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Review paper

Salt effects on the soil microbial decomposer community and their role in organic carbon cycling: A review

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ABSTRACT

Salinization of soil is recognised as one of the most pressing environmental challenges to resolve for the next century. We here conduct a synoptic review of the available research on how salt affects decomposer microbial communities and carbon (C) cycling in soil. After summarizing known physiological responses of microorganisms to salinity, we provide a brief overview and qualification of a selection of widely applied methods to assess microorganisms in soil to date. The dominant approaches to characterise microbial responses to salt exposure have so far been microbial biomass and respiration measurements. We compile datasets from a selection of studies and find that (1) microbial biomass-carbon (C) per C held in soil organic matter shows no consistent pattern with long-term (field gradients) or short-term (laboratory additions) soil salinity level, and (2) respiration per soil organic C is substantially inhibited by higher salt concentrations in soil, and consistently so for both short-term and long-term salinity levels. Patterns that emerge from extra-cellular enzyme assessments are more difficult to generalize, and appear to vary with the enzyme studied, and its context. Growth based assessments of microbial responses to salinization are largely lacking. Relating the established responses of microbial respiration to that of growth could provide an estimate for how the microbial C-use efficiency would be affected by salt exposure. This would be a valuable predictor for changes in soil C sequestration. A few studies have investigated the connection between microbial tolerance to salt and the soil salinity levels, but so far results have not been conclusive. We predict that more systematic inquiries including comprehensive ranges of soil salinities will substantiate a connection between soil salinity and microbial tolerance to salt. This would confirm that salinity has a direct effect on the composition of microbial communities. While salt has been identified as one of the most powerful environmental factors to structure microbial communities in aquatic environments, no up-to-date sequence based assessments currently exist from soil. Filling this gap should be a research priority. Moreover, linking sequencing based assessments of microbial communities to their tolerance to salt would have the potential to yield biomarker sets of microbial sequences. This could provide predictive power for, e.g., the sensitivity of agricultural soils to salt exposure, and, as such, a useful tool for soil resource management. We conclude that salt exposure has a powerful influence on soil microbial communities and processes. In addition to being one of the most pressing agricultural problems to solve, this influence could also be used as an experimental probe to better understand how microorganisms control the biogeochemistry in soil.

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1. Introduction

The United Nations Rio+20 summit initiated the process to update the Millennium Development Goals, and committed the member nations to create new Sustainable Development Goals (SDG) for the new century. Recently, a first attempt strove to

identify and distil out a tentative list (Griggs et al., 2013). This work stressed that most central for achieving a sustainable planet is the stable functioning of the Earth systems – including biodiversity and biogeochemical cycles. A sustainable planet must build on this foundation. Out of six identified targets for 2030 by the pioneering authors, three – sustainable food security, sustainable water security, and sustaining biodiversity and ecosystem services – are directly dependent on a mechanistic understanding for how the microbial regulation of soil biogeochemistry is affected by salinization.

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Soil salinization is a term used for the accumulation of salt in soils at a level that negatively impacts agricultural productivity, environmental health and economic welfare (Rengasamy, 2006b). Generally, a soil is described as saline if the electrical conductivity measured in a saturated soil paste (EC_e) is higher than 4 dS m^{-1} (US Laboratory Staff, 1954). The Food and Agriculture Organisation of the United Nations (FAO) estimates that globally over 830 M ha of arable land are affected by salinization (Szabolcs, 1989; Martinez-Beltran and Manzur, 2005), corresponding to about 10% of the globe's arable land (Szabolcs, 1989). Salinization affects up to 3 M ha land in Europe, the 17 western states of the USA, >5% of the land in Africa, about a fifth of the arable land of West Asia, and 30% of the Australian land area (Chhabra, 1996; Rengasamy, 2006b; UNEP, 2007; Ladeiro, 2012), making it a world-wide environmental challenge. Of the global threats that collectively compromise about 10 ha arable land per minute (Griggs et al., 2013), salinization contributes about 30% (Buringh, 1978).

In the context of this review on the effects of salt, we refer to salts as ionic compounds composed of an equal number of anions and cations. Ionic bonds between the oppositely charged ions form through electrostatic attraction. Most salts are easily soluble in water, leading to the presence of ions in solution. In soils, the pore water contains a variety of dissolved ions such as Na^+ , Ca^{2+} , NH_4^+ , Cl^- or SO_4^{2-} . As soil water content decreases, dissolved ions become more concentrated. Salt accumulation in the surface soil is often found in agricultural areas in arid and semi-arid regions, where it is caused by irrigation with brackish or saline water in poorly drained soils (Allison, 1964). In areas with a shallow groundwater body evaporating ground water can also lead to higher salt concentration in the soil surface layer (Rengasamy, 2006b). In addition, soil salinization can be the result of changes in vegetation cover that alter ecosystem water balances. For instance, in Australia extensive areas are undergoing dryland salinization as a consequence of the replacement of native, deep-rooted perennial vegetation with shallow-rooted agricultural plants. This led to lower evapotranspiration of rainfall and waterlogging of areas with saline groundwater (Clarke et al., 2002). A vegetation change in the opposite direction, from grassland to forest, can also lead to soil salinization, when evapotranspiration exceeds groundwater recharge (Jobbagy and Jackson, 2004; Jackson et al., 2005). Salt water intrusion from marine environments is also an important cause for soil salinization (Chandrajith et al., 2014), which has resulted in the salinization of 53% of coastal regions in e.g. Bangladesh (Haque, 2006).

Salinization leads to physical changes in soil. High salt concentrations result in flocculation or dispersion of soil particles, which influences soil organic matter (SOM) solubility (Shainberg and Letey, 1984; Wong et al., 2009, 2010). In addition, the type of salt predominantly present in the soil also plays a role in determining SOM solubility. Multivalent cations in the soil solution, such as Ca^{2+} , can link together negatively charged clay particles and organic compounds (Oades, 1984). Thereby the presence of multivalent cations can increase the sorption of organic matter to soil particles (Mikutta et al., 2007; Mavi et al., 2012) and thus reduce the amount of organic matter available for decomposition (Oades, 1988; Six et al., 2000). Monovalent cations such as Na^+ form much weaker bonds. Soils with a high concentration of Na^+ are called sodic soils. Soils are normally considered to be sodic if they have a sodium absorption ratio (SAR) > 13. If a sodic soil also has an electrical conductivity $>4 \text{ dS m}^{-1}$ it is classified as saline-sodic (US Salinity Laboratory Staff, 1954). In sodic soils the sorption of organic compounds to the soil matrix is reduced (Setia et al., 2013). If a higher percentage of exchange sites are occupied by monovalent cations, cross-linking between organic molecules and mineral surfaces is decreased. Soils become more liable to erosion and

leaching, and organic matter is less protected from decomposition (Sumner and Naida, 1998; Wong et al., 2010). Dispersion of soil particles can also affect oxygen availability with consequences for microbial activity (Bronick and Lal, 2005).

Soil salinization naturally has direct impacts on plants, and has subsequently been a research priority for crops for decades (Ayers and Westcot, 1976; Chhabra, 1996; Katerji et al., 2003; Arshad, 2008; Stevens and Partington, 2013). For instance, salt exposure is known to reduce crop yield under greenhouse and field conditions in e.g. barley (Pal et al., 1984; Richards et al., 1987), wheat (Richards, 1983; Bajwa et al., 1986), cotton (Meloni et al., 2001; Soomro et al., 2001), sugar cane (Choudhary et al., 2004), rice (Bajwa et al., 1986), maize (Bajwa et al., 1986) and sugar beet (Ghoulam et al., 2002). Crops and cultivars differ in their tolerance to salinity, and this is also modulated by environmental and soil factors. Furthermore, indirect consequences of salinization are ion imbalance and nutrient deficiency (Marschner, 1995), further aggravating the negative effects on plant productivity. Although crop resistance to salt exposure is a promising development (e.g. Bennett et al., 2013), overall plant productivity will be impeded by salinization. However, less is known about the effects of salinity on soil microorganisms. This review will therefore focus on responses of the microbial decomposer community and soil C cycling to salinity.

Soil is the habitat for a huge concentration of microorganisms. According to estimates, 1 g of soil contains up to ten billion bacterial cells (Torsvik and Ovreas, 2002; Horner-Devine et al., 2004) and kilometres of fungal hyphae (Bååth and Söderström, 1979; De Boer et al., 2005). Microorganisms are the principal drivers of all nutrient cycles, and especially for the decomposition of SOM, thereby regenerating plant nutrients. Consequently, any effects by salt on microbial processes will have large implications for SOM dynamics, ecosystem biogeochemical cycling, and plant nutrition (Marschner, 1995; Raich and Potter, 1995; Schlesinger, 1997; Rustad et al., 2000; Setia et al., 2010; Setia et al., 2012). SOM decomposition is influenced by a range of abiotic and biotic factors, such as temperature and moisture (Waksman and Gerretsen, 1931; Davidson and Janssens, 2006), as well as pH (Blagodatskaya and Anderson, 1998; Rousk et al., 2011a), redox conditions (Schmidt et al., 2011) and the community composition of microbes, plants and fauna (Wardle et al., 2004). Salinity is an environmental factor that is receiving increasing attention, but our understanding of the effect of soil salt concentrations on the structure and functioning of the soil microbial community is still fragmented and incomplete.

With this review we intend to provide a synoptic review of the available literature to date on how salt exposure influences decomposer microorganisms and decomposer microbial processes relating to the C cycle in soil. While comprehensive reviews on the effects of salinization on the soil N cycle, along with literature reviews on how salinization effects can be mitigated through land management are not available, either of these subjects deserve separate treatment and will and should encompass extensive research compilations. Furthermore, it should be noted that the ecosystem consequences of salinization will be a balanced outcome of the effects on both the plant community and the below-ground soil microbial decomposer community. This review will not specifically focus on the effects on the plant community, and for interested readers we refer to an already existent body of work in e.g. Zhu (2001) and Parida and Das (2005).

Our endeavour to review salt effects on the soil microbial decomposer community and C cycling necessitates brief summaries of how salinity can affect the microbial physiology, along with an overview and qualification of current methods used to assess microorganisms in salt-exposed soil. We will review what insights systematic application of these methods has revealed about the

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