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## Element cycling as driven by stoichiometric homeostasis of soil microorganisms



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### Abstract

Cycling of carbon (C), nitrogen (N) and phosphorus (P) at the ecosystem scale is largely driven by microbial activity. A major factor that controls element cycling is the stoichiometric relationship between the microbial biomass and its substrate. I review recent advances in the field of ecological stoichiometry in terrestrial ecology with emphasis on processes performed by non-mycorrhizal soil microorganisms. The review shows that key processes of element cycling are driven by the property of microorganisms to maintain their biomass element ratio by (I) adjusting rates of element acquisition processes (organic matter decomposition, N<sub>2</sub> fixation and P solubilization) in order to acquire missing elements, and by (II) adjusting element partitioning and turnover times of elements in the microbial biomass to ratios of available elements. The review also shows that turnover times of elements in the microbial biomass have been neglected in ecological stoichiometry so far, although they are likely of high importance for microorganisms that thrive on substrates with extremely high C:nutrient ratios. Long turnover times of nutrients in the microbial biomass may explain why net nutrient mineralization also occurs at very high substrate C:nutrient ratios. In conclusion, ecological stoichiometry provides a conceptual framework for predicting relationships between the cycling of several key elements at the ecosystem scale, whose potential has not fully been exploited in terrestrial ecology yet.

### Zusammenfassung

Der Kohlenstoff (C)-, Stickstoff (N)- und Phosphor (P)-Kreislauf werden stark durch mikrobielle Aktivitäten angetrieben. Ein Hauptfaktor, der die Stoffkreisläufe beeinflusst, ist das Verhältnis zwischen der Stöchiometrie der Bodenmikroorganismen und der Stöchiometrie ihrer Umwelt. Der Artikel gibt einen Überblick über aktuelle Forschungsergebnisse auf dem Gebiet der Ökologischen Stöchiometrie in terrestrischen Ökosystemen. Zentrale Stoffumsetzungsprozesse werden von der Eigenschaft der Bodenmikroorganismen angetrieben, ihre Biomasse konstant zu halten, indem sie (i) die Raten der Nährstoffakquise oder (ii) Element-Partitionierung und die Verweilzeiten der Elemente in der mikrobiellen Biomasse an die Verhältnisse der verfügbaren Elemente anpassen. Der Überblick über die aktuelle Forschung zeigt, dass Verweilzeiten von Elementen in der mikrobiellen Biomasse bisher nicht ausreichend in der Ökologischen Stöchiometrie berücksichtigt wurden, obwohl sie vermutlich eine wichtige Rolle spielen, vor allem für Mikroorganismen, die von Substrat mit hohen C:Nährstoff-Verhältnissen leben. Lange Verweilzeiten von Nährstoffen in der mikrobiellen Biomasse erklären möglicherweise, warum N- und P-Mineralisierung auch auf Substraten mit sehr hohen C:Nährstoff-Verhältnissen erfolgen. Der Artikel zeigt, dass Ökologische Stöchiometrie einen

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konzeptionellen Ansatz bietet, der erlaubt, das Verhältnis von Umsatzprozessen verschiedener Elemente vorauszusagen, und dessen Potential in der terrestrischen Ökologie noch nicht vollständig ausgeschöpft ist.

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## Introduction

Although the microbial biomass only comprises a small proportion of organic matter in soil, it largely drives the cycling of carbon (C), nitrogen (N) and phosphorus (P) at the ecosystem scale (Van Der Heijden, Bardgett, & Van Straalen, 2008). One major factor that controls microbial processes is the stoichiometric relationship between microbial communities and their environment as proposed by Ecological Stoichiometry (ES). Based on the finding by Redfield (1934) that plankton maintains a stable biomass C:N:P ratio, Reiners (1986) was among the first to propose stoichiometric relationships between organisms and their environment as a general framework for ecosystem functioning. In the following decades, ES has been developed further mostly in the study of food webs and organic matter decomposition in the pelagic zone of lakes (Elser & Urabe, 1999; Sterner & Elser, 2002; Hessen, Elser, Sterner, & Urabe, 2013). ES provides a basis for predicting the cycling of several key elements and their relationships in ecosystems. Key processes of element cycling are explained by microorganisms, maintaining their biomass stoichiometry despite a strong mismatch between their biomass element ratio and the element ratio of their substrate. Notwithstanding the success of ES to predict processes of element cycling in aquatic ecosystem, a stoichiometric view has only recently been adopted in terrestrial ecology (Cleveland & Liptzin, 2007; Mulder & Elser, 2009; Mooshammer et al., 2012; Mulder et al., 2013; Zechmeister-Boltenstern et al., 2015). The purpose of this article is to review recent advances of ES in terrestrial ecology, showing that ES allows to integrate several key processes of element cycling beyond decomposition and provides a framework for predicting the cycling of several key elements. For the sake of brevity, the article is restricted to processes performed by non-mycorrhizal soil microorganisms.

The basis of ES is the concept of stoichiometric homeostasis, which refers to the property of an organism to keep its biomass element ratio relatively stable independently of its substrate. The soil microbial biomass, which is defined as the biomass of the soil microbial community (fungi, bacteria, archaea and protozoa), has a relatively well constrained C:N:P ratio, similar to the Redfield ratio found in planktonic biomass (Redfield, 1934) in a range between 60:7:1 and 42:6:1 (Cleveland & Liptzin, 2007; Xu, Thornton, & Post, 2013). Slight shifts in the microbial biomass stoichiometry can be caused, first, by changes in the microbial community composition (Fanin, Fromin, Buatois, & Hättenschwiler,

2013; Tischer, Potthast, & Hamer, 2014; Heuck, Weig, & Spohn, 2015), and second, by storage of C and P present in excess with respect to the microbial demands (Hessen & Anderson, 2008; Mooshammer, Wanek, Zechmeister-Boltenstern, & Richter, 2014). Yet, despite some variation, microbial biomass element ratios are relatively constrained, especially compared to the ratio of elements that are bioavailable in soil. Terrestrial decomposer communities grow on a wide range of substrates, which rarely ever meet their nutritional demands in terms of stoichiometry. For example, the litter in temperate coniferous forests has an average molar C:P ratio of 2350 (McGroddy, Daufresne, & Hedin, 2004), whereas the average molar C:P ratio of the soil microbial biomass is 60 (Cleveland & Liptzin, 2007). Likewise, the C:N ratio of the soil microbial biomass amounts to about 7 (Cleveland & Liptzin, 2007), whereas the average C:N ratio is 88 in temperate coniferous forest litter (McGroddy et al., 2004). Given these large differences between substrate and decomposer biomass stoichiometry, how do microbes maintain their biomass stoichiometry, and how does this affect element cycling at the ecosystem scale?

In this short review of recent advances to answer these two questions, I propose to differentiate between two kinds of processes by which microorganisms maintain their biomass stoichiometry; on the one hand processes of element acquisition, and on the other hand element partitioning and turnover of elements in the microbial biomass pool (Fig. 1). Soil microbial communities maintain their biomass stoichiometry (i) by adjusting the rates of processes of element acquisition in order to acquire missing elements and (ii) by adjusting element partitioning and element turnover times in the microbial biomass to ratios of available elements. Both types of processes strongly affect element cycling at the ecosystem scale.

## Element partitioning and turnover time

### Element partitioning

One way by which microbial communities maintain their biomass stoichiometry is the regulation of the partitioning of elements taken up into the microbial biomass. C, N and P taken up are partitioned between growth (buildup of biomass) and release in the form of CO<sub>2</sub>, inorganic N and P (Fig. 1). The partitioning of organic C taken up between biomass buildup and respiration is captured by the microbial

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