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Do fungi need salt licks? No evidence for fungal contribution to the Sodium Ecosystem Respiration Hypothesis based on lab and field experiments in Southern Ecuador



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ABSTRACT

Though typically discussed in the context of salinity, a shortage of sodium in tropical forests has been demonstrated in recent years, inhibiting soil biota with impacts on decomposition processes (Sodium Ecosystem Respiration hypothesis). So far, sodium limitation has been shown for soil fauna, whereas a potential role in saprotrophic fungi remains unknown. We tested the hypothesis that fungi have sodium demands at low levels resulting in reduced activity in tropical soils, analyzing fungal responses to sodium availability. Despite careful experimentation and the usage of different fungal strains we did not find evidence for fungal sodium demands using controlled nutrient media, not even in the absence of potassium. Likewise, there was no significant fungal response to sodium additions in litter samples, though decomposition rates were positively affected. These findings suggest that sodium is not essential for osmoregulation of tested fungal strains, which are hence not affected by sodium limitation.

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1. Introduction

Soil fungi represent a highly diverse group with important roles in ecosystem functioning, especially with respect to carbon and nutrient cycling (Nannipieri et al., 2003; van der Heijden, 2008). Disentangling the environmental drivers which determine fungal activity and growth is thus fundamental for our understanding of ecosystem functioning, especially in understudied tropical forests. In this context soil nutrient limitations have an essential role and especially nitrogen and phosphorus (co-)limitations are often discussed as a prevalent factor controlling ecosystem dynamics (Elser et al., 2007; Vitousek et al., 2010; Camenzind et al., 2017), though in

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the case of fungal activity carbon availability also plays an important role (Kamble and Baath, 2014; Reischke et al., 2014). Interestingly, the influence and interplay of other elements has often been overlooked, and in certain tropical areas elements such as potassium, molybdenum and calcium have been shown to limit tree growth as well as microbial activity (Wright et al., 2011; Wurzburger et al., 2012; Wullaert et al., 2013; Kaspari and Powers, 2016). Very recently, sodium (Na) has also received attention in tropical rainforests, and has been revealed as a limiting factor controlling decomposition rates (Kaspari et al., 2009; Dudley et al., 2012).

Though Na is globally primarily discussed in relation to its toxic effects in saline environments (e.g. Omar et al., 1994; Evelin et al., 2009), certain areas especially in the tropical biome receive very low Na inputs. Studies in the Amazon basin demonstrated decreasing Na inputs by rainfall with increasing distance from the

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ocean (Stallard and Edmond, 1981; Tardy et al., 2005). Na availability may become extremely low in inland tropical soils, in concert with generally highly weathered parent material (Walker and Syers, 1976). This phenomenon was previously described for mammals or birds and their usage of salt licks (Dudley et al., 2012). Kaspari et al. (2008b: 2009: 2014) and Clav et al. (2014, 2015) expanded these findings to ants and termites, but also other soil fauna, which responded positively to Na additions. They further discovered that this sodium shortage was accompanied by important shifts in a highly relevant ecosystem process - the decomposition of plant litter. Na additions enhanced the decomposition of different litter types, and based on these findings Kaspari et al. (2014) formulated the Sodium Ecosystem Respiration (SER) hypothesis for tropical forests, which states that "Na is critical for consumers but not plants, that Na shortfall is more likely on highly weathered soils inland from oceanic aerosols, and that this shortfall results in decreased decomposer activity". So far, this hypothesis has been confirmed in several tropical forest sites across the globe (Kaspari et al., 2009, 2014; Clay et al., 2015; Jia et al., 2015; Risch et al., 2016). The Na shortage arises from a discrepancy in Na levels in plant litter resources - since plants use potassium (K) instead of Na to regulate osmolarity - and the high Na demand of its animal consumers (Clay et al., 2014; Ott et al., 2014). The affected process of litter decomposition is highly relevant for ecosystem productivity in tropical forests, since nutrient recycling plays a predominant role for plant nutrition in these partly nutrient scarce soils (Walker and Syers, 1976; Quesada et al., 2010; Cleveland et al., 2013). Thus, Na limitation, even though only relevant for decomposers, may exert control on the whole ecosystem.

Litter decomposition is a highly complex process, mediated by soil fauna but also microbes such as saprobic fungi (Gonzalez and Seastedt, 2001; Hättenschwiler et al., 2005; Powers et al., 2009). Fungi have so far not been explicitly addressed in the context of the SER hypothesis, though their potential contribution to litter decomposition processes may be of fundamental importance (Hättenschwiler et al., 2005; van der Heijden, 2008). Preliminary findings by Kaspari et al. (2014) using basic assessments of hyphal abundance showed a positive trend following Na additions, though these effects were not significant. Based on the available literature there is no clear information about potential fungal Na demands at low concentrations (Scharnagl et al., 2017), whereas a large amount of studies documented salinity effects on fungal growth and activity (e.g. Tresner and Hayes, 1971; Gleason et al., 2006; Hammer et al., 2011). From an ecological perspective, the few available comparative studies on Na concentrations in soil, plant and fungal tissues point towards higher Na contents in fungi compared to plant material, especially in a tropical site (Stark, 1972; Cromack et al., 1979; Scharnagl et al., 2017), though still below values reported for soil fauna (Cromack et al., 1979). Additionally, several laboratory experiments have been conducted evaluating the effects of varying Na concentrations on fungal growth. These studies, however, clearly focused on high/toxic salt conditions and methods were adapted accordingly (e.g. Tresner and Hayes, 1971, Fig. 1; Gleason et al., 2006). Nevertheless, these experiments partly also indicate a slight increase in fungal growth at the lowest Na concentration applied, pointing towards fungal Na demands at low concentrations (lones and Jennings, 1965; Chen et al., 2001; Matsuda et al., 2006; Smolyanyuk et al., 2013). Regarding fungal physiology, analyses of cell transport systems and osmoregulation of fungi show patterns similar to plants - a preferential usage of K for cell functioning (Jones and Gadd, 1990; Rodriguez-Navarro, 2000). Fungal K transport systems are well described (Rodriguez-Navarro and Ramos, 1984; Benito et al., 2004; Corratge-Faillie et al., 2010) and K is known to be important for fungal growth (Yuan et al., 2005; Husekova et al., 2016). Still, Na uptake systems have likewise been characterized for fungi (Benito et al., 2004, 2011; Corratge-Faillie et al., 2010) and few studies indicate a potential substitution of K by Na in low K conditions (Camacho et al., 1981; Ortega and Rodriguez-Navarro, 1986), a mechanism which was also reported for plants growing on K deficient soils (Subbarao et al., 1999; Wakeel et al., 2011).

Here, we aimed to evaluate the Na demand of several fungal strains and its potential ecological impact at a low Na tropical site in Southern Ecuador. We tested the hypotheses that: (1) fungi need Na at low concentrations as indicated by positive growth responses to very low Na doses (Fig. 1) and a substitution of K by Na additions; and (2) this may lead to reduced fungal activity in low Na environments and a fungal contribution to the SER hypothesis in tropical rainforests. To do this, we analyzed the response of fungal growth and activity of strains isolated from a tropical low Na environment to Na additions under different growth conditions, which covered the range from controlled laboratory to realistic field conditions (see Fig. 2).

2. Materials and methods

First, the effects of Na limitation and fungal substitution of K by Na was tested by analyzing the growth of ten fungal isolates in response to various Na concentrations in defined growth media, in part in a factorial design with K as an additional factor. Beforehand, a first insight was gained on general fungal responses to Na additions by experimental testing of three fungal isolates from a temperate grassland, covering different fungal phyla (Supplementary Material S1). These pre-experiments were also used to elaborate experimental designs applied here, namely to identify the range of Na concentrations potentially representing Na limitations and to optimize growth media to ensure only Na was the limiting



Fig. 1. Illustration of the addressed hypothesis that fungi need sodium at low concentrations. Toxic concentrations given are based on values provided in the literature (Tresner and Hayes, 1971; Estaun, 1990; Gleason et al., 2006; Matsuda et al., 2006; Tang et al., 2009).

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