Microbial respiration per unit microbial biomass depends on litter layer 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 was negatively related with the litter nitrogen (N) concentration. The positive relation between the qCO_2 and the 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. The reasons for the observed relationship between the qCO_2 and the litter layer C:N ratio could be microbial N mining, overflow respiration or the inhibition of oxidative enzymes at high N concentrations. In conclusion, the results show that the qCO_2 increases with the litter layer C:N ratio. 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 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, i.e., respiration without the production of energy, has been shown to occur in several microbial species in laboratory incubations (Russell and Cooks 1995; Teixeira de Mattos and Neijssel, 1997; Vemuri et al., 2006). The relevance of microbial overflow respiration in ecosystems has recently been questioned by several studies. It has been argued, first, that for disposing of C via the respiratory chain, N for the proteins of the respiratory chain has to be invested, and therefore it might be more beneficial for microorganisms to dispose of excess C by releasing DOC (Hessen and Anderson, 2008). Second, it has been pointed out 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 has been shown to occur in laboratory incubations and seems to be likely from a stoichiometric perspective, the relevance of this process in ecosystems 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 on litter layer properties was compiled.

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 respiration rate 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 (C_{mic}), 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 (N_{mic}),

litter P, microbial biomass P, and temperature and soil water capacity at which the respiration measurement had been 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. In order to evaluate the influence of the incubation temperature and the soil water content on the qCO_2, the following linear regression models were fitted.

$$qCO_2 = a_1 \times C{:}N\ ratio + \varepsilon$$

$$qCO_2 = b_1 \times C{:}N\ ratio + b_2 \times temperature + \varepsilon$$

$$qCO_2 = c_1 \times C{:}N\ ratio + c_2 \times temperature + c_3 \times soil\ water\ content + \varepsilon$$

where a_i, b_i, and c_i are coefficients and ε is the error term. Furthermore, I fitted a linear model with all litter properties and the latitude of the study site of the form

$$qCO_2 = d_1 \times C{:}N\ ratio + d_2 \times temperature + d_3 \times soil\ water\ content + d_4 \times C + d_5 \times N + d_6 \times C_{mic} + d_7 \times N_{mic} + d_8 \times latitude + \varepsilon$$

where d_i are coefficients and ε is the error term. 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

117 respiration and the C:N ratio (slope=1.47, r=0.71, p<0.001, Fig. 3), and no effect of the litter
118 C:N ratio on the microbial biomass C concentration (r=0.16, p>0.05, Table 2). The incubation
119 temperatures, at which the respiration rates had been determined ranged from 14 to 25°C. The
120 qCO_2 was positively correlated with the incubation temperature (slope=0.25, r=0.55, p<0.001,
121 Table 2). Moreover, the latitude was negatively related with the litter N concentration (r=-0.51,
122 p<0.001, Table 2). Other statistically significant correlations, such as between respiration rate
123 and qCO_2, and N concentration and C:N ratio (Table 2), were due to the intrinsic dependence
124 of the variables. No significant relation between the litter C:N ratio and the microbial C:N ratio
125 was found (r=0.11, p>0.05, Table 2). Unfortunately, only very few studies reported litter P or
126 microbial P concentrations, rendering the inclusion of these parameters into the analysis
127 impossible.

128 The linear regression model of the qCO_2 with the C:N ratio as the only predicting variable had
129 a R^2=0.61 (p<0.001). If the incubation temperature was included in the model of the qCO_2 the
130 R^2 increased to R^2=0.72 (p<0.001). The R^2 slightly increase further if the soil water content was
131 additionally included as predicting variable (also R^2=0.73, p<0.001). If all assessed litter layer
132 properties (C:N ratio, temperature, soil water content, C, N, C_{mic}, N_{mic}) and the latitude were
133 included in the linear model as predicting variables, the R^2 increased to R^2=0.87 (p<0.001).

134

135 ## 4 Discussion

136 Here it was found that soil microbial respiration rate both in absolute terms and per unit
137 microbial biomass was positively correlated with the soil litter C:N ratio. The findings are in
138 accordance with previous studies that reported a positive correlation between litter C:N ratio
139 and respiration (Othonen, 1994; Gödde et al., 2002; Michel and Matzner, 2002), and a negative
140 relation between respiration and available N (Craine et al., 2007). The findings also agree with
141 results from litterbag studies on litter decomposition in relation to litter C:N ratio (Berg and
142 Matzner, 1997; Berg and McClaugherty, 2003). Moreover, the findings go in line with a
143 positive correlation between the qCO_2 and the soil C-to-nutrient ratios in beech, spruce and
144 mixed forests found recently (Spohn and Chodak, 2015).

145 There are at least three explanations for the observed relationships. A first explanation might
146 be that microorganisms mine litter for N, i.e., they burn readily available C in order to gain
147 energy to acquire N from more recalcitrant forms of organic matter (Craine et al., 2007) or in
148 order to have physical access to the N incorporated in organic compounds. However, it can be

questioned whether microorganisms that suffer from N limitation can afford to invest N into the production of exoenzymes and release them to acquire C, especially in N poor soils where the pay-off in terms of N is very small. A second explanation might be overflow respiration, which means that microorganisms uncouple respiration from energy production and only respire C to dispose it of (Russel and Cook et al., 1995; Manzoni et al., 2008, 2010). Overflow respiration has been observed in many microbial species in lab incubations (Russell and Cooks 1995; Teixeira de Mattos and Neijssel, 1997). However, the relevance of microbial overflow respiration in ecosystems has been questioned for two reasons (Hessen and Anderson, 2008). First, the disposal of C via respiration requires N to maintain the proteins of the respiratory chain, and thus it would be more beneficial for microorganisms to dispose of excess C by releasing DOC (Hessen and Anderson, 2008). Second, 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. Yet, it has to be taken into account, first, that the buildup of structural defenses, viral repellents or establishment of symbiosis also requires N, and second, that there are limits to the amounts of C that microbes can store and likely also to the amounts of C microbes can invest into buildup of structural defenses, viral repellents or establishment of symbiosis. 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). All three mechanisms – N mining, overflow respiration, and enzyme inhibition – could explain the observed relationship between the qCO_2 and the litter layer C:N ratio; and based on the data presented here it cannot be concluded which of the three mechanisms is most relevant to the observed relationships.

The positive relationship between the incubation temperature and the qCO_2 indicates that the qCO_2 increases with temperature. This influence of the temperature on the qCO_2 is supported by the higher R^2 of the model of the qCO_2 as a function of the C:N ratio and temperature (R^2=0.72) compared to the model of the qCO_2 as a function of only the C:N ratio (R^2=0.61). The finding that the qCO_2 increased with temperature is in accordance with Xu et al. (2006).

The findings about the litter layer stoichiometry and the qCO_2 seem to be in agreement with findings about the microbial carbon use efficiency. With increasing litter C:N ratio, microbial carbon use efficiency decreases because the microorganisms do not have enough N to build up

as much biomass as the C concentration would allow them (Manzoni et al., 2010; Cotrufo et al., 2013; Sinsabaugh et al., 2013). This seems to agree with the positive correlation between the qCO_2 and the litter C:N ratio. However, it has to be taken into account that the qCO_2 cannot directly be converted into the CUE since the qCO_2 is the ratio of a flux and a pool, and the CUE is a ratio of two fluxes, or in other word since the qCO_2 does not tell how much C was taken up by the microorganisms. Thus, based on the findings presented here no conclusions about microbial carbon use efficiency can be drawn.

One further way in which microorganisms can react to imbalanced substrate stoichiometry, is to gradually adjust the microbial biomass stoichiometry to the substrate 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 layer stoichiometry.

There are several implication soft the relationships found here. The positive corelation 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 that reported that long-term N deposition and fertilization, resulting in decreased 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. The present 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. Another implication of the results presented here concerns soil and ecosystem models. In these models, the proportion of C emitted per unit decomposer biomass is usually thought to be constant (Manzoni and Porporato, 2009). However, here it was shown that it is highly dependent on the soil litter layer C:N ratio.

5 Conclusions

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

Appendix A

A list of the publications used for data extraction can be found in the supplementary material.

Acknowledgements

I would like to thank Egbert Matzner, Rainer G. Joergensen, and Carlos A. Sierra for constructive comments on previous versions of this manuscript.

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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 obtained from each reference. A detailed list of the publications, from which data was extracted is given in the supplementary material.

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* & Legumes	10
Fisk and Fahey, 2001	44°N	*Fagus & 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 & 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

Table 2. Pearson's correlation coefficient of the latitude of the study site, the pH_{H2O} 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). *, **, *** denote levels of significance at $p<0.05$, 0.01 and 0.001.

	Latitude	**pH_{H2O}**	**C**	**N**	**C:N**	**C_{mic}**	**N_{mic}**	**C_{mic}:N_{mic}**	**Temp**	**Resp**	**qCO_2**
Latitude											
pH_{H2O}	-0.39*										
C	0.52***	-0.16									
N	-0.51***	-0.14	0.00								
C:N	0.38**	0.17	0.51*	-0.81***							
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***	-0.39*				
Temp	-0.42**	0.39*	0.17	-0.38*	0.30*	-0.06	0.40**	0.03			
Resp	0.17	0.19	0.35*	-0.56***	0.71***	0.52***	0.38*	0.07	0.33*		
qCO_2	0.13	0.36*	0.26	-0.72***	0.78***	0.01	0.22	0.05	0.55***	0.64***	

Figures

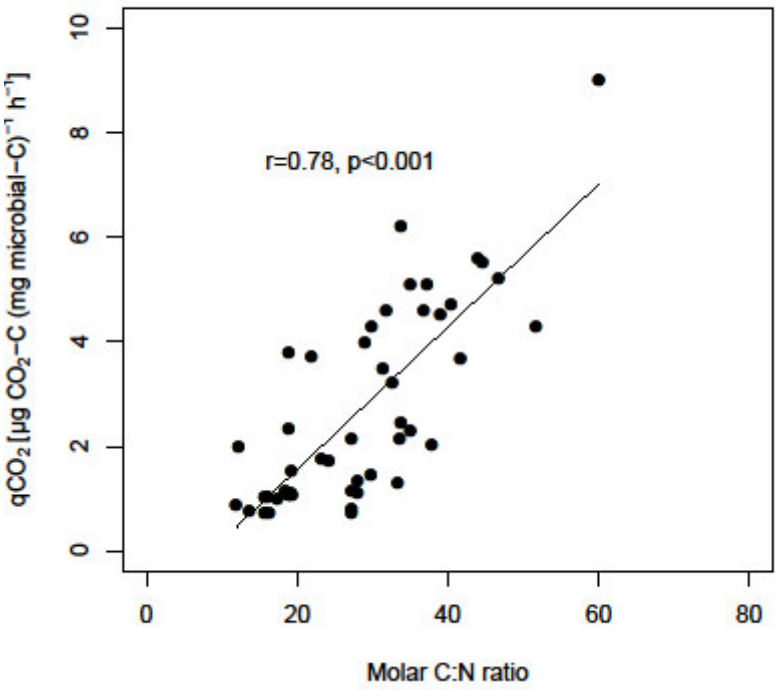
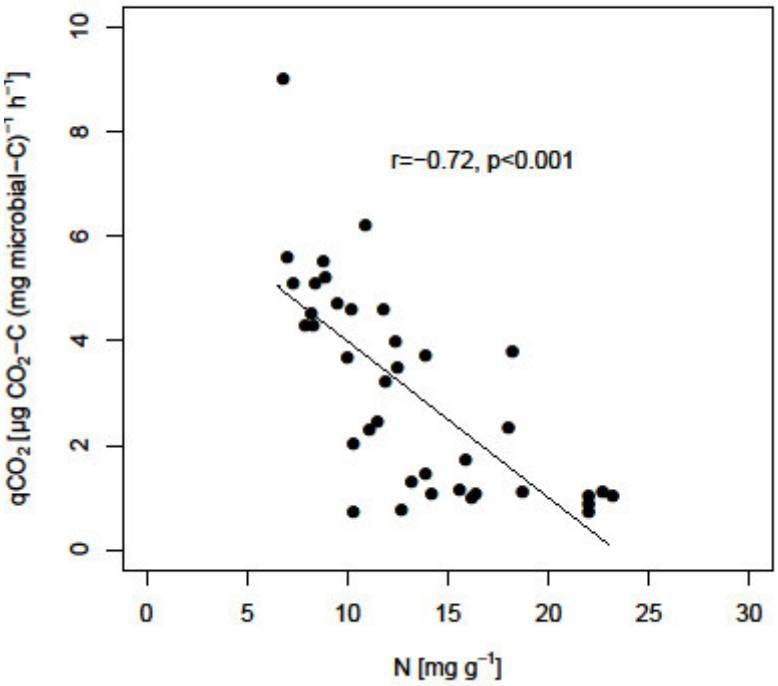


Figure 1. Correlation between the metabolic quotient (qCO_2) and the molar carbon-to-nitrogen ratio (C:N) of the soil litter layer



335

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

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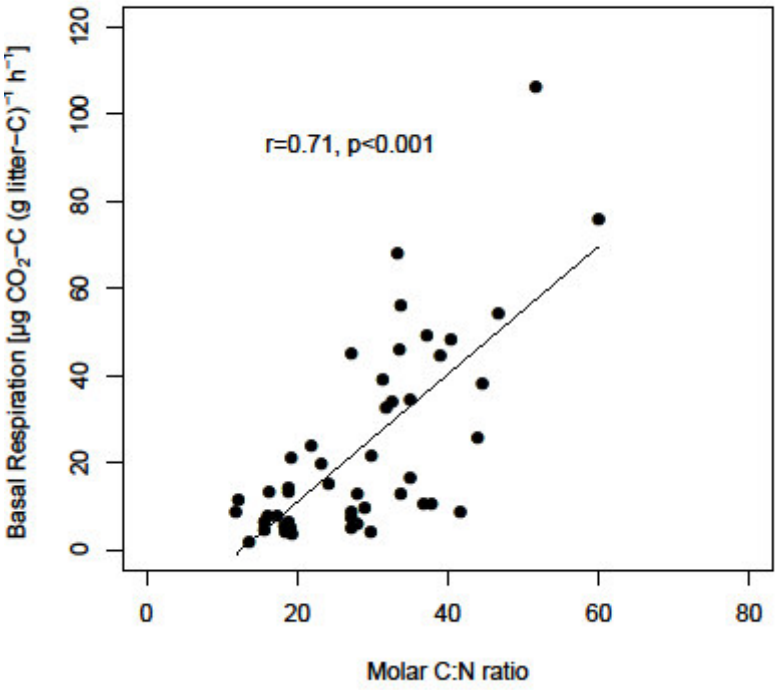

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340 Figure 3. Correlation between the basal respiration rate and the molar carbon-to-nitrogen ratio
341 (C:N) of the soil litter layer