Plant access to inositol phosphates in soil

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Phosphorus deficiency is a major constraint to the growth of plants in many natural and agricultural ecosystems throughout the world. Plants have therefore developed mechanisms to enhance the availability of soil phosphate. These include changes to root structure, association with mycorrhizal fungi and other soil microorganisms, and biochemical processes at the root-soil interface (Jakobsen *et al*., 2005). Mineralization of phosphate from soil organic P by phosphatase enzymes is of particular significance, as organic P accounts for a major proportion (generally 40 to 80%) of the total P in most soils, occurring primarily as inositol phosphates (Turner *et al.*, 2002). However, our understanding of the utilization of specific organic P substrates in soil, and the role of plant and/or microbial phosphatases to organic P mineralization is limited (Richardson *et al.*, 2005). Similarly, it is unclear whether mycorrhizae provide plants increased access to soil organic P above that of their benefit in increasing soil exploration (Joner *et al*., 2000). Importantly, and despite the predominance of inositol phosphates in most soils, we have little understanding of their biological availability.

A number of studies using controlled growth conditions have shown that inositol phosphates are a potential source of P for plants. However, their contribution is dependent on the P-fixation capacity of the soil or growth media used (Adams and Pate, 1992; Findenegg and Nelemans, 1993; Hayes *et al*., 2000). Inositol phosphates are subject to adsorption and precipitation reactions in soil (see paper by Celi *et al.*) which are major factors in determining their availability. Using a range of species grown in sterile culture, we have also shown that plants have limited ability to directly access P from inositol phosphates, which is associated with insufficient extracellular phytase activity of roots (Richardson *et al*., 2000). Growth and P nutrition of plants was improved significantly by the addition of either purified phytase or inoculation with phytase-producing microorganisms (Hayes *et al*., 2000; Richardson *et al*., 2001a). Transgenic plants (arabidopsis, tobacco, potato and subterranean clover) that express heterologous phytase genes (eg, *phyA* from *Aspergillus*), and release extracellular phytase from their roots, also show significantly increased ability to acquire P from inositol phosphates when supplied as an available substrate (Richardson *et al.*, 2001b; Zimmermann, e*t al*., 2004; George *et al.*, 2004; George *et al.*, 2005a).

However, the importance of extracellular phytase for improving the P nutrition of plants grown in soil is less evident. Whilst some studies have shown that plant utilization of inositol phosphates can be improved by microbial inoculation, other studies have indicated little or no benefit (Tarafdar and Marschner, 1995; Martin 1973; Richardson *et al*., 2001a). Using transgenic subterranean clover that express *phyA*, no P nutrition response was observed when plants were grown in an unamended acidic and P-deficient pasture soil (George *et al.*, 2004). Transgenic tobacco similarly showed no response in this soil when unamended, but had 14 to 32% greater P content relative to control plants when grown in P-fertilized soil. The P nutrition of tobacco was also increased by up to 52% when inositol phosphate was added (as Ca-phytate) to the soil, although absolute growth of the plants was still significantly less than that for plants that received an equivalent amount of inorganic P (George *et al.*, 2005a). The

importance of substrate availability to the P nutrition of plants that express *phyA* has further been investigated using soils with differing organic P contents. In separate experiments, consistently greater P accumulation by plants that express *phyA* has been observed in soils with naturally high organic P contents (George *et al*., 2005b).

Mineralization of inositol phosphates in the rhizosphere of plants has recently been demonstrated using NMR-spectroscopy (Chen *et al*., 2004). Although the extent of mineralization was dependent on soil type, greater depletion was observed in soils under radiata pine compared to ryegrass, and it was suggested that this may be due to association with ectomycorrhizal fungi and greater phosphatase activity in the rhizosphere. We have also observed specific depletion of monoester-phosphates in the rhizosphere of transgenic clover plants that release extracellular phytase (George *et al.*, 2005c). Interestingly, depletion of organic P by the plants appeared to be greatest from recently synthesized organic P as determined by radioactive tracer. This suggests that microbial synthesis of inositol phosphates was apparent and that plants exuding the microbially-derived phytase have increased capacity to access this P. Such dynamics may also account for the greater response observed when transgenic plants were grown in fertilized soils, but further work to verify this is required.

Clearly there is a need to better understand the biological cycling of inositol phosphates in soil and the factors that affect their synthesis and degradation. The importance of mycorrhizae and other soil microorganisms and their interaction with plant roots, and role of root exudates requires more detailed investigation. Better understanding of the efficacy of inositol phosphate-phytase interactions in soil is needed (see paper by George *et al*.), as is the need to apply appropriate analytical procedures to measure 'biologically-relevant' pools of inositol phosphates. Better knowledge of the behavior of inositol phosphates in soil may ultimately improve P-fertilizer management and provide economic and environmental benefit for a more sustainable agriculture.

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