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Review paper

Plant–soil interactions in metal contaminated soils

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ABSTRACT

The legacy of industrialization has left many soils contaminated. However, soil organisms and plant communities can thrive in spite of metal contamination and, in some cases, metabolize and help in remediation. The responses of plants and soil organisms to contamination are mutually dependent and dynamic. Plant–soil feedbacks are central to the development of any terrestrial community; they are ongoing in both contaminated and healthy soils. However, the theory that governs plant–soil feedbacks in healthy soils needs to be studied in contaminated soils. In healthy soils, negative feedbacks (*i.e.* pathogens) play a central role in shaping plant community structure. However to our knowledge, the nature of feedback relationships has never been addressed in contaminated soils. Here we review literature that supports a plant–soil feedback approach to understanding the ecology of metal-contaminated soil. Further, we discuss the idea that within these soils, the role of positive as opposed to negative plant–soil feedbacks may be more important. Testing this idea in a rigorous way in any ecosystem is challenging, and metal contamination imposes an additional abiotic constraint. We discuss research goals and experimental approaches to study plant–soil interactions applicable to metal-contaminated soils; these insights can be extended to other contaminated environments and restoration efforts.

1. Introduction

Recent decades have seen a growing interest in the role of facilitation on plant community development and composition with respect to stressful environments (Stachowicz, 2001; Kivlin et al., 2013). Twenty years ago, Bertness and Hacker (1994) demonstrated that the success of a salt-marsh plant community was determined by facilitation from neighbor plants in stressful or anoxic sediments. Since then, the role of facilitation from neighboring plants has been tested along environmental stress gradients (Espeland and Rice, 2007), and the use of 'nurse plants' in facilitating plant community development has been applied to restoration in limiting and harsh environments (Padilla and Pugnaire, 2006; Eränen and Kozlov, 2007). Moreover, recent evidence has shown that facilitation between species within the plant community can enhance phytoremediation of metals in contaminated soils (Wang et al., 2014). The mechanisms of facilitation and remediation are rooted in soils, and this review is focused specifically on plant–soil interactions in metal-contaminated-soils. The contributions by soil microorganisms to remediate metal contamination and the biology of the microbes and their host plants have been well documented (Ma et al., 2011; Sessitsch et al., 2013); this topic is not covered here. However, the dynamic relationships among plants, soil organisms, and metal contamination have not been sufficiently explored. Plant–soil feedbacks, the bidirectional relationships between plants and their soils, can be affected by abiotic factors (Clarholm and Skyllberg, 2013) that pose a selective force on the community. Research has shown that major drivers like climate change (van der Putten et al., 2010; Rajkumar et al., 2013) can affect the plant–soil relationship. Metal contamination, another important stressor on soils, has also been found to alter the nature of plant and soil community interactions (Pawlowska et al., 1997; Zhang et al., 2007).

The global increase in human development and land use is rapidly changing our world (DeFries et al., 2004). When soils accumulate contaminants, the health of the ecosystem is influenced (Effland and Pouyat, 1997). Soil ecologists have well-developed theories of plant–soil feedbacks (Wardle, 2002; Bardgett and Wardle, 2010). Traditionally, plant–soil feedback theory suggests that negative feedbacks, such as pathogens or nematode and insect pests from the soil, drive plant community

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structure and diversity. This idea has been studied extensively and recently reviewed (Bever et al., 2012; van der Putten et al., 2013). Indeed, experiments in many different systems, including a meta-analysis of grassland soil data, have shown that negative feedbacks from soil are the primary force affecting plant community succession, distribution, composition and diversity (Packer and Clay, 2000; Engelkes et al., 2008; Kulmatiski et al., 2008; Mangan et al., 2010). In contrast, facilitation, a positive feedback from the soil to the plant, is frequently associated with biological invasions (van der Putten et al., 2013). When soil metal contamination exerts an abiotic stress on a biotic community, selection will favor organisms with resistance traits over those with strong competitive ability. Relationships within these communities tend toward facilitation (Bertness and Callaway, 1994; Wagner, 2004).

Contamination can mean many things; this review is focused on soils contaminated with metals. Soil organic matter (SOM) is central to metal remediation and nutrient cycling and must be considered in the context of soils with metal contaminants. However, studying SOM levels can be complicated for two reasons. First, many sites contaminated with metals are also contaminated with organic pollutants complicating accurate measurements of SOM in the field. Second, as contaminated sites become re-vegetated, SOM will naturally accumulate in the soil, affecting the relationship between the plants, soil microbes and metals. It is undeniable that SOM plays an important role in mediating the interactions of plants, soil microbes and metals. In this review however, we focus only on the literature and our experiences with metal contamination, rather than organic pollution, as we tie a recent and relevant case study to literature surrounding plant and microbe community responses to metals in soils.

As an introduction, we highlight an ongoing case study from Liberty State Park (LSP) in Jersey City, New Jersey, USA, a previously industrial site affected by metal and organic contamination that is now undergoing natural succession. We then review the literature on the response of soil organisms to metal contamination, and make the argument that contaminated systems must be studied within the context of feedbacks, among plants, soil organisms and soil metals (Fig. 1). We also suggest that facilitation, within the context of metal-contaminated soils, may be more important than historical paradigms focused on negative plant–soil feedbacks would suggest. This is a hypothesis in need of testing. Bruno et al. (2003) have identified the role of facilitation in the succession and establishment of plant communities in stressful environments that result from naturally occurring ecological changes. Metal contamination in soils, on the other hand, is likely not caused by naturally occurring ecological changes. Studying effects of metals on plant and soil communities is important and has applications to restoration and natural recovery of disturbed or postindustrial land. We review literature here that describes metal-contaminated soil with respect to both mono-specific experiments or plots and whole diverse plant communities and at various stages of succession (van der Putten et al., 2013). We conclude by describing some possible approaches to address this increasingly important and highly relevant question in soil ecology, and discuss methodologies to increase our understanding of the mechanisms driving succession, remediation and community composition.

2. Liberty State Park – a case study in the ecology of metal-contaminated soils

Postindustrial landscapes are increasingly providing the opportunity for restoration and adaptive reuse. However, developing long-term solutions to metal-contaminated soils requires a deep understanding of the ecology of the site. The state of the plant and soil communities with respect to their contaminant is dynamic. Metal contamination may serve as a direct and negative filter on both the soil and plant communities. At the same time, the bottleneck of this filter results in a community that is resilient to metals

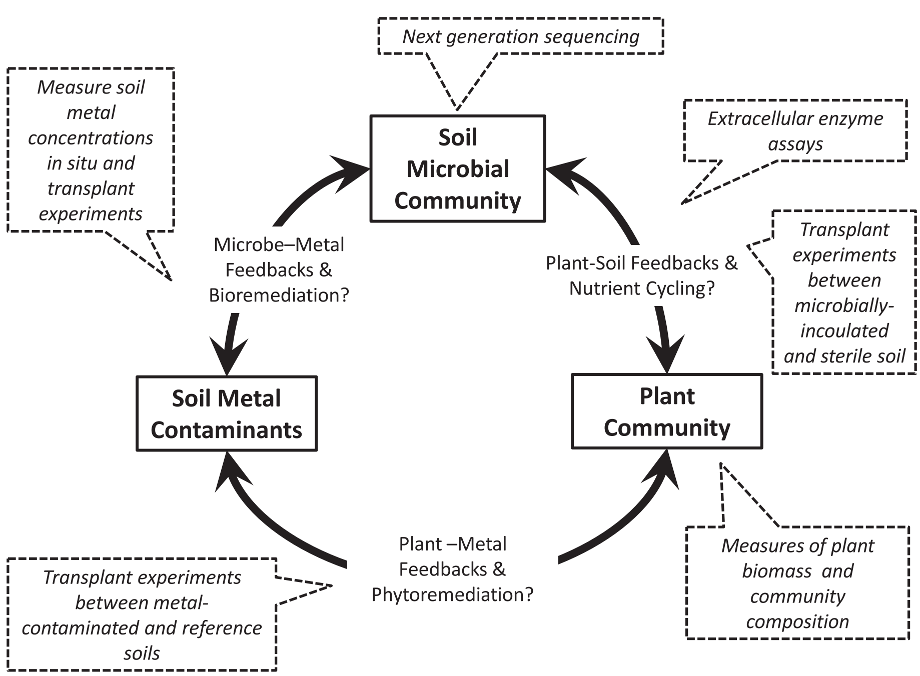

Fig. 1. Scheme showing the dynamic three way relationship among plants, soil organisms and metal contamination. Boxes with solid lines contain the three pools (plants, soil metals, and soil organisms) connected by two-way arrows indicating feedback relationships. Important research questions are noted across the arrows between the pools. Possible experimental methods to address the questions are marked in dashed-line call-out-boxes. These methods, when applied to a well designed experiment or field study along a concentration gradient, will resolve the mechanisms of interaction among plants, soil microbes and metal contamination in soils. Some of the questions that can be answered include, but are not limited to: 1.) Does a unique microbial community form as a result of contamination; 2.) Does the unique microbial community lead to increased nutrient cycling or remediation? and 3.) At what levels of contamination do we see changes in the plant and soil communities?