**	**1.33–3.44**	6	1.24	0.91–1.70	7
	Mineral soil	All	**0.72**	**0.55–0.96**	13	**0.78**	**0.61–0.99**	12
		Temperate forest	1.15^{a}	0.75–1.64	5	**0.73^{a}**	**0.56–0.96**	10
		(Sub-)tropical forest	**0.47^{b}**	**0.38–0.58**	6	**1.08^{b}**	**1.07–1.10**	2
		Grassland	**0.78^{a}**	**0.77–0.79**	2	–	–	–
Extractable P	Mineral soil	All	0.82	0.65–1.04	7	1.16	0.98–1.47	5
		Temperate forest	1.09^{a}	0.84–1.43	2	1.07^{a}	0.96–1.19	2
		(Sub-)tropical forest	**0.71^{a}**	**0.54–0.94**	4	1.01^{a}	0.96–1.07	2

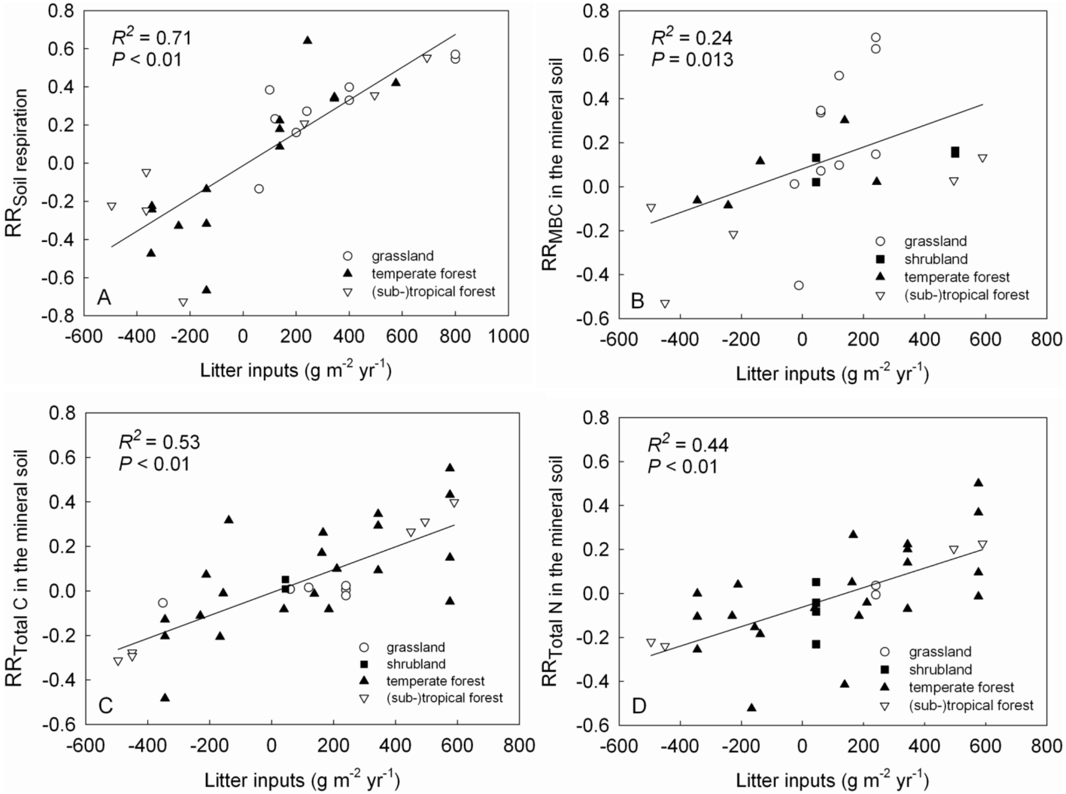

Fig. 1. Relationships between the amounts of litter manipulation and the response ratios (RR) of **(A)** soil respiration; **(B)** MBC in the mineral soil; **(C)** total C in the mineral soil; **(D)** total N in the mineral soil.

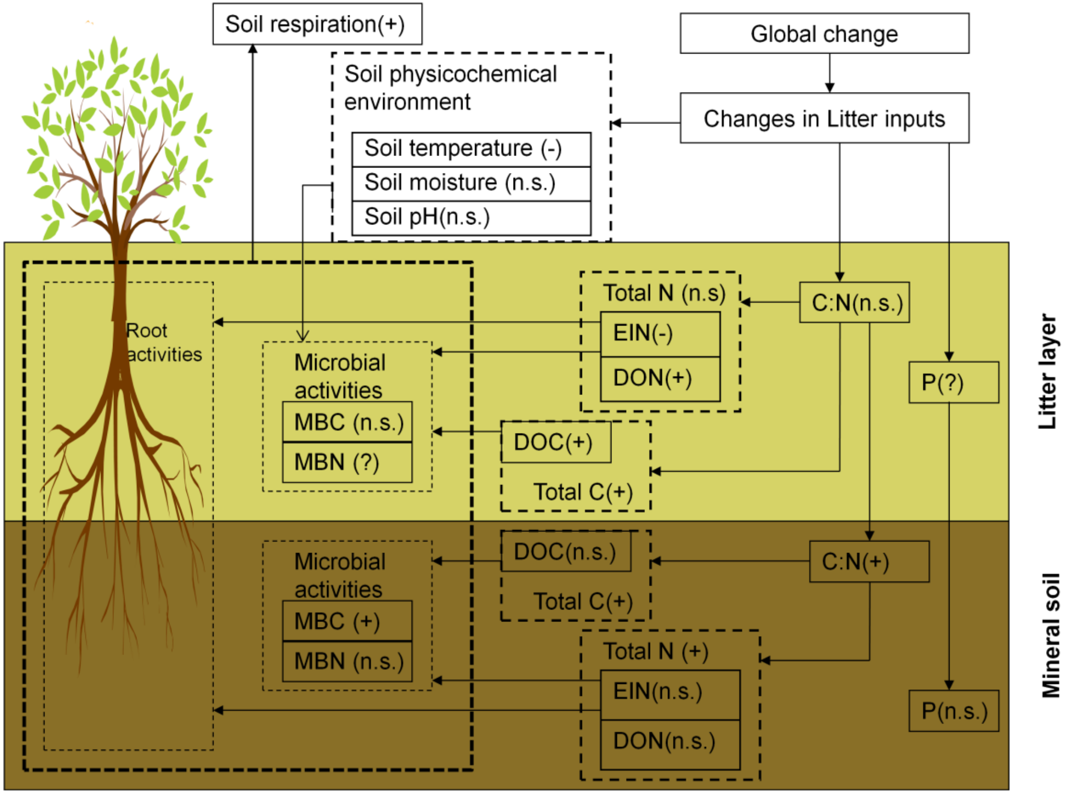

Fig. 2. The response of soil carbon and nutrient cycling to changes in litter inputs. The relationship between the response ratio of each parameter and the amounts of litter manipulation is shown in parentheses. "+" indicates a significant positive linear correlation; "–" indicates a significant negative linear correlation; n.s. is non-significant; "?" indicates an unknown relationship because of data limitation.