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Element cycling as driven by stoichiometric homeostasis of soil microorganisms



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Marie Spohn*

Department of Soil Ecology, Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Germany

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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, N₂ 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

*Tel.: +49 0921 55 5762; fax: +49 0921 55 5799.

E-mail address: marie.spohn@uni-bayreuth.de

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 CO₂, inorganic N and P (Fig. 1). The partitioning of organic C taken up between biomass buildup and respiration is captured by the microbial

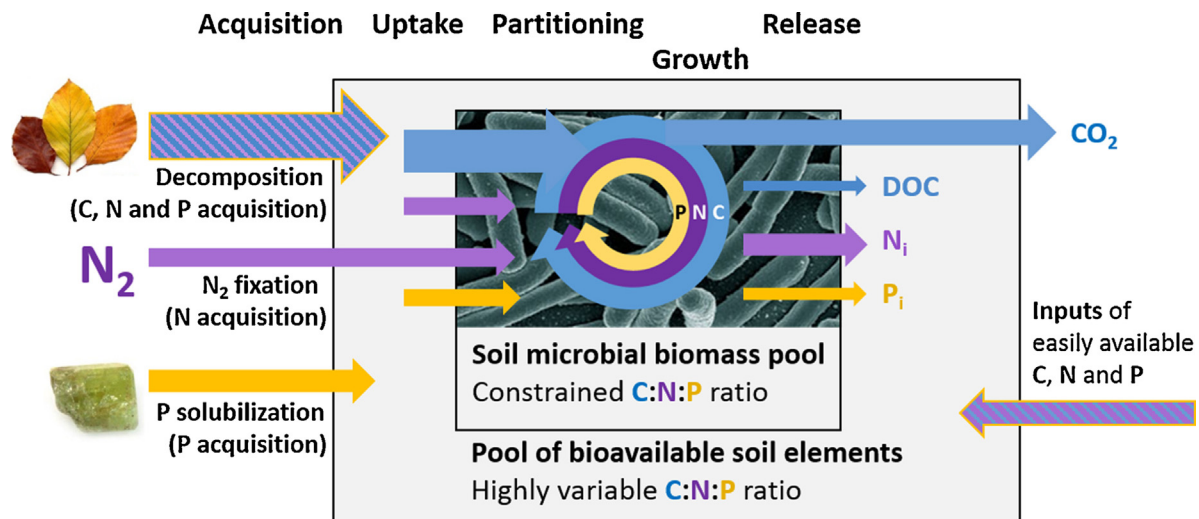


Fig. 1. The soil microbial biomass has a relatively stable stoichiometry compared to the pool of available elements in soil. Soil microbial communities maintain their biomass stoichiometry either by adjusting the rates of element acquisition processes (organic matter decomposition, N₂ fixation and P solubilization) to acquire missing elements or 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. DOC stand for dissolved organic carbon, N_i stands for inorganic nitrogen and P_i stands for inorganic phosphorus.

C use efficiency (CUE; also called gross growth efficiency or assimilation efficiency) defined as the ratio of C allocated to biomass production to C taken up (Manzoni, Taylor, Richter, Porporato, & Ågren, 2012; Sinsabaugh, Manzoni, Moorhead, & Richter, 2013). Theoretically, microbial CUE is restricted to 0.88 by thermodynamics (Gommers, Van Schie, Van Dijken, & Kuenen, 1988), meaning that not more than 88% of the C that microorganisms take up can be invested into growth, because microorganisms need at least 12% of it for energy production by respiration to maintain their biomass and acquire unavailable elements. Yet, the microbial CUE in soil is thought to hardly ever reach the theoretical maximum because environmental conditions usually request more than minimum energy investment for biomass maintenance and growth (Manzoni et al., 2012; Sinsabaugh et al., 2013). Among the factors that request additional investment of energy and C is an unfavorable stoichiometry of the available elements that forces microorganisms to allocate larger proportions of C and energy to C or nutrient acquisition (Spohn, Klaus, Wanek, & Richter, 2016; Spohn, Pötsch, et al., 2016). Several studies found that elevated N availability increased microbial CUE, likely because it allows microorganisms to allocate less C and N to N acquisition and more to buildup of biomass. Thiet, Frey, and Six (2006) reported an increase in microbial growth yields in soil amended with N by 13%. Furthermore, it was observed that bacterial growth efficiency was higher in fertilized agricultural soils than in non-fertilized forest soils (Lee & Schmidt, 2014). In a long term fertilization experiment in a temperate grassland, N fertilization but not P or K fertilization increased the microbial CUE by 38% (Spohn, Pötsch, et al., 2016).

It has been derived from models that during decomposition of forest litter, microorganisms have much more

C available in relation to N, and thus cannot use it for the buildup of biomass but release it via so-called overflow respiration, which strongly decreases their CUE (Manzoni, Jackson, Trofymow, & Porporato, 2008; Manzoni, Trofymow, Jackson, & Porporato, 2010). Overflow respiration is respiration uncoupled from the production of energy that serves to dispose of C and is known to occur in microorganisms under laboratory conditions on substrates with very high C:nutrient ratio (Russell & Cook, 1995). Yet, it is still under discussion whether overflow respiration exists *in situ* (Hessen & Anderson, 2008). From an evolutionary point of view, it seems more reasonable that microorganisms use C they cannot allocate to growth for the formation of compounds that increase their fitness or for the establishment of symbiosis instead of just disposing it (Hessen & Anderson, 2008; Hessen et al., 2013; Spohn, 2015). In a recent study it was shown that microbial CUE in the litter layer was not decreased compared to mineral soil, indicating that no overflow respiration took place despite very high C:nutrient ratios (Spohn, Klaus, et al., 2016). It should be considered that microorganisms can grow on organic matter with very high C:nutrient ratios, not only by decreasing their CUE, but potentially also by extending the mean turnover time of nutrients in the microbial biomass (see below).

Analogous to microbial CUE, microbial N use efficiency can be defined as the ratio of N allocated to the buildup of biomass and N taken up by the microbial community. Mooshammer, Wanek, Hämmerle, et al. (2014) showed that microbial N use efficiency was higher in litter, which has a high C:N ratio, than in mineral soil. Thus, the finding indicates that microbial communities regulate their N use efficiency according to the availability of N, in the way that they use N more efficiently when its availability is low.

Turnover times of elements in the microbial biomass

While the element use efficiency denotes the proportion of an element taken up that is allocated to the production of biomass, the turnover time (=mean residence time) indicates how long the element remains in the microbial biomass pool. The turnover time of an element in the microbial biomass likely increases with decreasing availability of the element (Oberson & Joner, 2005; Kaiser, Franklin, Dieckmann, & Richter, 2014), similar to the turnover time of nutrients in plants, which also increases with decreasing nutrient availability (Aerts & Chapin, 2000). This can occur at the level of a single cell as well as at the level of the microbial biomass as a biogeochemical pool, consisting of several cells. In an arable soil of the temperate zone, C had a turnover time of 82–95 days in the microbial biomass, while P had a turnover time in the same microbial biomass of 37–42 days (Kouno, Wu, & Brookes, 2002), indicating that C was more efficiently retained in the microbial biomass than P. This finding is in accordance with the generally observed C limitation of microorganisms in mineral soil. Cheng (2009) reported turnover times of the microbial biomass C of 48 and 35 days in planted soils, and 97 days in unplanted soils, suggesting that the presence of roots stimulated the turnover of microbial biomass C, likely due to the release of exudates, i.e. easily available C. Other studies on P in the microbial biomass showed rather short turnover times, suggesting that the element is quickly turned over (McLaughlin et al., 1988; Oehl et al., 2001). The efficient retention of nutrients in the biomass pool should be especially important during the decomposition of nutrient-poor organic matter as for example wood and forest litter, in which the C:nutrient ratios exceed by far the C:nutrient ratios of the microbial biomass. The immobilization of nutrients in the microbial biomass strongly affects the amounts of nutrients available for plants (Van Der Heijden, Bardgett & Van Straalen, 2008; Richardson, Barea, McNeill, & Prigent-Combaret, 2009), and thus element cycling at the ecosystem scale. However, despite its importance, the turnover times of elements in the microbial biomass have been overlooked in studies on organic matter decomposition (Manzoni et al., 2008, 2010). Yet, the adjustment of the turnover time is likely critical for microorganisms that thrive on substrates that do not match their nutritional needs in terms of element ratios, and may explain why net nutrient mineralization also occurs at very high substrate C:nutrient ratios (see below).

Element acquisition

Decomposition and mineralization

Decomposition of organic matter is a central process of element cycling which ends with the mineralization of

nutrients and organic C fixed during photosynthesis. Element ratios of organic matter have been investigated for many decades as important controls of decomposition processes mostly in litter decomposition studies (Berg & Matzner, 1997; Berg & McClaugherty, 2003). However, only few studies also considered the stoichiometry of the decomposer communities and the internal cycling of elements in the microbial biomass (Bosatta & Staaf, 1982; Manzoni et al., 2008, 2010; Zechmeister-Boltenstern et al., 2015), showing that organic C, N and P mineralization and immobilization in the microbial biomass is strongly determined by the relationship between the substrate stoichiometry on the one hand and the microbial biomass stoichiometry on the other hand. The critical substrate C:N and C:P ratio at which decomposers shift from being C-limited to being nutrient-limited or *vice versa* is called threshold element ratio (TER). When microorganisms decompose substrate with a C:N or C:P ratio beyond their TER, N and P are taken up into the microbial biomass, while below the TER net mineralization occurs (Bosatta & Staaf, 1982; Olsen et al., 1986; Urabe & Watanabe, 1992; Sterner & Hessen, 1994). The TER can be calculated as follows

$$\text{TER}_{\text{C:X}} = \frac{\text{MBC}}{\text{MBX}} * \frac{\text{XUE}}{\text{CUE}} \quad (1)$$

where CUE is the microbial C use efficiency, XUE is microbial nutrient use efficiency with X being a specific nutrient (N or P), MBC is the microbial biomass C concentration, and MBX is the microbial biomass nutrient (N or P) concentration. In agreement with these theoretical considerations, it has been shown that the stoichiometry of forest litter strongly affects rates of net organic C, N and P mineralization (Manzoni et al., 2008, 2010), gross organic C, N and P mineralization (Mooshammer et al., 2012), and organic C mineralization per unit microbial biomass (Spohn & Chodak, 2015; Spohn, 2015).

It has been concluded that decomposition of litter with high C:nutrient ratios is only possible when microorganisms strongly decrease their CUE by releasing excess C (Manzoni et al., 2010). However, it should be considered that microorganisms might also be able to grow on substrate that strongly exceeds the C:nutrient ratio required for microbial nutrition, by retaining nutrients very efficiently in their biomass, and thus increasing the turnover time of the nutrients in the biomass. This can be seen best from the equation of the TER under steady state conditions which can be written as follows

$$\text{TER}_{\text{C:X}} = \frac{C_{\text{Uptake}} \times T_{\text{C}}}{X_{\text{Uptake}} \times T_{\text{X}}} \quad (2)$$

where T_{C} and T_{X} are the turnover times of C and X in the microbial biomass, respectively (for details see Appendix A). This shows that low N or P uptake can be compensated by a long turnover time of the nutrients in the microbial biomass. The regulation of the turnover time of elements in the microbial biomass may explain why even at a very high

substrate C:nutrient ratio, as for example during the decomposition of deadwood, net nutrient mineralization occurs (Bantle, Borken, & Matzner, 2014; Ricker, Lockaby, Blosser, & Conner, 2016).

Moreover, microorganisms likely selectively feed on fractions of the soil organic matter that matches their nutritional needs (Arsuffi & Suberkropp, 1989; Hood, McNeely, Finlay, & Sterner, 2014). The co-metabolism of N-rich compounds might allow the decomposition of nutrient-poor substrate (Hood et al., 2014), and the metabolism of energy-rich compounds might provide the necessary energy to decompose more recalcitrant fractions of the soil organic matter (Craine, Morrow, & Fierer, 2007). The use of selected fractions of the organic matter affects the soil organic matter quality on the long-term.

The decomposition of organic matter and the mineralization of organic P is a C and N consuming process because it is based on the production and the release of N-rich exoenzymes. Marklein and Houlton (2012) showed in a meta-analysis that N inputs to soil either in the form of fertilizer or in the form of biologically fixed N₂ accelerated the activity of phosphatases in a wide range of terrestrial ecosystems. These results suggest that microbial communities allocate more C and N to P acquisition when there is an N input to soil.

N₂ fixation

N₂ fixation by free-living bacteria is nearly ubiquitous in terrestrial ecosystems, and it is the largest natural N input to terrestrial ecosystems. Free-living N₂-fixers may meet their N demands by fixing N₂, by acquiring mineral N from their environment or by organic matter decomposition. When inorganic forms of N are readily available in the environment, many N₂-fixing organisms switched off N₂ fixation in incubation studies (Reed, Cleveland, & Townsend, 2011). This is in accordance with an inverse relationship between N₂ fixation by free-living bacteria and N availability in several ecosystems (Smith, 1992), and a negative effect of N fertilization on free-living diazotrophs (Zackrisson, DeLuca, Nilsson, Sellstedt, & Berglund, 2004; Cusack, Silver, & McDowell, 2009). N₂ fixation is one of the metabolically most costly processes on Earth, and can require 16 mole adenosine triphosphate, i.e. 48 mole P, per one fixed mole N₂ (Simpson & Burris, 1984). This high demand for ATP may explain the high P requirements of N₂-fixing organisms (Vitousek et al., 2002). Many fertilization studies have observed a stimulatory response of N fixation by free-living bacteria to added P (Eisele, Schimel, Kapustka, & Parton, 1989; Vitousek & Hobbie, 2000; Reed, Cleveland, & Townsend, 2007), and P availability has been found to constrain N₂ fixation by free-living bacteria in tropical forest soils (Wurzburger, Bellenger, Kraepiel, & Hedin, 2012; Reed, Cleveland, & Townsend, 2013). N₂-fixation could be quantitatively predicted based on the ratio of available P:N in soil as N₂-fixation is suppressed at high soil N availability, and increases with the soil P:N ratio

(Eisele et al., 1989). The production of ATP requires energy, stored in the form of organic C. Consequently, N₂-fixation by free-living microorganisms is stimulated by organic compounds such as sugars that typically form part of root exudates (Bürgmann, Meier, Bunge, Widmer, & Zeyer, 2005). N₂ fixation might be especially important during decomposition of N-poor substrate such as deadwood because it provides additional N (Sollins, Cline, Verhoeven, Sachs, & Spycher, 1987).

Solubilization of bound inorganic P

Solubilization of bound mineral P is a central process by which P becomes bioavailable (Richardson et al., 2009; Jones & Oburger, 2011). Bound inorganic P is solubilized (i) by acidification through the release of protons (ii) by complexation of metals such as iron by the release of organic acid anions, and (iii) by exopolysaccharides and siderophores that both work as chelators (Welch, Taunton, & Banfield, 2002; Jones & Oburger, 2011). The capacity to solubilize P is widely spread among microorganisms, and more than half of all cultivatable bacteria were able to solubilize P in temperate croplands (Browne et al., 2009). Microorganisms solubilized P more actively when C sources were available (Hameeda, Reddy, Rupela, Kumar, & Reddy, 2006; Patel, Archana, & Kumar, 2008). Since the release of bound inorganic P is caused by organic acids and siderophores that contain C and N (Jones & Oburger, 2011), the solubilization of P should also underlay stoichiometric constraints. Yet, ES has never been applied to the release of nutrients such as P from minerals or bound inorganic forms.

Conclusion

ES provides a conceptual framework that allows for integrating several key processes of element cycling. Being based on element ratios, which by definition are dimensionless, ES offers to compare biological systems across a wide range of spatial scales where quantities differ greatly. This short review of current research showed that stoichiometric homeostasis of soil microorganisms is a driver of element cycling in terrestrial ecosystems. Processes of terrestrial element cycling can be predicted based on the ratio of elements in the environment and element partitioning and turnover of elements in the microbial biomass. Moreover, the review shows that turnover times of elements in the microbial biomass have been rather neglected in ES so far, although they might be of importance for microorganisms that thrive on substrates with extremely high C:nutrient ratios, and may explain why net nutrient mineralization also occurs at very high substrate C:nutrient ratios. Taken together, ES offers a conceptual basis for predicting the cycling of several key elements that still has not fully been exploited in the study of element cycling in terrestrial ecosystems yet.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.baec.2016.05.003>.

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