



## Microbial respiration per unit biomass increases with carbon-to-nutrient ratios in forest soils



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### ABSTRACT

The ratio of carbon-to-nutrient in forest floors is usually much higher than the ratio of carbon-to-nutrient that soil microorganisms require for their nutrition. In order to understand how this mismatch affects carbon (C) cycling, we investigated the respiration rate per unit soil microbial biomass – the metabolic quotient ( $qCO_2$ ) – in relation to the soil carbon-to-nitrogen (C:N) and carbon-to-phosphorus (C:P) ratio in temperate forests. For this purpose, cores of beech, spruce, and mixed spruce-beech forest soils were cut into slices of 1 cm from the litter layer down to 5 cm in the mineral soil, and the relationship between the  $qCO_2$  and the soil C:N and the soil C:P ratio was analyzed. We found that the  $qCO_2$  was positively correlated with soil C:N ratio in spruce soils ( $R = 0.72$ ), and with the soil C:P ratio in beech ( $R = 0.93$ ), spruce ( $R = 0.80$ ) and mixed forest soils ( $R = 0.96$ ). We also observed a close correlation between the  $qCO_2$  and the soil C concentration in all three forest types. Yet, the  $qCO_2$  decreased less with depth than the C concentration in all three forest types, suggesting that the change in  $qCO_2$  is not only controlled by the soil C concentration. We conclude that microorganisms increase their respiration rate per unit biomass with increasing soil C:P ratio and C concentration, which adjusts the substrate to their nutritional demands in terms of stoichiometry.

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### 1. Introduction

Large amounts of organic carbon (C) are transformed, stored and respired by microorganisms in soil. The microbial C partitioning between respiration and biomass growth depends on environmental conditions such as temperature and moisture, and on substrate stoichiometry (Manzoni et al., 2008, 2012). However, little is known about how soil carbon: nitrogen: phosphorus (C:N:P) stoichiometry affects the mineralization rate per unit soil microbial biomass, termed the metabolic quotient ( $qCO_2$ ).

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

vary, the stoichiometry of the soil microbial biomass at a global scale is less flexible and converges towards a C:N:P ratio between 60:7:1 and 42:6:1 (Cleveland and Liptzin, 2007; Xu et al., 2013). The ratio between the substrate stoichiometry and the microbial biomass stoichiometry determines which element limits microbial growth. The critical substrate carbon-to-nutrient (C:X) ratio at which decomposers shift from being C limited to being nutrient limited is also called threshold element ratio (TER). The TER is thought to be a function of the decomposer biomass stoichiometry and the decomposers' C and nutrient use efficiency (Urabe and Watanabe, 1992; Berg and McClaugherty, 2003; Frost et al., 2006; Sinsabaugh et al., 2013; Kaiser et al., 2014). This ratio can be expressed as,

$$TER_{C:X} = \frac{XUE}{CUE} * \frac{C_{mic}}{X_{mic}} \quad (1)$$

where CUE is the microbial C use efficiency, XUE is microbial nutrient use efficiency with X being a specific nutrient (N or P),  $C_{mic}$

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is the microbial biomass C concentration, and  $X_{\text{mic}}$  is the microbial biomass nutrient (N or P) concentration. CUE is defined as,

$$\text{CUE} = \frac{C_B}{C_U} \quad (2)$$

where  $C_B$  is C used for biomass production (sometimes also termed growth), and  $C_U$  is C taken up by microorganisms per unit time. Accordingly, XUE is defined as,

$$\text{XUE} = \frac{X_B}{X_U} \quad (3)$$

where  $X_B$  is the nutrient used for biomass production, and  $X_U$  is the nutrient taken up by microorganisms.

Currently, there is no reliable method for the determination of the soil microbial CUE (Sinsabaugh et al., 2013). CUE efficiency is measured by determining the incorporation and respiration of C from a specific  $^{13}\text{C}$ -labeled substrate (Frey et al., 2013). However, in this approach, microbial C use efficiency is confounded with the specific use efficiency of a given substrate (Sinsabaugh et al., 2013). Moreover, this approach is associated with a large uncertainty since soil microorganisms do not only take up C from the labeled compound, but also from soil organic matter (SOM), and they may use both sources at very different rates. In contrast, the  $q\text{CO}_2$  can be measured unambiguously in soil. The  $q\text{CO}_2$  is defined as follows,

$$q\text{CO}_2 = \frac{C_R}{C_{\text{mic}}} \quad (4)$$

where  $C_R$  is the basal respiration rate and  $C_{\text{mic}}$  is the microbial biomass C (Anderson and Domsch, 1993, 2010). The  $q\text{CO}_2$  was introduced as a measure for the ecophysiological status of soil microorganisms (Anderson and Domsch, 1993; reviewed in Anderson and Domsch (2010)). It has been used in a large number of studies, for example in relation to soil development (Insam and Haselwandter, 1989) and heavy metal contamination (Brookes, 1995). While both the CUE and the  $q\text{CO}_2$  are related to C use, they cannot directly be converted into each other.

A common model assumption for microbial element use efficiencies is  $\text{XUE} = 1$  and  $\text{CUE} = 0.5$  (Manzoni et al., 2012). This means that microorganisms are absolutely efficient in using nutrients they take up for biomass production, but only use 50% of the C they take up for biomass production. Based on this assumption,  $\text{TER}_{\text{C:N}}$  ranges from 10 to 24, assuming microbial biomass C:N ratios between 5 and 12 (see Eqn 1). Accordingly, assuming a microbial biomass C:P ratio between 40 and 80,  $\text{TER}_{\text{C:P}}$  ranges from 80 to 160.

Microorganisms growing on substrate with a higher C:X ratio than  $\text{TER}_{\text{C:X}}$  have not enough nutrients to build up as much biomass as the C concentration would allow them. Thus, it has been stated that when growing on nutrient poor substrate, microorganisms dispose of C via overflow respiration as  $\text{CO}_2$  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. Hessen et al. (2013) argued that for disposing of C via the respiratory chain, N for the proteins of the respiratory chain has to be invested. Hence, it would be more advantageous for the organism to dispose C as dissolved organic C (DOC) rather than as  $\text{CO}_2$  (Hessen and Anderson, 2008). Moreover, it has been argued that the energy that would be 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). Kaiser et al. (2014) recently showed in a theoretical model that decomposers can overcome stoichiometric imbalance between

substrate and their biomass through adjustments of the relative turnover rates of C- and N-rich pools in their biomass. Hence, while overflow respiration seems to be very likely from a stoichiometric perspective, the existence of this process is still under discussion (Hessen et al., 2013).

In forest soils, microorganisms face extreme substrate imbalances since the C:X ratios of woody plants are very high compared to the microbial biomass C:X ratio. While in phytoplankton and macroalgae, the molar C:N ratios amount to approximately 10, wood has a molar C:N ratio of up to 400 and also much higher C:P ratios than aquatic plants (Cebrian, 1999; Sterner and Elser, 2002). It has been found in meta-analysis on the C:N and C:P ratios of leaf litter collected in litter traps that the average leaf litter C:N ratio was 58 in temperate broadleaf forests and 87 in temperate coniferous forests (McGroddy et al., 2004). The molar leaf litter C:P ratio was 1702 in temperate broadleaf forests and 2352 in temperate coniferous forests (McGroddy et al., 2004). Hence, the C:N ratio, and especially the C:P ratio of temperate leaf litter is much higher than the estimated microbial  $\text{TER}_{\text{C:N}}$  and  $\text{TER}_{\text{C:P}}$ , respectively. During the decomposition of detritus, organic matter derived from woody plants changes its stoichiometry very strongly because C is mineralized, and nutrients are enriched relative to the soil mass until in the mineral subsoil the ratio of C:N:organic P gets very similar to the microbial C:N:P ratio (Kirkby et al., 2011).

In this study, we investigated how the  $q\text{CO}_2$  changes with soil C:X ratio at different depths of the organic layer and the upper cm of the mineral soil in three forest types. First, we hypothesized that the  $q\text{CO}_2$  decreases with the soil C:X ratio because microorganisms growing in nutrient-poor soil respire more C than microorganisms in nutrient-rich soil in order to match the substrate to their nutritional demands. Second, we hypothesized that in all forest soils, the  $q\text{CO}_2$  is correlated with the C:P ratio, while in soils of spruce forests, which are usually poorer in N, the  $q\text{CO}_2$  is additionally determined by the soil C:N ratio.

## 2. Material and methods

### 2.1. Study site

Samples were taken from pure beech (*Fagus sylvatica* L.), pure spruce (*Picea abies* L. Karst.), and mixed spruce-beech sites in the mountain range Solling, Lower Saxony, Germany (51° 42' 32"–51° 47' 47" °N and 9° 26' 20"–9° 39' 06" °E). Geologically, the Solling is built from tertiary sandstone covered by a layer of loess with a thickness of 20–80 cm. The soils are Cambic Podzols and Dystric Cambisols. The sites are located at an elevation of 400–490 m asl. The average annual precipitation is 1050 mm and the annual mean temperature 6.5 °C.

### 2.2. Sampling and sample preparation

We sampled 5 beech sites, 6 spruce sites, and 11 mixed beech-spruce sites. At each site, ten undisturbed soil cores were taken using plastic tubes of 15 cm diameter and 20 cm height. The organic layer and the upper 5 cm of the mineral soil were cut into 1 cm slices. Samples (except for the L layer) were sieved (<2 mm), and roots were removed. For chemical analyses, samples were dried at 60 °C and grounded. Subsamples for microbial analysis were stored at 0 °C.

### 2.3. Chemical and microbial analyses

Total C and N were measured by dry combustion using a CN analyzer (Vario, Elementar). Total P was determined by ICP-AES (Spectro, Analytical Instruments) after pressure digestion in

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