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Review

Soil salinity: A neglected factor in plant ecology and biogeography

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ABSTRACT

This paper argues that soil salinity needs to be more broadly acknowledged as a driving factor in plant ecology—not only in the ecology of halophytes—in order to understand and make more accurate predictions for the impact of environmental change on biodiversity and vegetation patterns throughout the semi-arid world. It summarizes recent research on soil salinity and plant distributions in semi-arid environments throughout the world: there is empirical as well as experimental evidence that soil salinity, even at low levels, is an abiotic stress factor that influences vegetation patterns and diversification. Lines of evidence demonstrating salinity's potential influence as a selective agent in East Africa and North America are presented. The paper then synthesizes recent results from spatial ecology, plant and insect systematics and behavioral ecology, focusing on Australia, that support a role for salinity in evolutionary ecology of *Acacia*. On a shorter time scale, soil salinity may play a role in weed invasion and woody vegetation encroachment in Australia.

1. Introduction

Recently there has been much activity related to predicting the impact of climate change on biodiversity, nevertheless the question of what determines the distribution of species, one of the most basic in ecology, is still unanswered for most of Australia and much of the rest of the world (Austin and Van Niel, 2011; Hughes, 2003; Kier et al., 2005). Five categories of factors that determine distribution and abundance of plant species are recognized (Mueller-Dombois and Ellenberg, 1974): climatic; edaphic; geographic-historic factors; species interactions; and perturbations. These factors also govern the composition and structure of plant communities. They also act as evolutionary stress factors.

That climatic and topographic data are not always sufficient to explain vegetation patterns is evident (e.g., Austin and Van Niel, 2011; Bertrand et al., 2012; Bui and Henderson, 2003; Dirnbock et al., 2002; Martin et al., 2006; Reed et al., 2009). Yet even when edaphic factors are taken into consideration by plant ecologists and biogeographic modelers, soil moisture/texture, pH, and nutrients are generally the only variables considered. Although soil salinity is recognized as a major limitation to cropping (e.g., Lauchli and Luttge, 2002; US Salinity Laboratory, 1969; Zhu, 2001) and the focus of many plant breeding efforts to produce salt-resistant crops (e.g., Flowers et al., 2010; Lauchli and Luttge, 2002; Parida and Das, 2005), generally, it is neglected as a factor in plant ecology, except in the ecology of deserts (salt pans and playas) and wetlands (salt marshes, mangroves) where its importance is obvious given the prevalence of halophytes.

This paper first considers definitions of saline soils and halophytes, and reviews the role of soil salinity in plant ecology and geography around the world but then focuses on Australia. It presents new evidence that salinity plays a role at the macro-level, in the diversification of the genus *Acacia*, with more than 900 native Australian species. Australia is one of the most biologically unique areas of the world, with one of the most extensive arid zones; natural salinity is widespread, with extensive playa lake systems and saline and sodic soils (Northcote and Skene, 1972; Rengasamy, 2006).

1.1. What is soil salinity?

The definition of saline soil is confusing.[1] Soils are considered saline if they contain salt in a concentration sufficient to interfere with the growth of most crop species. Saline soils have an electrical conductivity >4 dS m^{-1} (~36 mM NaCl) measured on a saturated soil paste extract at 25 °C (US Salinity Laboratory, 1969). Electrical

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[1] Soil scientists distinguish **saline** soils with an electrical conductivity >4 dS m^{-1}, pH < 8.5, and Na < 15% of total exchangeable cations from **sodic** soils with Na > 15%, and in older literature, **alkali** soils with pH > 8.5. Here I will be discussing broadly **salt-affected soil**: soil that has been adversely modified for the growth of most crop plants by the presence of soluble salts, with or without high amounts of exchangeable Na (SSSA glossary, https://www.soils.org/publications/soils-glossary#). Salt-affected soils can be saline and alkaline.

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conductivity is a measure of the ease with which electrical current will pass through water: the greater the salinity, the greater the conductivity; however, the relationship is a function of the specific ions present in the solution and their concentrations. Depending on the soil texture, the relative water and salt content, and osmotic pressure of the saturation extract can be very different (Fig. 7, US Salinity Laboratory, 1969). When soil water content less than saturation, plants will experience salt concentration higher than that measured in the test for soil salinity. Salinity level will change down a soil profile with seasonal moisture fluctuations and relative soil water content but salt is generally localized below the root zone. Expressing salinity as a soil profile-integrated value (e.g. Bui and Henderson, 2003) dilutes the presence of salt concentrated in a single horizon only.

Salt accumulation is a phenomenon that is not unique to any particular soil type in many soil classifications but it is typically associated with "Soils influenced by water" especially Solonetz (alkaline) and Solonchak (salt enrichment upon evaporation) Soil Groups in the World Reference Base (IUSS, 2006). It occurs where evaporation is high relative to precipitation (there is a seasonal water deficit) and leaching is insufficient to move salts out of the soil profile (Duchaufour, 1982; Schofield and Kirkby, 2003). Secondary salinization can arise when salts accumulate near the soil surface as a result of rising water tables due to land management practices such as irrigation or tree clearing (Cisneros et al., 1999; Rengasamy, 2006; Runyon and D'Odorico, 2010; Silburn et al., 2009; Williamson, 1986). Thus a large fraction of natural and secondary salinity occurs in desert and grassland biomes, in savanna ecosystems, which are often used as rangelands, and are closely associated with semi-arid, seasonally contrasted climates in the tropics and sub-tropics. Nevertheless the occurrence of salt-affected soils is not a perfect match with climate, even when also taking lithology (a potential source of solutes released by weathering) into account (Schofield and Kirkby, 2003). Saline and sodic soils often occur in or near local topographic lows in the landscape where soluble salts accumulate under endorheic drainage conditions, thus they are often seasonally waterlogged and can be associated with wetlands. Approximately 10% of the Earth's total land surface may be salt-affected (Schofield and Kirkby, 2003).

Soil salinity can imply the presence of chlorides, sulfates, nitrates, (and bicarbonates) of sodium (Na), calcium (Ca), magnesium (Mg), and potassium (K). High levels of carbonates are reflected by soil pH >8.3. Saline soils often have a typical sequence of horizon chemistry that reflects the position and salt content and chemistry of the underlying water table, the dominant upward trend of water movement through the profile, and the solubility of salts (e.g., Fig. 1). Microbial activity can also influence saline soil chemistry and vice versa (Miletto et al., 2008; Whittig and Janitsky, 1963; Wolicka and Jarzynowska, 2012). Vegetation zonation is demarcated as a function of salts and their chemical composition (e.g., Cisneros et al., 1999; Richardson et al., 1994; Stewart and Kantrud, 1972) and changes in vegetation cover lead to changes in the soil hydrology and chemistry (e.g., Cisneros et al., 1999; Runyon and D'Odorico, 2010; Silburn et al., 2009).

Global patterns of salinization have changed over geologic time with climate (Kershaw et al., 2003). Importantly, as Schofield and Kirkby (2003) have shown, climate change will impact on the spatial pattern of soil salinity by changing patterns of precipitation and evapotranspiration, and landscape hydrology.

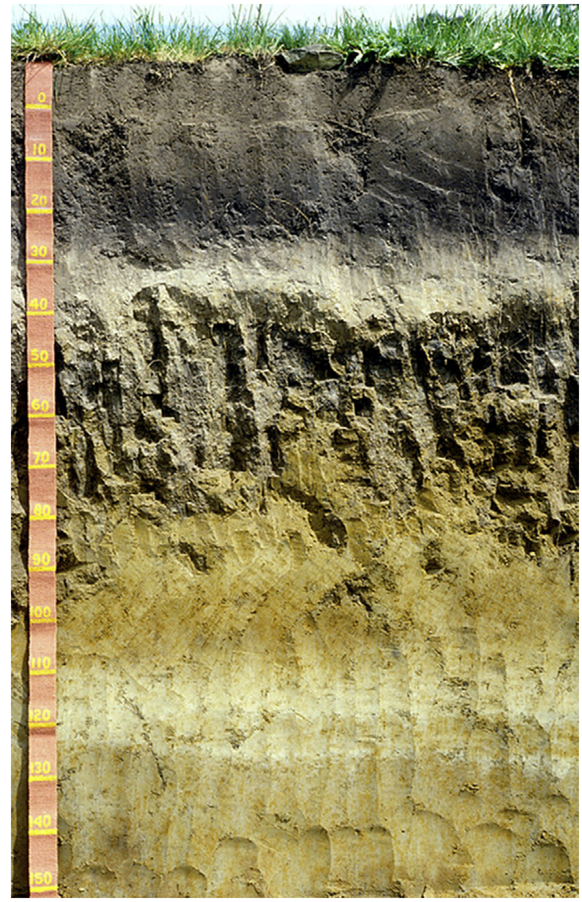

Fig. 1. Well developed Solonetz at Keyneton, South Australia with a typical horizon sequence: a brown or black surface horizon with organic matter dispersed by Na cations; pale (*albic*) eluviation horizon directly over a horizon with exchangeable Na >15% (*natric*), columnar structure, and pH of about 8.5 (indicative of the presence of free sodium carbonate); a horizon with Ca-carbonate (*calcic)* is present below the *natric* horizon. The sequence of mineral precipitates in the profile follows the Hardie and Eugster (1970) sequence for the evolution of closed basin brines thus indicating the presence of a shallow (~2 m) water table with Ca < CO_3 during the soil's formation. (Photo courtesy of Rob Fitzpatrick). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

1.2. Plant response to soil salinity

Most plants are glycophytes that tolerate only low concentrations of salt before they are adversely affected as evidenced by decrease in productivity and/or death. The threshold salt concentration that separates halophytes from glycophytes has been set at different levels by different authors. Flowers et al. (2010) use a threshold of 200 mM NaCl which corresponds roughly to 20 dS m^{-1} but others have used 80 mM NaCl (~8 dS m^{-1}) to distinguish between halophytes and non-halophytes. Obligate halophytes require saline conditions to grow whereas facultative halophytes are found in less saline habitats and are characterized by broader physiological diversity that enables them to cope with saline and non-saline conditions[2] (Parida and Das, 2005). Salt-tolerant glycophytes exhibit some physiological mechanisms to reduce sodium toxicity although they are not halophytes (e.g. Flowers et al., 2010; Hamilton et al., 2001; Parida and Das, 2005).

Even low soil salinity levels (<4 dS m^{-1}) can exert physiological stress on plants by affecting osmotic potential, ion toxicity (Na, Cl, and other ions could be toxic), photosynthesis (reduction in

[2] Thus they apparently show phenotypic plasticity (the ability of a single genotype to produce multiple phenotypes in response to variation in the environment) as defined by Pfennig et al. (2010). Phenotypic plasticity can promote diversification because the developmental pathways that underlie environmentally induced phenotypes consist of many genetic components that can potentially respond to selection.