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Using systems modelling to explore the potential for root exudates to increase phosphorus use efficiency in cereal crops

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ABSTRACT

Enhanced citrate release from crop roots has been one of the recent breeding targets for increased phosphorus (P) use efficiency (PUE), due to the potential of root citrate to solubilise soil P. However, it is unclear about the level of citrate efflux required to significantly impact on crop PUE in different soils. This paper presents a modelling approach to assess the field level impact of root exudates on crop PUE. The farming systems model, APSIM, was modified to include the effect of root citrate efflux on P availability in soil, crop P uptake and growth. With parameters derived from literature, the model was used to simulate the long-term impact of root citrate across soil and climatic conditions. Preliminary results showed contrasting long-term and short-term impacts due to either the accumulated effect of solubilisation or the depletion of soil P reserve. The major impact of enhanced citrate efflux is to increase the efficiency of applied P. The enhanced model enables simulations of a wide range of combinations of Genotype by Environment by Management (GxExM) scenarios, to address knowledge gaps, and to assist in design of field testing for validating the performance of new wheat varieties across environments.

1. Introduction

Phosphorus (P) is a macro nutrient required by crops, and inputs of P are needed to maintain soil fertility. Modern agriculture is dependent on P derived from phosphate rock, which is a non-renewable resource, and needs to be well-managed to avoid over-exploitation (Cordell et al., 2009; Cornish, 2010). For a single season, only 10–20% of the applied P in fertilisers is directly used by crops due to the reaction of soluble P fertilisers with soil constituents, while the rest is bound with soil particles as adsorbed P, as sparingly-soluble precipitates of P or as organic P, some of which is recalcitrant to mineralisation (Cornish, 2009). Subsequent use of residual P depends largely on soil types and management, rarely exceeds 50% in most Australian soils (Holford, 1997; Bünemann et al., 2006). On some loam soils with optimal management, the long-term recovery of applied P can reach 80% (Wang et al., 2010; Song et al., 2010). The balance is mostly found to be 'tightly bounded' with soil, which is 'unavailable' or only slowly available to plants. On acid and alkaline soils, the recovery of applied P by crops is much lower, due to reaction of P with Al (acidic soil) and Ca (alkaline soil) to form insoluble compounds. While application of P fertilisers is needed to achieve maximum crop production, continued addition of P into soil could also lead to build-up of P in soil and potentially cause environmental problems. Therefore, increasing P use efficiency (PUE), particularly on soils with high P buffering capacity, is essential to maintain crop productivity, avoid negative impacts on the environment, and sustain the resource base.

Different approaches have been explored to increase the PUE of crops. Traditional methods include banded application of P fertilisers which increases the close contact of fertiliser to crop roots (Leikam et al., 1981; Santos et al., 2004), and deep placement of P fertilisers where the surface soil was dry (Jarvis and Bolland, 1990; Singh et al., 2005). Managing the rhizosphere to solubilise soil P and enhance crop uptake has also been explored through application of NH_4–N (Thomson et al., 1993) or intercropping with legumes (Li et al., 2008) to cause acidification of the soil, and through manipulation of rhizosphere microorganisms to increase microbiological activity to dissolve sparingly soluble inorganic P (Harvey et al., 2009). In addition, breeding efforts aimed at selection of genotypes that have larger or more efficient root systems and that have an enhanced efflux of root exudates (mainly citrate) to solubilise soil P are considered to have great potential to increase PUE (Jones,

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1998; Richardson et al., 2009, 2011). While some of these measures have been shown to be effective (e.g., banding, deep placement), some still remain uncertain, particularly the ones related to plant manipulation such as root structure modification and enhancement of root exudation of organic anions (Ryan et al., 2001).

The assumed benefits of citrate efflux for solubilising P in soils were based on the fact that organic anions can enhance P mobilisation into soil solution (Jones, 1998; Khademi et al., 2010) and that some legume plants that posses relatively large root system (Ali et al., 2002) or higher efflux of citrate from roots (e.g., white lupin) (Hocking et al., 1997; Dinkelaker et al., 1989; Neumann et al., 1999) are able to grow better in P deficient environments. For breeding or selecting new genotypes of other crops, like wheat, it still remains unclear: 1) what level of citrate efflux is needed to have significant impact on crop PUE in different soils, 2) how the citrate solubilisation effect on soil P interacts with enhanced root growth to affect crop P uptake, and 3) what data are needed to quantify these processes and their system-wide impacts. Along with the increased investment into breeding and selection programs, there is an urgent need for new approaches to integrate knowledge and information gained from molecular biology and plant physiology to understand the significance of individual processes to the performance of the whole system (Dunlop and Phung, 2002).

In this paper, we discuss an integrated approach based on crop systems modelling to assess the potential impact of new plant traits on PUE across different climate and soil environments. We will: 1) briefly review the current understanding and available data on citrate release from plant roots and its impact on PUE, with a particular focus on modelling, 2) show how a modelling approach helps understand how solubilisation effect on soil P by root exudates interacts with enhanced root growth to affect PUE of crops, and 3) discuss the potential of combining farming system modelling and crop breeding to advance our understanding.

2. Knowledge of root exudates, their impact and data availability for modelling

It is widely believed that the release of organic anions from plant roots can solubilise unavailable inorganic soil P, thus enhance P mobilisation into soil solution, and improve the plant P uptake and growth (Jones, 1998; Khademi et al., 2010). This is particularly important under P limiting conditions, because the release of citrate, malate and oxalate from roots of some plant species increases with the onset of P deficiency (Jones, 1998; Vance et al., 2003; Ryan et al., 2001). It has been reported that release of organic acid, particularly citrate, increased in *Brassica napus* (Hoffland et al., 1989), white lupin (*Lupinus albus*) (Dinkelaker et al., 1989), and the Proteaceae family of plants (Roelofs et al., 2001) in response to P deficiency. The organic anion excretion also helps enhance tolerance to Al toxicity (de la Fuente et al., 1997). The apparent rates of citrate excretion from the roots of rice plants has a range of 155–337 nmol g^{-1} fresh root weight (FW) h^{-1} (Kirk et al., 1999b) with the maximum rate in the order of 360 nmol g^{-1} FW h^{-1} (Kirk et al., 1999a). For wheat, a lower range of 1.3–3.1 pmol g^{-1} FW s^{-1} (1 pmol $= 10^{-3}$ nmol) was reported by Jones (1998) based on calculations from Delhaize et al. (1993). Much higher values of 75–185 nmol g^{-1} FW h^{-1} (40–100 pmol per 4 mm root apex per hour) were reported for a Brazilian wheat genotype Carazinho (Ryan et al., 2009). The highest rates appear to occur in white lupin (1656–2376 nmol g^{-1} FW h^{-1}) and members of the Proteaceae (3600–9000 nmol g^{-1} FW h^{-1}) (Roelofs et al., 2001). More data on efflux from roots of different crops are summarised in Jones (1998), Ryan et al. (2001) and Roelofs et al. (2001). As a summary, the maximum rate of citrate exudation from roots in naturally occurring plants is approximately 200, 300, 2000, and 9000 nmol g^{-1} FW h^{-1} for wheat, rice, white lupin and Proteaceae, respectively.

Despite many studies indicating the impact of organic anion release from roots on P use efficiency, there is a lack of field data on comparison of the performance of different species/genotypes in P deficient soils. Most studies compare genotypes grown in hydroponics, artificial media or occasionally P-deficient soils in glasshouse conditions. In a pot experiment with alkaline soil, López-Bucio et al. (2000) measured enhanced phosphorus uptake in transgenic tobacco plants that expressed a *Pseudomonas aeruginosa* citrate synthase gene and overproduced citrate, which also produced 15% more biomass at flowering time and 23–35% more biomass at completion of fruit set under P limiting treatments, as compared to a normal tobacco plant. However, Delhaize et al. (2001) indicated that expression of the *P. aeruginosa* citrate synthase gene did not lead to enhanced citrate release, thus questioned the results of López-Bucio et al. (2000). By growing a single wheat plant in rhizosphere microcosms filled with calcareous soil, injection of oxalate resulted in a several-fold enhancement in plant P uptake, however, injection of citrate had no effect due to rapid mineralization of citrate in this soil (Khademi et al., 2010). Strom et al. (2002) showed that local injection of citrate and oxalate into the rhizosphere led to increased P uptake by maize. In addition, Gerke (1994) demonstrated that the presence of these carboxylates in the rhizosphere could increase the diffusion coefficient of P in soil solution by two or three orders of magnitude. It is obvious that there is significant uncertainty about the impact of citrate released from plant roots on PUE in different soils. To the best of our knowledge, there are no data available to compare performance of genotypes with different efflux of citrate release or across different soils.

Kirk (1999) and Kirk et al. (1999a,b) studied the effect to solubilise P by citrate released from rice plants grown in a controlled thin-layer system packed with weathered humic clay soil, and discussed three possible mechanisms by which the excretion of organic anions from roots may solubilise P: 1) by changing the soil pH, 2) by displacing P from adsorption sites, and 3) by chelating metal ions that would otherwise immobilise P or form soluble metal–chelate complexes with P. They further pointed out that changes in pH are only important where the anion is excreted in association with protons and in large quantities; and likewise, displacement of adsorbed P is only important where large amounts of organic anions are excreted. Through modelling of the diffusion and decomposition of organic anions released from rice plants and their reaction with soil in solubilising phosphate, Kirk (1999) showed that the organic anion excretion could account for the observed phosphate solubilisation and plant P uptake, and that plant P uptake increases linearly with citrate efflux, with the rate of increase determined by the increase in P concentration in soil solution due to unit increase in citrate concentration. They further concluded that the main mechanism of solubilisation involved chelation of metal ions and formation of soluble citrate-metal-P complexes or both (Kirk et al., 1999a, 1999b). In another study, Devau et al. (2010) suggested that other root-induced chemical process, the uptake of Ca, was also controlling P nutrition under P-deficient soils. However, current modelling of the interactions of organic anions with metal ions in soils is hindered by poor understanding of the basic chemistry of organometallic complexes and biodegradation of the organic anions in soil (Ryan et al., 2001).

The modelling study of Kirk (1999) provides useful insights into understanding of the processes related to P solubilisation and enhanced crop P uptake as affected by citrate release from the root system. It shows that for a given efflux of organic anion, the increase in plant P uptake is sensitive to the relative rates of diffusion