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Influence of salinity and water content on soil microorganisms

Nan Yan[a,b,*], Petra Marschner[c], Wenhong Cao[a,b], Changqing Zuo[a,b], Wei Qin[a,b]

[a]*Department of Sediment Research, China Institute of Water Resources and Hydropower Research, Beijing 100048, China*
[b]*Research Centre on Soil and Water Conservation of the Ministry of Water Resources, Beijing 100048, China*
[c]*School of Agriculture, Food & Wine, The Waite Research Institute, The University of Adelaide, Adelaide, SA 5005, Australia*

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Abstract

Salinization is one of the most serious land degradation problems facing world. Salinity results in poor plant growth and low soil microbial activity due to osmotic stress and toxic ions. Soil microorganisms play a pivotal role in soils through mineralization of organic matter into plant available nutrients. Therefore it is important to maintain high microbial activity in soils. Salinity tolerant soil microbes counteract osmotic stress by synthesizing osmolytes which allows them to maintain their cell turgor and metabolism. Osmotic potential is a function of the salt concentration in the soil solution and therefore affected by both salinity (measured as electrical conductivity at a certain water content) and soil water content. Soil salinity and water content vary in time and space. Understanding the effect of changes in salinity and water content on soil microorganisms is important for crop production, sustainable land use and rehabilitation of saline soils. In this review, the effects of soil salinity and water content on microbes are discussed to guide future research into management of saline soils.

Keywords: Salinity; Water content; Soil microorganism

Contents

*Corresponding author at: China Institute of Water Resources and Hydropower Research, Beijing 100048, PR China. Fax: +86 68416371.
E-mail address: yannan8521@sina.com (N. Yan).
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1. Introduction

It is predicted that the human population will reach 8 billion in 2025. To avoid or minimize food shortage, saline soils have to be rehabilitated and managed to meet the food demand of an ever growing human population (Ladeiro, 2012). Soil microorganisms constitute less than 0.5% (w/w) of the soil mass, but they play a key role in soil properties and processes. Salinity affects plants and microbes via two primary mechanisms: osmotic effect and specific ion effects (Oren, 1999; Chhabra, 1996). Another factor influencing plants and microbes is soil water content. Soil water potential which relates to the energy level by which the water is held in the soil also closely related to soil salinity, it is influenced by osmotic potential in the soil solution.

2. The importance of soil microorganisms for nutrient cycling

Soil microorganisms constitute less than 0.5% (w/w) of the soil mass, but they play a key role in soil properties and processes. Soil microbes include bacteria, archaea, fungi, protozoa and viruses (Tate, 2000). Microorganisms participate in oxidation, nitrification, ammonification, nitrogen fixation, and other processes which lead to decomposition of soil organic matter and transformation of nutrients (Amato & Ladd, 1994), they can also store C and nutrients in their biomass which are mineralized after cell death by surviving microbes (Anderson & Domsch, 1980). Our understanding of these processes increased considerably in recent years with advances in molecular and analytical methodologies which have led to more successful strategies to modify them for a range of ecosystem services (Frey, Six, & Elliott, 2003; Gessner et al., 2010; Rillig & Mummey, 2006).

Nutrient cycling is the flux of nutrients within and between the various biotic or abiotic pools in which nutrients occur in the soil environment (Brady & Weil, 2002). Microorganisms have a major impact on the cycling of elements, most of which are essential for the growth of living organisms. Bacteria, archaea and fungi, in particular, are crucial for the cycling of several important inorganic nutrients in soils. Through oxidation, ammonification, nitrogen fixation and other processes, organic materials are decomposed, releasing essential inorganic plant nutrients to the soil. Nitrate (through nitrification), sulfate (through sulfur oxidation), phosphate (through phosphorus mineralization) are present in soils primarily due to the action of microorganisms. Therefore, microbes are essential to maintain a productive and valuable soil system. Disturbance of the soil environment, such as land use change or soil cultivation, can shift microbial communities and can have detrimental effects on soil nutrient cycling (French et al., 2009).

In addition, the emission of CO_2 from soils, which includes respiration from soil organisms and roots, contributes approximately 10% to atmospheric CO_2 (Raich & Potter, 1995). Microbes also play an essential role in the formation of humic substances which are stable forms of organic C and critical for organic C sequestration in soils (Burns et al., 1986). (Fig. 1).

3. Soil salinity

3.1. Soil salinity definition

A soil that contains excess salts so as to impair its productivity is called a salt-affected soil. Salt in the soil can influence soil processes through the salt concentration in the soil solution (salinity) which determines the osmotic potential and the concentration of sodium on the exchange complex of the soil (sodicity) which influences soil structural stability. Salinity can, over time, lead to sodicity. The major soluble salts in soils are the cations Na^+ (sodium), Ca^{2+} (calcium), Mg^{2+} (magnesium) and K^+ (potassium), and the anions Cl^- (chloride), SO_4^{2-} (sulfate), HCO_3^- (bicarbonate), CO_3^{2-} (carbonate) and NO_3^- (nitrate) (Shi & Wang, 2005). There are several classification systems for salt-affected soils in the world, for example the USDA system, the USSR system and the Australian

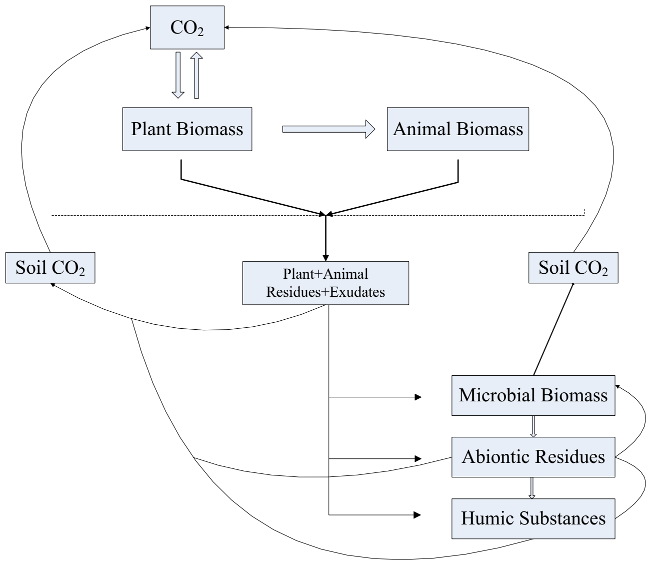

Fig. 1. Conceptual model of carbon cycle emphasizing transfers between major soil organic matter pools (Tate, 2000).

Table 1
Classification of salt-affected soils.

Salt-affected soil classification	EC_e ($dS\ m^{-1}$)	pH	Sodium adsorption ratio	Soil physical condition
Saline	> 4.0	< 8.5	< 13	Normal
Saline–sodic	> 4.0	< 8.5	> 13	Normal
Sodic	< 4.0	> 8.5	> 13	Poor

system (Chhabra, 1996). The USDA system classifies soils in three distinct categories (saline, sodic and saline–sodic soils). Saline soils have an electrical conductivity of the saturated paste (EC_e) > 4 dS m^{-1}, ESP < 15 or SAR < 13 and pH < 8.5. Sodic soils have an ESP > 15 or SAR > 13. Soils that have both detrimental levels of neutral soluble salts (EC_e > 4 dS m^{-1}) and a high-proportion of sodium ions (ESP > 15 or SAR > 13) are classified as saline–sodic soils (Brady & Weil, 2002; CISEAU, IPTRID, AGLL, & FAO, 2005) (Table 1). Salt-affected soils can be classified according to how the salinity developed: primary salinity which occurs naturally where the soil parent material is rich in soluble salts, or geochemical processes result in salt-affected soil. Secondary salinity is salinization of land and water resources due to human activities. Human activities which can induce salinization include poor irrigation management; insufficient drainage; improper cropping patterns and rotations; chemical contamination (Oldeman, Hakkeling, & Sombroek, 1990; UNEP, 2007).

3.2. Effects of salinity on microorganisms

High-concentrations of soluble salts affect microbes via two primary mechanisms: osmotic effect and specific ion effects.

Soluble salts increase the osmotic potential (more negative) of the soil water, drawing water out of cells which may kill microbes and roots through plasmolysis. Low osmotic potential also makes it more difficult for roots and microbes to remove water from the soil (Oren, 1999). Plants and microbes can adapt to low osmotic potential by accumulating osmolytes, however, synthesis of osmolytes requires large amounts of energy and this results in reduced growth and activity (Oren, 1999; Wichern, Wichern, & Joergensen, 2006). At high-concentrations, certain ions, including Na^+, Cl^-, and $HCO_3^-HCO_3^-$, are toxic to many plants (Chhabra, 1996).

Many studies showed that salinity reduces microbial activity, microbial biomass and changes microbial community structure (Andronov et al., 2012; Batra & Manna, 1997; Pathak & Rao, 1998; Rousk, Elyaagubi, Jones, & Godbold, 2011; Setia, Marschner, Baldock, Chittleborough, & Verma, 2011). Salinity reduces microbial biomass mainly because the osmotic stress results in drying and lysis of cells (Batra & Manna, 1997; Laura, 1974; Pathak & Rao, 1998; Rietz & Haynes, 2003; Sarig, Fliessbach, & Steinberger, 1996; Sarig & Steinberger, 1994; Yuan, Li, Liu, Gao, & Zhang, 2007a). Some studies showed that soil respiration decreased with increasing soil EC (Adviento-Borbe, Doran, Drijber, & Dobermann, 2006; Wong, Dalal, & Greene, 2009; Yuan et al., 2007b). Setia, Marschner, Baldock, and Chittleborough (2010) found that soil respiration was reduced by more than 50% at $EC_{1:5} \geq 5.0$ dS m^{-1}. However, Rietz and Haynes (2003) reported that soil respiration was not significantly correlated with EC, but as EC increased, the metabolic quotient (respiration per unit biomass) increased. The sensitivity of soil enzyme activities to salinity varies: activities of urease, alkaline phosphatase, β-glucosidase were strongly inhibited by salinity (Frankenberger & Bingham, 1982; Pan, Liu, Zhao, & Wang, 2013), whereas dehydrogenase and catalase were less affected (Garcia & Hernandez, 1996).

As explained above, microorganisms have the ability to adapt to or tolerate stress caused by salinity by accumulating osmolytes (Del Moral, Quesada, & Ramos-Cormenzana, 1987; Quesada, Ventosa, Ramoscormenzana, & Rodriguezvalera, 1982; Sagot et al., 2010; Zahran, Moharram, & Mohammad, 1992). Proline and glycine betaine are the main organic osmolytes and potassium cations are the most common inorganic solutes used as osmolytes accumulated by salinity tolerant microbes (Csonka, 1989). However, the synthesis of organic osmolytes requires high-amounts of energy (Killham, 1994; Oren 2001). Accumulation of inorganic salts as osmolytes can be toxic therefore it is confined to halophytic microbes which evolved salt tolerant enzymes to survive in highly saline environments. Fungi tend to be more sensitive to salt stress than bacteria (Gros, Poly, Monrozier, & Faivre, 2003; Pankhurst, Yu, Hawke, & Harch, 2001; Sardinha, Muller, Schmeisky, & Joergensen, 2003; Wichern et al., 2006), thus the bacteria/fungi ratio can be increased in saline soils. Differences in salinity tolerance among microbes results in changes in community structure compared to non-saline soils (Gros et al., 2003; Pankhurst et al., 2001).

4. The effects of soil water availability on microorganisms

4.1. Forms of water in soils

Substantial volumes of water are commonly stored in soils. For example, 1ha of medium textured soil (1 m deep) with a water content at field capacity of 20% can store 8.0×10^5 L water (Or & Wraith, 2000). Plants and organisms rely heavily on water in soils and water is essential for nutrient cycling. However, soil water content varies both in time and in space which not only influences water availability to plants and microbes but also has a major effect on the rate of diffusion of solutes and gases (Adl, 2003).

The status of soil water can be described in two ways: the soil water content, which indicates how much water is present, and soil water potential, which relates to the energy level by which the water is held in the soil. The water potential is the amount of pressure that needs to be applied to transport a solution of known molarity from a referenced elevation to that of pure water (McKenzie, 2002), mainly including matric, osmotic and gravitational potential. Processes dealing with water balance are usually more related to water content; whereas processes related to water movement are mainly related to soil water potential (Warrick & Or, 2007).

4.2. Effect of water content on microbes

Water is not only an essential transport medium for substrates, it is also an important participant in hydrolysis processes. Therefore soil water content controls microbial activity and is a major factor that determines the rates of mineralization (Paul et al., 2003). However, excess soil water content results in limited O_2 diffusion because O_2 diffusion in water is much lower (about 10^4 times) than in air which will reduce the activity of aerobic microorganisms (Kozlowski, 1984; Skopp, Jawson, & Doran, 1990), but could increase the activities of anaerobes. Lack of water reduces microbial activity and growth (Bottner, 1985; Kieft, Soroker, & Firestone, 1987), C and N mineralization (Pulleman & Tietema, 1999; Sleutel et al., 2008) and shifts microbial community structure (Hueso, Garcia, & Hernandez, 2012; Sorensen, Germino, & Feris, 2013). Cells retain sufficient water for cell turgor and metabolism by maintaining a higher osmotic potential (more negative) in the cytoplasm than that of the surrounding environment (Martin, Ciulla, & Roberts, 1999). At low water content (high water potential), soil microbes can accumulate organic and inorganic compounds which increases the osmotic potential inside their cells. Therefore the principal tolerance mechanism for low water content and high-salinity is the same: accumulation of osmolytes. Further as soils dry out, substrate supply becomes increasingly limited because the pores drain and water films around aggregates become thinner and disconnected (Ilstedt, Nordgren, & Malmer, 2000; Stark & Firestone, 1995).

Fungi, Gram-positive bacteria and archaea can better tolerate high matric potential than Gram-negative bacteria because they have stronger cell walls (Fierer, Schimel, & Holden, 2003; Martin et al., 1999; Schimel, Balser, & Wallenstein, 2007; Vasileiadis et al., 2012).

4.3. Effect of fluctuating water content on soil microorganisms

Soil moisture and the distribution of water within a soil profile vary with seasonal cycles of rainfall, irrigation periods (farm lands) and temperature. In semi-arid and Mediterranean ecosystems, surface soils frequently experience long dry periods followed by a relatively rapid wetting (Fierer & Schimel, 2002). The effects of drying and rewetting on soil microbial processes have been studied (Griffiths, Whiteley, O'Donnell, & Bailey, 2003; Herron, Stark, Holt, Hooker, & Cardon, 2009; Ilstedt et al., 2000; Schimel et al., 2007; Xiang, Doyle, Holden, & Schimel, 2008). The concentration of available substrate and microbial activity peak in the first 24 h after rewetting (Fierer & Schimel, 2003). This is because, upon rewetting, cells of sensitive microbes lyse, whilst other microbial genotypes release the organic solutes they accumulated during the dry phase (Halverson, Jones, & Firestone, 2000). Furthermore, soil aggregates break down and their previously protected organic matter is exposed and can then be decomposed. Microbial biomass, activity and nitrification decrease with increasing number of dry and rewetting cycles (Mikha, Rice, & Milliken, 2005; Nelson, Ladd, & Oades, 1996; Wu & Brookes, 2005). The decrease in microbial biomass with increasing number of drying and rewetting cycles may be due to the higher microbial biomass turnover (Van Gestel, Merckx, & Vlassak, 1993) and the loss of C during the flush in respiration upon rewetting (Fierer & Schimel, 2003). However, the response of microbial activity to drying and rewetting varies with soil type (Jin, Haney, Fay, & Polley, 2013) which may be due to the interaction of soil moisture and soil type, aggregation and the concentration of potentially bioavailable soil organic matter (Anderson & Ingram, 1993). However, drying and rewetting can also kill some microbes and change microbial community structure which, in turn, could influence nutrient cycling (Fierer et al., 2003; Schimel et al., 2007). Butterly, Bunemann, McNeill, Baldock, and Marschner (2009) found that drying and rewetting induced a reduction in fungi and an increase in Gram-positive bacteria (Butterly et al., 2009).

5. Conclusion

Soil salinity is a threat world-wide to agricultural production and ecosystems because it reduces plant growth and microbial functioning. The effects of salinity and soil water content on soil microbes have been studied extensively, but usually separately, in saline soils, the water content also influences the salt concentration in the soil solution (osmotic potential), the study of interaction between soil water content and salinity on soil microbes is needed. Further in the field, soil salinity and water content are not constant in time and space. Therefore, experiments are needed to better understand the effect of fluctuating salinity and soil water content on soil microbes. Synthesis of osmolytes requires large amounts of energy. Therefore addition of organic materials such as plant residues or manures as nutrient sources for microbes may be an important strategy to ameliorate saline soils. Future research could investigate the effect the properties of organic materials such as decomposability and nutrient content on microbial tolerance to osmotic stress.

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