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Microbial respiration per unit microbial biomass depends on soil litter carbon-to-nitrogen ratio

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Abstract

Soil microbial respiration is a central process in the terrestrial carbon (C) cycle. In this study I tested the effect of the carbon-to-nitrogen (C : N) ratio of soil litter layers on microbial respiration in absolute terms and per unit microbial biomass C. For this purpose, a global dataset on microbial respiration per unit microbial biomass C – termed the metabolic quotient (qCO_2) – was compiled form literature data. It was found that the qCO_2 in the soil litter layers was positively correlated with the litter C : N ratio and negatively related with the litter nitrogen (N) concentration. The positive relation between qCO_2 and litter C : N ratio resulted from an increase in respiration with the C : N ratio in combination with no significant effect of the litter C : N ratio on the soil microbial biomass C concentration. The results suggest that soil microorganisms respire more C both in absolute terms and per unit microbial biomass C when decomposing N-poor substrate. Thus, the findings indicate that atmospheric N deposition, leading to decreased litter C : N ratios, might decrease microbial respiration in soils.

1 Introduction

Large amounts of organic carbon (C) are transformed, stored and respired by microorganisms in soil. Hence, gaining insight into the factors controlling the respiration rate per unit soil microbial biomass is crucial to understand the terrestrial C cycle. The respiration rate per unit microbial biomass C – termed the metabolic quotient (qCO_2) – is as a measure for the ecophysiological status of soil microorganisms (Anderson and Domsch, 1993). Although a large number of studies on the qCO_2 has been published (reviewed by Brookes, 1995; Bastida et al., 2008; Anderson and Domsch, 2010), little is known about how the qCO_2 is affected by soil C : N : P stoichiometry.

The soil microbial biomass shows a relatively well constrained stoichiometry similarly to the Redfield ratio found for planktonic biomass (Redfield, 1934). Although the stoichiometry of individual phylogenetic groups may vary, the molar C : N ratio of the

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soil microbial biomass at a global scale converges towards 6–8 (Cleveland and Liptzin, 2007; Xu et al., 2013). The C : N ratio of soil litter layers is in the range of 12–80 (Berg and McClaugherty, 2003). Thus, microorganisms decomposing litter with a high C : N ratio are confronted with a surplus of C in relation to N. Compared to other ecosystems, microorganisms in forests face extreme substrate imbalances since the C : N ratios of woody plants are extremely high compared to the microbial biomass C : N ratio. While, for example, in phytoplankton and magroalgae the C : N ratio amounts to approximately 10, woody plants have a C : N ratio of up to 400 (Cebrian, 1999; Sterner and Elser, 2002).

When growing on N-poor substrate, microorganisms have not enough N to build up as much biomass as the C concentration would allow. Thus, it has been argued that microorganisms can dispose of C via overflow respiration as CO_2 to make the substrate meet their nutritional demands (Manzoni et al., 2008, 2010; Sinsabaugh et al., 2013). Overflow respiration is thought to be respiration without the production of energy. The concept of overflow respiration has recently been criticized by several studies. It has been argued, first, that for disposing C via the respiratory chain, N for the proteins of the respiratory chain has to be invested and, second, that the energy lost by disposing of C could be invested into storage, anti-viral defense or other processes, which increase the fitness of the organism (Hessen and Anderson, 2008; Hessen et al., 2013). Hence, while overflow respiration seems to be likely from a perspective of stoichiometric models, the existence of this process is still under discussion.

The objective of this study was to use data of published studies on the qCO_2 in soil litter layers to learn about how litter C : N stoichiometry affects the respiration rate per unit decomposer biomass. Following stoichiometric theory, I tested the hypothesis that the qCO_2 increases with litter C : N ratio and decreases with litter N concentration. For this purpose, data from literature on the qCO_2 in soil litter layers and litter properties was compiled.

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2 Material and methods

Literature searches were conducted using Google Scholar, Web of Science, and Scopus in November and December 2013. I searched for the word "metabolic quotient" in combination with the following terms "litter decomposition", "litter layer", "leaf decomposition", "needle decomposition", "microbial activity", "forest floor", "microbial respiration", "tropical forest", "temperate forest", "boreal forest", "mediterranean forest", "plantation".

Based on the literature search, I selected studies that reported the qCO_2 measured in laboratory incubations on litter collected from the soil litter layer of forests, tree and palm plantations and heathlands. Studies that mixed litter with mineral soil were excluded because it is assumed that stabilization of the soil organic matter by sorption and aggregation possibly obscures relations between element concentrations and the qCO_2. If results for different treatments were reported, only the data for the control treatment were extracted. If time series were reported, I only extracted the first data point of the series in order to avoid pseudo-replication. In order to prevent confounding results due to different methods, the following criteria were applied for data selection. The qCO_2 had to be reported in unambiguous units as the rate of C mineralization per unit of microbial biomass C. Basal respiration had to be determined during incubations based on CO_2 measurements by gas chromatography or titration (but not, for example, O_2 consumption), and the microbial biomass C had to be determined by the fumigation-extraction method. Additionally, the studies had to report either the C : N ratio of the litter or both the C and N concentration. Besides the metabolic quotient, microbial biomass C, basal respiration, and the C : N ratio of the litter, the following parameters were collected if reported in the studies: latitude and mean annual temperature of the study site, classification of the litter layer, litter pH, plant species from which the litter was derived, microbial biomass N, litter P, microbial biomass P, and temperature and water holding capacity at which the respiration measurement had been

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performed. In case data was reported in the form of graphs, numbers were extracted using the open-source software DataThief (Tummers, 2006).

Units were converted to obtain microbial biomass C in mg (g litter)$^{-1}$, basal respiration in µg CO_2-C (g litter-C)$^{-1}$ h^{-1}, qCO_2 in µg CO_2-C (mg microbial-C)$^{-1}$ h^{-1}, and the C : N ratio in mol mol^{-1}. For all analyses including latitude, only the degree of latitude was considered, but no differentiation between Southern and Northern Hemisphere was made. The Pearson's correlation coefficients were calculated, and the significance of the correlation was tested by the Pearson test. All data analysis was conducted in R (R Core Team, 2013).

3 Results

Fourteen studies were found that met the above-mentioned criteria, resulting in 48 observations. The studies covered the tropical, temperate, and boreal climate zone, and included data on the qCO_2 measured on litter derived from seven tree genera. Additionally, two studies reported data on litter of mixed forests with non-characterized species composition, and two studies reported results on litter derived from a palm and legumes and a forb (Table 1).

The qCO_2 was positively related to the C : N ratio of the litter (slope = 0.14, $R = 0.78$, $p < 0.001$, Fig. 1) and negatively to the litter N concentration (slope = 0.30, $R = -0.72$, $p < 0.001$, Fig. 2). The positive relation between litter C : N ratio and qCO_2 resulted from a positive relation between respiration and the C : N ratio (slope = 1.47, $R = 0.71$, $p < 0.001$, Fig. 3), and no effect of the litter C : N ratio on the microbial biomass C concentration ($R = 0.16$, $p > 0.05$, Table 2). The incubation temperatures, at which the respiration rates had been determined, ranged from 14 to 25 °C. Some of the variation in the qCO_2 was due to the different incubation temperatures and the positive correlation between incubation temperature and qCO_2 (slope = 0.25, $R = 0.55$, $p < 0.001$, Table 2). Moreover, the latitude was negatively related with the litter N concentration ($R = -0.51$, $p < 0.001$, Table 2). Other statistically significant correlations, such as be-

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tween respiration rate and qCO_2, and N concentration and C : N ratio (Table 2), are due to the intrinsic dependence of the variables. No significant relation between the litter C : N ratio and the microbial C : N ratio was found ($R = 0.11$, $p > 0.05$, Table 2). Unfortunately, only very few studies reported litter P or microbial P concentrations, making the inclusion of these parameters into the analysis impossible.

4 Discussion

Here it was found that soil microbial respiration both in absolute terms and per unit microbial biomass is positively correlated with the soil litter C : N ratio. The findings are in accordance with previous studies that reported a positive correlation between litter C : N ratio and respiration (Othonen, 1994; Gödde et al., 2002; Michel and Matzner, 2002), and a negative relation between respiration and available N (Craine et al., 2007). The findings also agree with results from litterbag studies on litter decomposition in relation to litter C : N ratio (Berg and Matzner, 1997; Berg and McClaugherty, 2003). Several explanations for this negative relationship between respiration and C : N ratio have been proposed. A first explanation might be that microorganisms mine litter for N, i.e., they burn readily available C in order to gain energy to acquire N from more recalcitrant forms of organic matter (Craine et al., 2007) or in order to have physical access to the N incorporated in organic compounds. A second explanation is based on stoichiometry theory. It states that excess C is burned through "overflow respiration", which means that microorganisms uncouple respiration from energy production and only respire C to dispose it (Russel and Cook et al., 1995; Manzoni et al., 2008, 2010). However, this argument has been criticized for two reasons (Hessen and Anderson, 2008). First, microorganisms may use C that is in surplus to their demands of somatic growth for promoting their fitness by C storage, buildup of structural defenses, viral repellents or establishment of symbiosis. Second, it seems that the disposal of C via respiration may need nutrients to maintain the proteins of the respiratory chain (Hessen and Anderson, 2008). A third explanation for decreased respiration at low litter C : N ratios could be that the activity of oxidative enzymes involved in the degradation of aromatic compounds decreases with N concentration (Carreiro et al., 2000; Saya-Cork et al., 2002; Michel and Matzner, 2003; Gallo et al., 2004). Decreased lignolytic activity might decrease microbial respiration in litter with low C : N ratios (Carreiro et al., 2000; Eiland et al., 2001; Saya-Cork et al., 2002).

One further way in which microorganisms can react to imbalanced substrate stoichiometry, is to gradually adapt the microbial biomass stoichiometry as recently shown for microorganisms in tropical litter (Fanin et al., 2013). However, in this study, I did not find a significant relation between the litter C : N ratio and the microbial C : N ratio, indicating that the microbial community did not adapt its biomass composition to the litter stoichiometry.

The positive relation between qCO_2 and litter C : N ratio resulted from an increase in respiration with the C : N ratio in combination with no significant effect of the litter C : N ratio on the soil microbial biomass C concentration. The findings of this study indicate that atmospheric N deposition, leading to decreased litter C : N ratios, might decrease microbial respiration in soil litter layers both in absolute terms and per unit microbial biomass. This is in accordance with studies reporting that long-term N deposition and fertilization, resulting in decreases in plant litter C : N ratios, increased soil C sequestration in forests (Magnani et al., 2007; Pregitzer et al., 2008; Janssens et al., 2010). Pregitzer et al. (2008) and Janssens et al. (2010) found that the major reason for the positive effect of N deposition on C sequestration is reduced respiration with decreasing soil C : N ratio. This study suggests that this reduction in respiration rates is not due to a lower microbial biomass concentration, but due to a reduced respiration rate per unit microbial biomass.

5 Conclusions

This analysis of literature data shows that microbial respiration per unit microbial biomass in litter layers increases with the litter C : N ratio, highlighting the importance

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of soil stoichiometry for microbial mineralization processes. The findings indicate that atmospheric N deposition, leading to decreased litter C : N ratios, might decrease microbial respiration in soils.

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Table 1. References considered in the analysis together with the latitude of the study site, the plant genus from which the litter was derived and the number of data points gained from each reference. A detailed list of the publications, from which data was extracted is given in the Supplement.

Reference	Latitude	Plant	Data points
Chang and Trofymow (1996)	50° N	*Cedrus*	3
Chapman et al. (2003)	57° N	*Pinus*	1
Dinesh et al. (2006)	10° S	*Cocos* and *Legumes*	10
Fisk and Fahey (2001)	44° N	*Fagus* and *Betula*	1
Karneva and Smolander (2007)	66° N	*Picea*, *Pinus*, *Betula*	8
van Meeteren et al. (2007)	52° N	Forbs	1
Ndaw et al. (2009)	21° S	Various broadleaf trees, *Eucalyptus*	4
Pietikainen and Fritze (1996)	65° N	*Picea*	3
Ross and Sparling (1993)	36° S	*Pinus*	4
Ross and Tate (1993)	36° S	*Fagus*	2
Ross et al. (1996)	43° S	*Fagus*	2
Ross et al. (1999a)	38° S	Various trees, *Pinus*	4
Ross et al. (1999b)	61° N, 42° S, 40° S, 36° S	*Pinus*	4
Schimel et al. (1999)	64° N	*Betula*	1

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Table 2. Spearman's correlation coefficient of the latitude of the study site, the pH_{H_2O} of the soil litter layer, the C and N concentration and the C : N ratio of the soil litter layer, the microbial biomass C and N concentration (C_{mic} and N_{mic}), the microbial biomass C : N ratio, the incubation temperature at which the respiration rate was determined (Temp), the respiration rate (Resp), and the metabolic quotient (qCO_2). [a], [b], [c] denote levels of significance at $p < 0.05$, 0.01 and 0.001.

	Latitude	pH_{H_2O}	C	N	C : N	C_{mic}	N_{mic}	$C_{mic} : N_{mic}$	Temp	Resp	qCO_2
Latitude											
pH_{H_2O}	−0.39[a]										
C	0.52[c]	−0.16									
N	−0.51[c]	−0.14	0.00								
C : N	0.38[b]	0.17	0.51[a]	−0.81[c]							
C_{mic}	0.22	−0.12	0.24	−0.01	0.16						
N_{mic}	−0.01	0.25	0.13	−0.20	0.22	0.08					
$C_{mic} : N_{mic}$	0.04	−0.07	0.18	0.00	0.11	0.54[c]	−0.39[a]				
Temp	−0.42[b]	0.39[a]	0.17	−0.38[a]	0.30[a]	−0.06	0.40[b]	0.03			
Resp	0.17	0.19	0.35[a]	−0.56[c]	0.71[c]	0.52[c]	0.38[a]	0.07	0.33[a]		
qCO_2	0.13	0.36[a]	0.26	−0.72[c]	0.78[c]	0.01	0.22	0.05	0.55[c]	0.64[c]	

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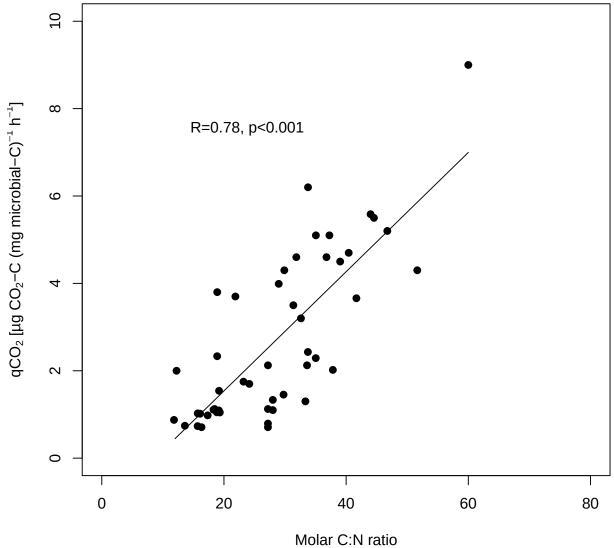

Figure 1. Correlation between the metabolic quotient (qCO_2) and the molar carbon-to-nitrogen ratio (C : N) of the soil litter layer.

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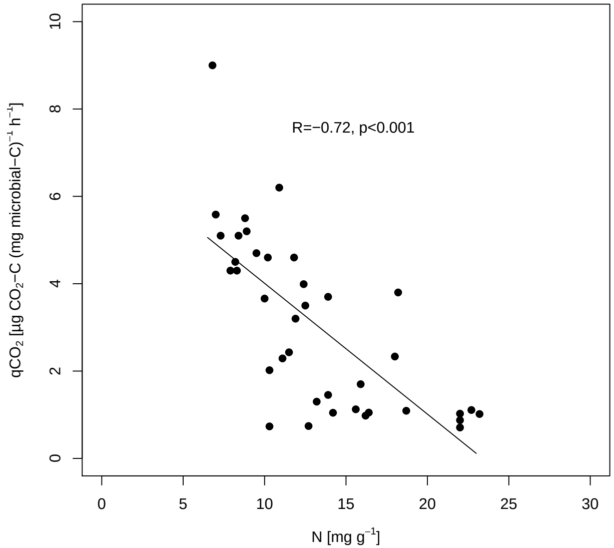

Figure 2. Correlation between the metabolic quotient (qCO_2) and the soil litter layer nitrogen (N) concentration.

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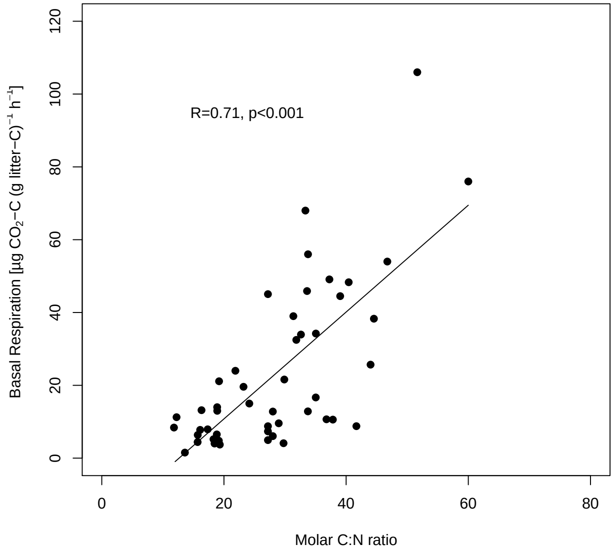

Figure 3. Correlation between the basal respiration rate and the molar carbon-to-nitrogen ratio (C : N) of the soil litter layer.

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