Plant Soil (2014) 379:217–229
DOI 10.1007/s11104-014-2033-9

REGULAR ARTICLE

Interactions between leaf litter and soil organic matter on carbon and nitrogen mineralization in six forest litter-soil systems

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Received: 2 September 2013 / Accepted: 9 January 2014 / Published online: 26 February 2014

Abstract
Background and aims Leaf litter decomposes on the surface of soil in natural systems and element transfers between litter and soil are commonly found. However, how litter and soil organic matter (SOM) interact to influence decomposition rate and nitrogen (N) release remains unclear.
Methods Leaf litter and mineral soil of top 0–5 cm from six forests were incubated separately, or together with litter on soil surface at 25 °C for 346 days. Litter N remaining and soil respiration rate were repeatedly measured during incubation. Litter carbon (C) and mass losses and mineral N concentrations in litter and soil were measured at the end of incubation.
Results Net N transfer from soil to litter was found in all litters when incubated with soil. Litter incubated with soil lost more C than litter incubated alone after 346 days. For litters with initial C: N ratios lower than 52, net N_{min} after 346 days was 100 % higher when incubated with soil than when incubated alone. Litter net N_{min} rate was negatively related to initial C: N ratio when incubated with soil but not when incubated alone. Soil respiration rate and net N_{min} rate did not differ between soil incubated with litter and soil incubated alone.
Conclusions We conclude that soils may enhance litter decomposition rate by net N transfer from soil to litter. Our results together with studies on litter mixture decomposition suggest that net N transfer between decomposing organic matter with different N status may be common and may significantly influence decomposition and N release. The low net N_{min} rate during litter decomposition along with the small size of litter N pool compared to soil N pool suggest that SOM rather than decomposing litter is the major contributor to plant mineral N supply.

Keywords Litter decomposition · N release · N transfer · N immobilization · Stoichiometry

Responsible Editor: Stefano Manzoni.

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Introduction

In natural systems, litter decomposes on the surface of soil, and C and nutrient transfer (such as N, P, S and base cations) between litter and soil through fungal hyphae are commonly found (Frankland et al. 1990; Wells and Boddy 1995; Connolly and Jellison 1997; Frey et al. 2000). Filamentous fungi are able to utilize spatially

separated resources in a heterogeneous environment due to their extensive hyphal networks. The litter-soil systems represent a good example of such resource heterogeneity. Fresh litter is well known to be N limited due to the high C concentration and low N concentration, and the reverse is true for soils (Demoling et al. 2007; Berg and McClaugherty 2008). Therefore, net N transfer from soil to litter is commonly found, evidenced by the increased total litter N content (i.e. N immobilization) during litter decomposition (Parton et al. 2007; Li and Fahey 2013). The amount of net N transfer from soil to litter can be up to 150 % of initial litter N content (Parton et al. 2007; Manzoni et al. 2008). By contrast, transfer of C from litter to soil by fungi is often found. For example, incubations of 1.3 g ^{13}C-labeled plant residues with 150 g soil for 5 weeks resulted in the transfer of litter C to soil through fungal hyphae, which amounted to 4.7 % of total soil C (Frey et al. 2003).

Substantial C and N transfers between litter and soil may change the availability of C and N to decomposing microbes on the recipient and thus influence decomposition rate and N release rate of litter-SOM systems. Labile C addition is known to have a stimulating effect on SOM decomposition, namely priming effect which is partly induced by enhanced microbial turnover and altered microbial community (Kuzyakov et al. 2000; Fontaine et al. 2007; Cheng 2009). On the other hand, N addition has been reported to increase litter decomposition rate due to balanced C and N availability for decomposing microbes (Hobbie and Vitousek 2000; Liu et al. 2010). According to stoichiometry theory, microbial growth and biomass production require a balance among elements (i.e. C, N, P, etc.), therefore, the relative abundance of C and nutrients in detritus should regulate microbial activity and thus influence litter decomposition rate (Sterner and Elser 2002; Cleveland and Liptzin 2007). Enhanced decomposition rate and net N_{min} rate were commonly found in litter mixtures compared with litter decaying alone, which was primarily due to C and N transfers from litters rich in these elements to litters with low concentrations (Finzi and Canham 1998; Gartner and Cardon 2004; Song et al. 2010). However, it remains unclear whether the modified C and N availability due to C and N transfers between litter and soil affects the decomposition rates and N release patterns of litter-SOM systems.

Plants acquire mineral N from microbe-mediated decomposition of litter and more stabilized SOM. However, the relative contribution of litter decomposition vs. SOM decomposition in plant mineral N supply is unclear. It has been hypothesized that mineral N release during litter decomposition is an important source of plant N uptake such that species differences in litter decomposition rate may drive a positive feedback between plant species and soil N availability (Aerts and Chapin 2000; Ehrenfeld et al. 2005; Berendse and Scheffer 2009). However, increasing evidence shows that N release in litter decomposition may be limited. Studies using ^{15}N labeled foliar litter showed that only 3 %–20 % of litter-derived N was taken up by plants even after 2–3 years of decomposition (Zeller et al. 2000; Piatek 2011). Therefore, there may be a long time lag between litter decomposition and actual litter N release, which occurs only after litter decomposition has proceeded into the late stage and litter is converted into more stable SOM. The slow rate of N release from rapidly decomposing litter and the small size of litter N pool relative to soil N pool at the global scale suggest that immediate plant-soil N feedbacks through litter decomposition may be less important than previously thought, and that SOM decomposition may be the bottleneck of plant N supply (Knops et al. 2002, 2010).

The assumption of immediate plant uptake of litter N partly rests on the evidence that rapid litter N loss occurs simultaneously with mass loss during decomposition (Singh et al. 1999; Osono and Takeda 2004; Decker and Boerner 2006). However, litter net N_{min} during decomposition is not measured in most cases (Parton et al. 2007; Manzoni et al. 2008). The total litter N loss differs from litter net N_{min} because transport of litter fragments into the underlying soil by leaching or soil faunal activities under field conditions represents an important reason for litter mass loss and N loss. Studies attempting to measure these losses showed that the fraction of litter C lost to soil as organic residues may be twice as much as the fraction released as CO_2 to the atmosphere (Rubino et al. 2010). Therefore, litter mass loss and N loss from field litter decomposition studies may overestimate actual C and N mineralization (Prescott 2005). Amounts of N release during litter decomposition should be estimated as net N_{min} but not total N loss.

In this study, we incubated litter and soil samples from six forests across China separately and together for 346 days and measured C mineralization and net N_{min} of litter and soil. We hypothesized that: (1) litter incubated with soil would decompose faster than litter

incubated alone due to net N transfer from soil to litter that relieves microbial C : N stoichiometric imbalance during litter decomposition (Frey et al. 2000; Berg and McClaugherty 2008); (2) litter net N_{min} rate would be low and would not be related to decomposition rate due to strong microbial N immobilization (Knops et al. 2002); (3) soil incubated with litter would have higher respiration rates than soil incubated alone due to the transfer of C from litter to soil which induces a priming effect (Frey et al. 2000; Fontaine et al. 2007); and (4) soil net N_{min} rate would be related to C mineralization rate due to more balanced ratios of C and N in SOM (Weintraub and Schimel 2003).

Materials and Methods

Litter and soil sampling

Leaf litters and soils were sampled from six forests ranging from subtropical to boreal areas in China (Table 1). Two forests were selected from subtropical, temperate and boreal areas, respectively, one coniferous and the other broadleaved (or broadleaf-dominated). Except for the Heshan site in the subtropical area which was a 30-year old plantation, the other five forests were natural and mature with ages ranging from 50 to 400 years. Studied litter species dominated each forest. Fresh leaf litter was collected with litter traps during October to November in 2010 from an area of 1 hm^2 in each forest, and air-dried for 1 month. Twenty cores (5 cm in diameter and depth) of top 0–5 cm mineral soil were randomly sampled from the same area as litter sampling in each forest in late August and pooled as a composite sample. The soils were air-dried for 2 weeks and then sieved through 2 mm mesh to exclude roots and rocks. The initial C and N concentrations and C : N ratios of studied soils and litters, initial soil and litter inorganic N concentrations and soil pH were shown in Table 2 (n=3).

Microcosms and incubation

Microcosms were made of capped PVC pots that were 13 cm in diameter and 5.3 cm in height. Litter and soil samples from each forest were assigned to three treatments: litter incubated alone, soil incubated alone and litter incubated on the surface of soil. A set of 72 microcosms (3 treatments×4 replicates×6 forests) were set up for year-long incubation. Additional 72

Table 1 Characteristics of the six forests where leaf litter and soil were sampled

Site	Heshan	Dinghushan	Changbaishan	Changbaishan	Mohe	Genhe
Location	22°41′N, 112°54′E	23°10′N, 112°10′E	42°12′N, 128°32′E	42°12′N, 128°32′E	53°33′N, 122°27′E	50°49′N, 121°31′E
Forest type	Pure conifer plantation	Natural evergreen broadleaf mixture	Natural conifer mixture	Natural broadleaf-conifer mixture	Natural pure conifer	Natural secondary pure broadleaf
Forest age	years	400 years	200–300 years	200–300 years	> 80 years	~ 50 years
Mean annual temperature	21.7 °C	21.0 °C	3.5 °C	3.5 °C	−5.5 °C	−5.4 °C
Mean annual precipitation	1801 mm	1927 mm	700 mm	700 mm	431 mm	424 mm
Soil type	Acrisol	Acrisol	Haplic Luvisol	Haplic Luvisol	Humic Cambisol	Humic Cambisol
Soil texture	Sandy clay loam	Silt loam	Loam	Sandy loam	Loam	Loam
Litter species sampled	*Pinus massoniana*	*Schima wallichii* and *Castanopsis chinensis*	*Pinus koraiensis*	*Phellodendron amurense*	*Pinus sylvestris* var. mongolica	*Betula platyphylla*

Table 2 Initial chemical properties of studied soil and litter, and characteristics of microcosms

	PM	SW+CC	PK	PA	PS	BP
Soil C (%)	2.97 (0.18)^{d}	5.08 (0.16)^{c}	6.47 (0.28)^{b}	6.41 (0.03)^{b}	5.49 (0.04)^{c}	8.50 (0.12)^{a}
Soil N (%)	0.17 (0.016)^{e}	0.32 (0.009)^{bc}	0.30 (0.009)^{c}	0.56 (0.007)^{a}	0.25 (0.003)^{d}	0.34 (0.006)^{b}
Soil C : N ratio	17.7 (1.4)^{c}	15.6 (0.6)^{c}	21.8 (0.3)^{b}	11.5 (0.2)^{d}	22.0 (0.3)^{b}	25.0 (0.8)^{a}
Soil IN (mg/kg)	34.1 (2.0)^{a}	38.5 (2.6)^{a}	19.4 (0.005)^{b}	34.3 (0.5)^{a}	12.9 (0.9)^{b}	19.7 (5.5)^{b}
Soil pH	3.9 (0.01)^{e}	3.7 (0.01)^{f}	4.6 (0.02)^{c}	5.5 (0.02)^{b}	5.7 (0.36)^{a}	4.0 (0.03)^{d}
Litter C (%)	51.6 (0.14)^{a}	51.3 (0.42)^{a}	51.5 (0.19)^{a}	44.1 (0.14)^{c}	52.3 (0.65)^{a}	49.5 (0.36)^{b}
Litter N (%)	1.01 (0.04)^{b}	1.09 (0.05)^{b}	0.48 (0.05)^{d}	1.35 (0.06)^{a}	0.58 (0.03)^{d}	0.81 (0.03)^{c}
Litter C : N ratio	51.1 (2.08)^{c}	47.2 (1.76)^{cd}	109.9 (11.4)^{a}	32.9 (1.5)^{d}	90.9 (3.5)^{b}	61.3 (2.7)^{c}
Litter IN (mg/kg)	120.0 (1.0)^{a}	56.7 (9.67)^{b}	26.7 (16.7)^{c}	26.7 (13.3)^{c}	6.67 (4.3)^{d}	3.33 (0.5)^{d}
Soil C : litter C	1.9	3.3	4.1	4.9	3.5	5.7
Soil N : litter N	5.6	9.8	20.8	13.8	14.4	14.0
Soil moisture during incubation (%)	31.7(2.4)^{d}	41.7(1.7)^{bc}	50.1(2.2)^{a}	47.1(2.8)^{b}	38.4(1.1)^{c}	52.0(2.0)^{a}

Litter codes: PM (*Pinus massoniana*), SW+CC (*Schima wallichii* mixed with *Castanopsis chinensis*), PK (*Pinus koraiensis*), PA (*Phellodendron amurense*), PS (*Pinus sylvestris*) and BP (*Betula platyphylla*). Soil code is the same as the litter code in each forest. Soils or litters followed by different letters were significantly different at 0.05 level

Data are means (SE), n=3

microcosms (4 replicates×6 forests×3 sampling times) were set up for the treatment of litter incubated with soil, which were used for destructive samplings at 73 days, 138 days and 240 days after incubation for measurement of litter N remaining. Three grams of litter were put in a 2 mm-meshed nylon litterbag (12 cm in diameter) and placed on 100 g quartz sand (litter incubated alone) or on 100 g soil (litter incubated with soil). For soil incubated alone, 100 g soil was put in the microcosm. The ratios of soil C to litter C (1.9–5.7) and soil N to litter N (5.6–20.8) in microcosms (Table 2) were comparable to those in the field, because the organic matter pool and N pool in litter layer were one third and one eighth of the pools in soil, respectively, on average of 16 temperate and boreal forests (Cole and Rapp 1981; Knops et al. 2010). To initiate incubation, water content in quartz sand or soil was adjusted to 50 % of water-holding capacity, and de-ionized water was added monthly during incubation to keep the initial soil moisture content (Table 2). To prevent litter leaching, water was added to microcosms along the walls of the pots. Litter in each microcosm (whether incubated alone or with soil) was inoculated with microbes by spraying 5 ml of soil suspension over the litterbag. The soil suspension (of each forest) was prepared by dispersing 100 g soil in 500 ml de-ionized water and letting sit for 5 min before use. All microcosms were incubated at 25ºC throughout the experiment. The lid of each pot was fitted with a three-way stopcock (T-shaped) to keep the microcosm aerobic inside during incubation, and used for gas sampling during respiration measurement (as described below).

Respiration rate measurement

Soil respiration rate was measured at an interval of 6–8 days in the first month when respiration rate was high and changed rapidly, and at an interval of 20–50 days later on when respiration rate decreased to a relatively stable level. There were 13 gas samplings in total. Before gas sampling, the pots were open without lids and placed under a fuming hood for 10 min for complete gas exchange. During gas sampling, the pots were capped with lids and sealed with the three-way stopcocks. Headspace gas of 5 ml was collected using syringes fitted with a three-way stopcock at 0 min and 60 min (in the first 2 months when respiration rate was high) or 120 min (from the third month when respiration rate decreased to a low level) after pot sealing, assuming that the CO_2 concentration inside the pot increased linearly during pot sealing (Karhu et al. 2010; Wetterstedt et al. 2010). The linear increase of CO_2 concentration was tested on the day of our first measurement of respiration rate by taking gas samples at 0 min, 30 min and 60 min after pot sealing (data not shown). For pots with litter incubated with soil, the litterbags were taken out of the pots and gas samplings were taken for measurement of soil respiration

rate. After gas sampling, litterbags were put back to the pots. The CO_2 concentration in the gas samples was analyzed within 24 h with a gas chromatograph (HP 5890, Agilent Technologies), which was equipped with a flame ionization detector (FID) for CO_2 analysis. Four milliliters of sample gas were injected into the chromatograph, using pure N_2 (99.999 %) as the carrier gas and the concentration of the standard CO_2 was 417 ppmv.

Chemical analyses and calculations

After 346 days of incubation, litter in each microcosm was divided into two portions, one for the measurements of mass and total C and N, the other for the measurement of inorganic N concentration. The portion for the measurements of litter mass and total C and N was oven-dried at 60 °C to a constant weight and weighed before and after drying. Then the oven-dried litter was ground into powder for measurements of total C and N concentrations with an elemental analyzer (Vario EL, Elementar Analysensysteme GmbH, Germany). Inorganic N (NH_4^+, NO_3^-) concentrations of litter and soil were measured by extracting samples with 0.5 M K_2SO_4 followed by analyses with an autoanalyzer (BranLubee, Germany). Soil pH was measured with a 1:2.5 (w/v) ratio of soil to de-ionized water using a pH meter.

Litter decomposition rate was indicated by litter C loss or mass loss rate, and was calculated as the percent of total initial C or mass lost during incubation. Litter N_{min} rate was indicated as the percent of mineralized N (difference of litter inorganic N before and after incubation) in litter initial total N. Litter N immobilization rate was calculated as the percent increase of litter total N after incubation compared to initial total N. Litter net N_{min} rate was calculated as the difference of litter N_{min} rate and litter N immobilization rate. To calculate soil cumulative C mineralization, we assumed that the averaged soil respiration rate of the first 6 days was the same as the respiration rate at the first sampling date (6 days after incubation was initiated). This was done as the soil respiration rate of the first 6 days should have experienced a transition from a low level (at the beginning) to a pulse (immediately after incubation is initiated) and then a decrease. It is possible that this approach does not accurately capture the respiration rate over the first 6 days. However, given the limited contribution of 6 days to the total 346-day incubation, the influence on cumulative soil respiration for the entire incubation period would be limited. Soil cumulative C mineralization rate was calculated as the percent of cumulative CO_2-C produced during the 346-day incubation in initial total soil C. Since soil respiration rate was only measured on 13 dates, the respiration rate between measurement points was estimated by linear interpolation between the two closest measurement points. Soil net N_{min} rate was indicated as (1) the percent increase of soil inorganic N compared to initial total N, and (2) the increase of soil inorganic N per kg soil after incubation.

Statistical analyses

Difference of soil respiration rate between soil incubated alone (Ss) and soil incubated with litter (S_{L+S}) was determined by paired-samples *t* test with Ss and S_{L+S} at each sampling date as a pair. Differences of litter moisture, litter C loss, litter mass loss, litter N remaining, litter N_{min} rate, litter N immobilization rate, litter net N_{min} rate and soil cumulative C mineralization and soil net N_{min} after 346 days of incubation between treatments (incubated alone or litter incubated with soil) and among litter species or soils were determined by two-way ANOVAs followed by LSD tests to compare means among litter species or soils. Data were square-root or log transformed before analyses to alleviate heteroscedasticity and improve normality. Linear regression analyses were used to study the relationships between net N_{min} rate (% of initial N) and C mineralization rate (% of initial C) and between soil net N_{min} rate (mg inorganic N per kg soil) and soil N concentration. Multiple linear regression analysis was conducted on litter C loss rate against litter initial N concentration, initial C : N ratio, soil moisture and litter moisture at the end of incubation. All statistical analyses were conducted using SPSS 16.0 for windows.

Results

Litter decomposition rate

Litter C loss rate after 346 days of incubation was significantly higher when incubated with soil than when incubated alone ($p<0.01$; Fig. 1). Litter C loss ranged from 35.0 % to 61.3 % of initial C when incubated with soil and from 27.3 % to 58.7 % when incubated alone (Fig. 1). The highest litter C loss was found in *P. amurense* and the lowest was found in *P. koraiensis* ($p<0.001$; Fig. 1). Litter C loss represented almost all

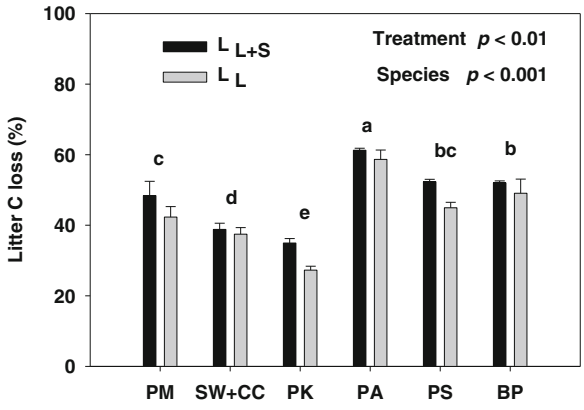

Fig. 1 Litter C loss after 346 days of incubation (mean±SE, n=4). L_L indicates litter incubated alone and L_{L+S} indicates litter incubated with soil. Litter codes: PM (*Pinus massoniana*), SW+CC (*Schima wallichii* mixed with *Castanopsis chinensis*), PK (*Pinus koraiensis*), PA (*Phellodendron amurense*), PS (*Pinus sylvestris*) and BP (*Betula platyphylla*). Litters with different letters (for both L_L and L_{L+S}) are significantly different at 0.05 level

mass loss, and therefore the magnitude and pattern of litter mass loss was almost the same as C loss (data not shown). Litter moisture was significantly higher when incubated alone than when incubated with soil (p<0.01; Table 3). Multiple linear regression analysis of litter C loss rate against litter initial N concentration, initial C : N ratio, soil moisture and litter moisture at the end of incubation showed that litter C loss rate was not related to any of these characteristics (data not shown).

Net N transfer between litter and soil and litter net N_{min} rate

During 346 days of incubation, net N transfer from soil to litter was found in all litters, leading to net increase of total N (i.e., litter N immobilization) (Fig. 2). For litters of *P. massoniana*, *S. wallichii* mixed with *C. chinensis*, and *P. amurense*, maximum N immobilization was found 138 days after incubation, ranging from 10 to 14 % of initial N, and then decreased to near zero at the end of incubation (Fig. 2). However, for litters of *P. koraiensis*, *P. sylvestris* and *B. platyphylla*, maximum N immobilization was found after 346 days of incubation, ranging from 21 to 33 % of initial N (Fig. 2; Table 3).

After 346 days of incubation, litter N_{min} rate was significantly higher in litters incubated with soil than litters incubated alone (p<0.001; Table 3). Litter net N_{min} rate ranged from zero to 10.1 % of initial N for litters of *P. massoniana*, *S. wallichii* mixed with *C. chinensis*, and *P. amurense*, when incubated alone or with soil (Table 3). Litter net N_{min} rate was 100 % higher when incubated with soil than when incubated alone for these litters. In contrast, negative net N_{min} rate occurred and ranged from 17.5 % to 24.0 % of initial N for litters of *P. koraiensis*, *P. sylvestris* and *B. platyphylla* when incubated with soil (Table 3). Net N_{min} was hardly found in these litters when incubated alone. Litter net N_{min} rate was negatively related to litter initial C : N ratio when incubated with soil (p<0.05; Fig. 3), but was not related to initial C : N ratio when incubated alone (data not shown) . After 346 days of incubation, litter net N_{min} rate was not related to litter C loss rate (Fig. 4a and b).

Soil C mineralization rate and net N_{min} rate

Soil respiration rate during incubation did not differ between soil incubated alone and soil incubated with litter (Fig. 5). After 346 days of incubation, soil cumulative C mineralization did not differ significantly between incubatiton with and without litter (Table 3). Percents of 3.56–7.61 % of initial soil C were mineralized when incubated alone, and 3.45–8.06 % of initial soil C was mineralized when incubated with litter (Table 3). Soils from temperate and boreal forests mineralized higher fractions of initial C than soils from subtropical forests (p<0.05; Table 3).

Soil total N content did not differ between soils incubated with and without litter (data not shown). Soil net N_{min} rate did not differ significantly between incubation with and without litter whether described as percent of initial N or based on soil weight (Table 3). Soil net N_{min} rate was not related to soil cumulative C mineralization rate when mineralization rate was described as percent of initial C or initial N (Fig. 6a and b). When soil net N_{min} was described based on soil weight, it was not related to cumulative soil C mineralization (% of initial C or mg C per kg soil; data not shown), but was positively related to soil initial N concentration (p<0.05; Fig. 6c and d).

Discussion

Litter decomposition rate and net N_{min} rate

As expected in our first hypothesis, litter decomposition rate was significantly higher in litters incubated with soil than incubated alone (Fig. 1), and this acceleration of C loss may be partially driven by the increased supply of

Table 3 Litter moisture and C and N mineralization of litter and soil after 346 days of incubation

	Treatment	PM	SW+CC	PK	PA	PS	BP
Litter moisture (%)	L_L A	76.3(0.6)	70.0(0.8)	71.4(0.8)	78.9(1.3)	78.3(0.4)	83.9(0.8)
	L_{L+S} B	72.2(4.1)^{bc}	64.2(2.4)^{d}	63.5(1.6)^{d}	71.5(0.6)^{b}	65.1(1.0)^{c}	77.0(0.7)^{a}
Litter N remaining (% of initial N)	L_L*	94.8(1.9)	95.7(2.7)	94.1(5.1)	96.5(4.8)	88.9(9.4)	93.9(1.3)
	L_{L+S}*	98.7(3.2)^{c}	101.2(4.8)^{bc}	133.0(8.3)^{a}	77.1(2.5)^{d}	121.9(5.6)^{ab}	120.7(3.3)^{a}
Litter N_{min} rate (% of initial N)	L_L B	4.30(1.1)	1.11(1.3)	0.0(0.2)	2.65(0.6)	0.18(0.04)	0.58(0.1)
	L_{L+S} A	10.10(1.8)^{a}	2.74(1.7)^{c}	8.93(2.1)^{b}	5.77(0.6)^{b}	4.43(0.4)^{c}	1.15(0.4)^{c}
Litter N immobilization rate (% of initial N)	L_L B	0 (0)	0(0)	0(0)	0(0)	0(0)	0(0)
	L_{L+S} A	1.97(2.0)^{c}	1.2(1.2)^{c}	33.0(8.3)^{a}	0(0)^{c}	21.9(2.8)^{ab}	20.7(3.3)^{b}
Litter net N_{min} rate (% of initial N)	L_L*	4.30 (1.1)	1.11(0.7)	0.0 (0.1)	2.65(0.6)	0.18(0.04)	0.58(0.1)
	L_{L+S}*	10.10 (1.8)^{a}	2.74(0.8)^{a}	−24.03(7.6)^{b}	5.77(0.6)^{a}	−17.45(2.4)^{b}	−19.52(3.4)^{b}
Soil cumulative C mineralization (% of initial C)	Ss A	4.88(0.06)	3.56(0.11)	7.34(0.06)	6.04(0.17)	7.61(0.10)	5.56(0.18)
	S_{L+S} A	4.82(0.24)^{e}	3.47(0.18)^{f}	6.90(0.14)^{b}	5.59(0.10)^{c}	8.06(0.24)^{a}	5.41(0.09)^{d}
Soil net N_{min} rate (% of initial N)	Ss	3.78(0.8)	2.5(0.17)	6.69(0.7)	8.67(0.6)	5.14(0.24)	7.51(0.28)
	S_{L+S} A	5.44(1.0)^{b}	1.87(0.07)^{c}	7.00(0.7)^{a}	9.32(0.9)^{a}	4.89(0.78)^{b}	6.19(0.91)^{a}
Soil net N_{min} rate(mg N kg^{-1} soil)	Ss A	95.0 (13)	115 (5.4)	218 (21)	520 (115)	140 (6.1)	237 (9.5)
	S_{L+S} A	123 (17)^{c}	94.5 (2.4)^{c}	227 (21)^{b}	553 (51)^{a}	134(19.5)^{c}	228 (31)^{b}

Litter codes: PM (*Pinus massoniana*), SW+CC (*Schima wallichii* mixed with *Castanopsis chinensis*), PK (*Pinus koraiensis*), PA (*Phellodendron amurense*), PS (*Pinus sylvestris*) and BP (*Betula platyphylla*). Soil code is the same as the litter code in each forest

Ss means soil incubated alone and S_{L+S} means soil incubated with litter. L_L means litter incubated alone and L_{L+S} means litter incubated with soil. Treatments followed by different upcase letters were significantly different at 0.001 level, and litters (both L_L and L_{L+S}) or soils (Ss and S_{L+S}) followed by different lowercase letters are significantly different at 0.05 level. * indicates significant difference between treatments but one treatment is not consistently higher or lower than the other across six litter-soil systems

Data are means (standard error), n=4

nutrients (particularly N) from the underlying soil because microbes decomposing fresh litter are frequently N-limited (Berg and McClaugherty 2008). Net N transfer

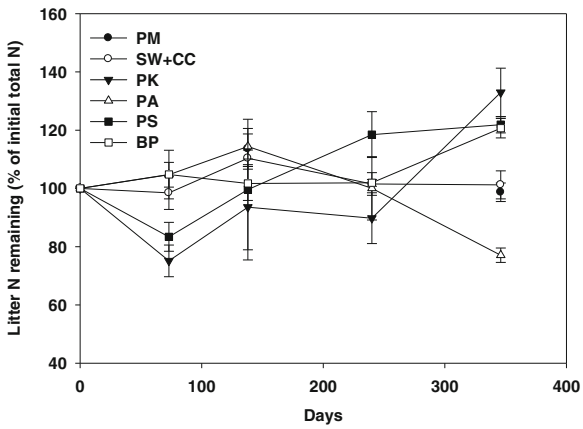

Fig. 2 Litter N remaining in litters incubated with soil during 346 days of incubation (mean±SE, n=4). Litter codes: PM (*Pinus massoniana*), SW+CC (*Schima wallichii* mixed with *Castanopsis chinensis*), PK (*Pinus koraiensis*), PA (*Phellodendron amurense*), PS (*Pinus sylvestris*) and BP (*Betula platyphylla*)

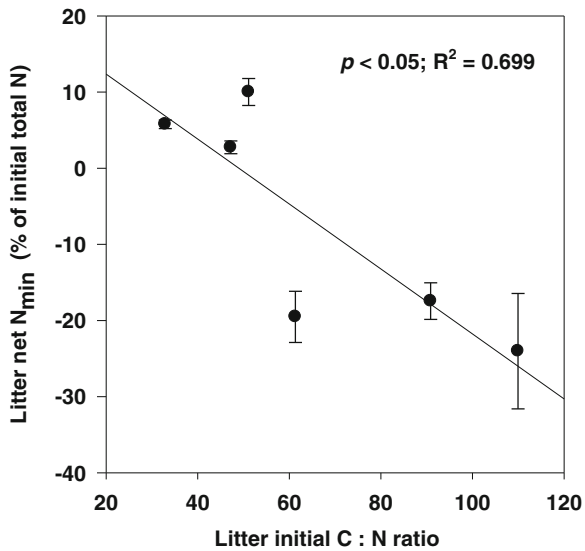

Fig. 3 Relation between litter net N_{min} rate and initial litter C : N ratio under the treatment of litter incubated with soil (mean±SE, n=4)

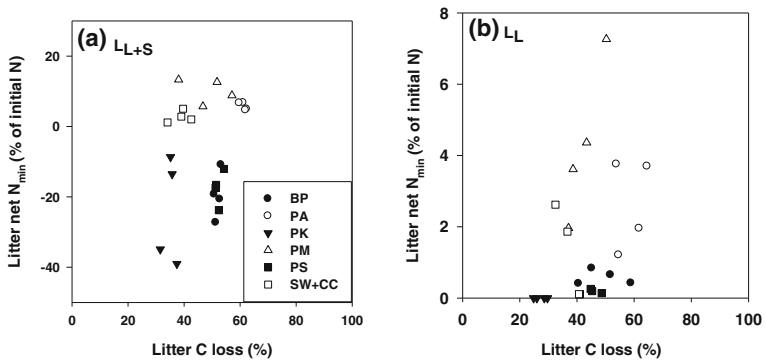

Fig. 4 Relation between litter net N_{min} and litter C loss (a, litter incubated with soil; b, litter incubated alone). *Litter codes*: PM (*Pinus massoniana*), SW+CC (*Schima wallichii* mixed with *Castanopsis chinensis*), PK (*Pinus koraiensis*), PA (*Phellodendron amurense*), PS (*Pinus sylvestris*) and BP (*Betula platyphylla*)

from soil to litter was indeed found in all litters when incubated with soil, even in *P. amurense* litter with an initial N concentration of as high as 1.35 % (with a C : N ratio of 32.9) (Fig. 2; Table 2). And this N transfer might have relieved the C : N imbalance in decomposing microbes and accelerated litter decomposition (Manzoni

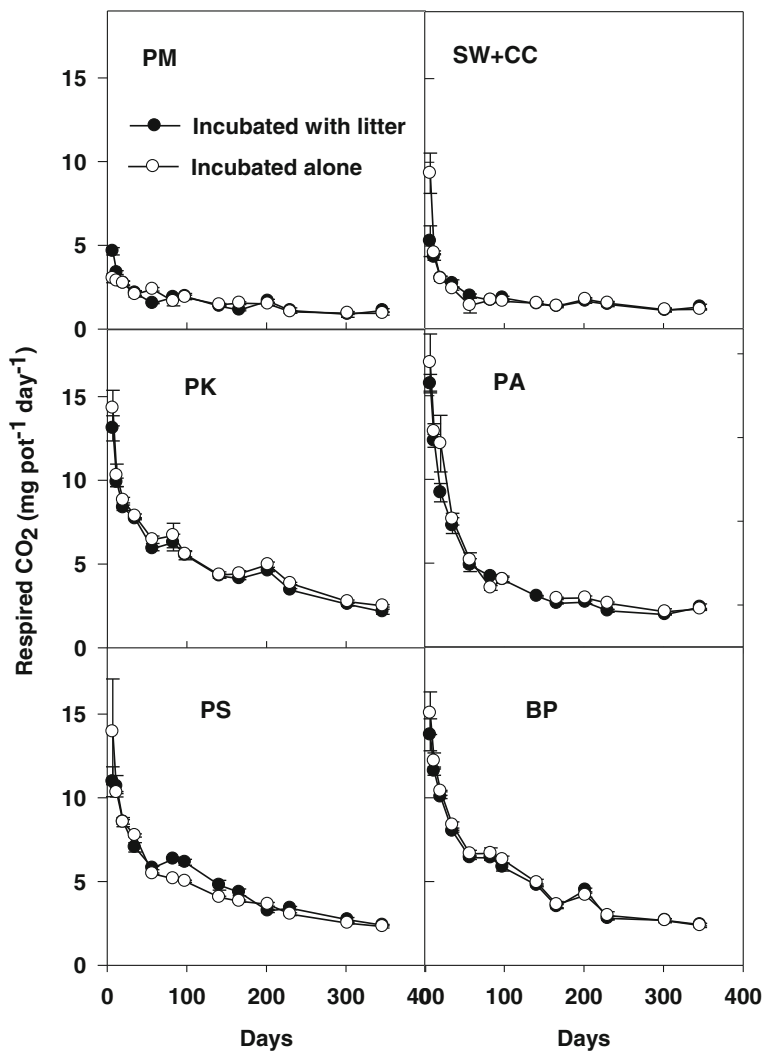

Fig. 5 Soil respiration rate throughout 346 days of incubation (mean±SE, n=4). Soil codes: PM (*Pinus massoniana*), SW+CC (*Schima wallichii* mixed with *Castanopsis chinensis*), PK (*Pinus koraiensis*), PA (*Phellodendron amurense*), PS (*Pinus sylvestris*) and BP (*Betula platyphylla*)

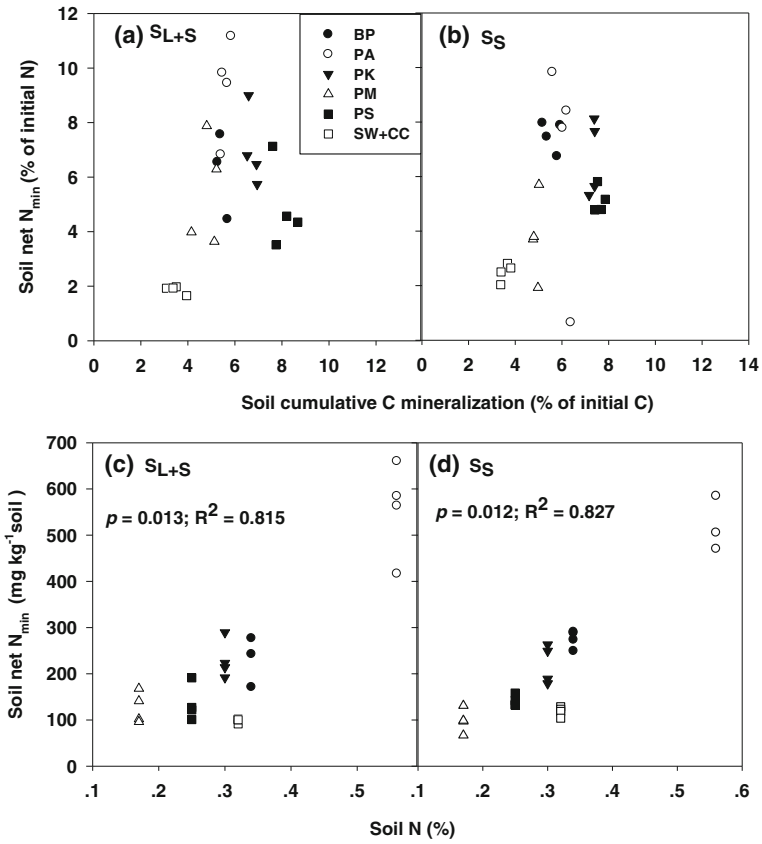

Fig. 6 Relation between soil net N_{min} and soil cumulative C mineralization (**a** soil incubated with litter; **b** soil incubated alone), and relation between soil net N_{min} (mg per kg soil) and soil N concentration (**c** soil incubated with litter; **d** soil incubated alone). *Soil codes*: PM (*Pinus massoniana*), SW+CC (*Schima wallichii* mixed with *Castanopsis chinensis*), PK (*Pinus koraiensis*), PA (*Phellodendron amurense*), PS (*Pinus sylvestris*) and BP (*Betula platyphylla*)

et al. 2008; Sinsabaugh et al. 2009). Our results are consistent with many other studies that N addition increased litter decomposition rate (Hobbie and Vitousek 2000; Vivanco and Austin 2011). Moreover, N transfer between different litters in litter mixtures has been suggested as the mechanism of synergistic effects of litter mixture on litter decomposition rate (Schimel and Hattenschwiler 2007; Hui and Jackson 2009). Nevertheless, Craine et al. (2007) showed that increased N availability stimulated the decomposition of litter labile C but decreased the decomposition rate of recalcitrant materials because microbial mining of recalcitrant organic matter for N was impaired by increased N. Our results did not contradict with the microbial N mining theory because litter decomposition is dominated by the decay of labile materials during early and middle stages of decomposition (Berg and McClaugherty 2008), as was the case in our study.

Moreover, litter net N_{min} after 346 days of incubation was 100 % higher when incubated with soil than incubated alone in litters of *P. massoniana*, *P. amurense* and *S. wallichii* mixed with *C. chinensis* (Table 3). The specific reason for the enhanced litter net N_{min} when incubating with soil was unclear, but one possible reason was the net N transfer from soil to litter. N addition was known to stimulate N mineralization in organic matter, a so called priming effect or added N interaction (Jenkinson et al. 1985; Lin et al. 2004). In addition, litter net N_{min} was negatively related to litter initial C : N ratio (Fig. 3), as previously suggested by Manzoni et al. (2008). Therefore, net N transfer from soil to litter might have impacted litter net N_{min} by altering litter C : N stoichiometry.

The mechanism of net N transfer from soil to litter observed in our study could not be addressed under our experimental setting, but might be due to the translocation by decomposing fungi. Although we did not measure the microbial community composition, fungal hyphae were observed in all litters whether incubated alone or incubated with soil. N transfer from soil to litter by decomposing fungi has been experimentally tested in Frey et al. (2000 and 2003), and was suggested as the mechanism of litter N immobilization in many studies (Parton et al. 2007; Manzoni et al. 2008). N diffusion

was considered as one possible reason for N transfer from soil to litter and diffusion rate has been reported to be positively related to soil moisture and the concentration gradient (Moldrup et al. 2001). However, the systems in which litter N immobilization was found earlier (i.e., PM and SW+CC) or N immobilization was highest (i.e., PK) (Fig. 2) had lower concentrations of inorganic N (primary form of diffusive N) in soil than in litter at the initiation of incubation and did not consistently have higher soil moisture (Table 2). Therefore, N diffusion might not be considered as the mechanism of net N transfer from soil to litter in our study.

Although none of the measured characteristics was related to litter C or mass loss rate, litter initial C quality might explain the different decomposition rates among different litters. Increasing evidence showed that litter C quality drives litter decomposition rate and litters with higher concentrations of acid-insoluble C fractions decompose slower (Hättenschwiler and Jørgensen 2010; Xiong et al. 2013). In our study, the highest and lowest decomposition rates were found in *P. amurense* litter and *P. koraiensis* litter, respectively. In accordance, *P. amurense* is among the litters with lowest acid-insoluble C fractions and *P. koraiensis* is among the litters with highest acid-insoluble C fractions (Li et al. 2007; Xiong et al. 2013).

Low net N_{min} rate during litter decomposition and limited role of decomposing litter in plant mineral N supply

In consistent with our second hypothesis, litter C loss rate and net N_{min} rate was decoupled during 1-year incubation (Figs. 4a and 5b). Moreover, little or negative net N_{min} occurred during litter decomposition. For example, litters of *P. sylvestris* and *B. platyphylla* lost ~50 % of initial C, but net N_{min} was near zero when incubated alone, and negative net N_{min} was found after 346 days when incubated with soil (Fig. 1 and Table 3). In our study, litter decomposition might have gone through the early and middle stages and should be incorporated into more stable SOM under field conditions. Since the moisture and temperature were kept at the most favorable level for microbial activity, the year-long incubation in our study should have led to a decomposition stage that may take year to reach under field conditions. In addition, litter C : N ratios of some litters approached soil C : N ratios (from 33 to 14 for *P. amurense* litter, and from 61 to 25 for *B. platyphylla* litter, and C : N ratios of their matching soils were 12 and 25, respectively), one more indication of the degree of decomposition. Slow net N_{min} rates during litter decomposition might be a general pattern given that the six litter species (or species combination) studied here represented a broad range of litter chemistry (Table 2). Limited net N_{min} (< 10 % of initial litter N) has also been observed in long-term laboratory incubation (up to 263 days at 25 °C) studies using diverse organic matter types ranging from wheat straw to humus (Wetterstedt et al. 2010).

Litter N pool has been reported to account for only one eighth of soil N pool across 16 temperate and boreal forests (Cole and Rapp 1981; Knops et al. 2010). During the entire incubation in our study, soil net N_{min} rate (from 1.87 % to 9.32 % of initial N) is comparable to litter net N_{min} rate (from negative to 10.1 % of initial N). Although we only studied net N_{min} rate of mineral soil of top 5 cm, the net N_{min} rate of soil below 15 cm depth has been reported to be higher than the top soil (Iversen et al. 2011). As such, the amount of mineral N release from decomposing litter might be less than 15 % of the amount of mineral N release from SOM. The low rates of litter net N_{min}, combined with the small size of litter N pool (relative to a large soil N pool) necessitate that the amount of plant available mineral N may be controlled by the size of soil N pool, and litter decomposition rate may only play a minor role in regulating total mineral N availability in the whole soil profile (litter plus SOM), as was suggested by Mueller et al. (2012).

Soil C mineralization rate and net N_{min} rate

In our second hypothesis we expected that soil incubated with litter would have higher respiration rates than soil incubated alone. However, no significant difference of soil respiration rate or cumulative C mineralization was found between soil incubated alone and soil incubated with litter (Fig. 5; Table 3). A priming effect was found when 1 g cellulose C was added to 1 kg of soil (Fontaine et al. 2007). Since the amount of added litter C in our study (about 1.5 g C to 100 g soil) was much larger than that added in Fontaine et al. (2007), the lack of litter effects on SOM mineralization might be due to no C transfer from litter to soil. Given that litter decomposed on the surface of soil in our study, which mimicked the case of leaf litter decomposition in the field, our results should not be extrapolated to root litter which is mixed with soil and therefore C transfer from litter to soil is more possible.

Soil cumulative C mineralization rate was significantly lower in soils from the subtropical forests than soils from temperate and boreal forests (Table 3), which might be related to the difference of soil organic C (SOC) quality among different climatic regions. SOC quality (relative proportion of active versus resistant C) has been found to decrease with increasing mean annual temperature across climatic regions (Fissore et al. 2008 and 2009) because active SOC is expected to accumulate at cold sites due to slow decomposition rate, while enhanced decomposition with increasing temperature may lead to the depletion of active SOC at warm sites (Hart and Perry 1999). Therefore, soils from subtropical forests might have lower SOC quality than soils from temperate and boreal forests and thus had lower C mineralization rates.

In contrast with our fourth hypothesis, soil net N_{min} rate was not related to C mineralization rate (Fig. 6a and b). The decoupled soil C mineralization rate and net N_{min} rate has also been found in other studies (Hart et al. 1994; Giardina et al. 2001; Nosshi et al. 2007), and might be induced by microbial stoichiometric requirements. Microbes would immobilize mineralized N to produce biomass when labile C is available, and therefore gross N_{min} rate are usually an order of magnitude greater than net N_{min} rates (Stark and Hart 1997; Verchot et al. 2001). Therefore, SOM with higher fractions of labile C usually has higher C mineralization rate but lower net N_{min} rate. For example, more C was mineralized from light fractions than from heavy fractions of SOM, but light fractions acted as a sink of mineral N whereas heavy fractions as a source of net N_{min} (Whalen et al. 2000).

Soil net N_{min} rate (mg N per kg soil) was positively related to soil initial N concentration (Fig. 6c and d). Although the regression was strongly influenced by the especially high soil N concentration (0.56 %) in *P. amurense* forest, this relationship was also found in other studies with soil N concentrations ranging from 0.09 % to 0.40 % (Wedin and Pastor 1993; Dessureault-Rompré et al. 2010). Therefore, soil N concentration can be considered as a good predictor of potential net N_{min} rate, as was previously shown in other studies (Schomberg et al. 2009; Dessureault-Rompré et al. 2010; Ros et al. 2011).

Conclusions

We demonstrated an enhancement of litter decomposition rate by the underlying soil in all litters when incubated with soil, which might be partially due to alleviated N limitation by net N transfer from soil to litter during incubation. Moreover, litter net N_{min} rate was also enhanced by incubating with soil in litters with a certain initial C : N ratio (lower than 52 in our study). However, litter did not influence soil C mineralization rate or net N_{min} rate under our experimental settings in which litter decomposed on the surface of soil, and this conclusion might not be applicable to root litter which is mixed with soil. Our study together with many others on litter mixture decomposition suggest that net N transfer between decomposing organic matter (litter or SOM) with different N status may be common and may play an important role in influencing the decomposition and N release of organic matter.

Although litter decomposition might have started to proceed into late stage after 346 days of incubation under our lab conditions, litter net N_{min} was limited or even negative despite substantial C loss. The low rate of litter net N_{min} during litter decomposition along with the small size of litter N pool compared to soil N pool suggest that the more stabilized SOM is the bottleneck of short-term soil mineral N availability at the ecosystem scale.

Acknowledgments We thank Dr. Mei Zhou for help in getting permissions for field sampling and thank Chengen Ma for assistance in the field. Thanks to Drs. Shenglei Fu, Xingliang Xu, Tim Seastedt and Fusheng Chen for constructive comments on an earlier draft of the manuscript. We also thank Dr. Stefano Manzoni and two anonymous reviewers for comments that greatly improved the manuscript. This research was funded by One-Hundred Talent Project of Chinese Academy of Sciences (No. KZZD-EW-TZ-11) and the Natural Science Foundation of China (NSFC grants 31200405 and 31021001).

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