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#### ABSTRACT

Crop production relies on continuous input of large amounts of phosphorus (P) in form of mineral fertilisers manufactured from phosphate rock (PR), a finite resource likely to be depleted within a century. Developing crop varieties with enhanced efficiency for P will make a key contribution to sustainable use of P resources. Crop yield (Y<sub>seed</sub>) in the context of nutrient-use efficiency can be expressed as a function of total accumulated nutrient in the plant (Nut<sub>accum</sub>), nutrient harvest index (NutHI, the fraction of total accumulated nutrient in the plant that is allocated to the seed), and seed nutrient concentration (%Nut<sub>seed</sub>): Y<sub>seed</sub> = Nut<sub>accum</sub> (NutHI/%Nut<sub>seed</sub>). In this paper, we review the physiological traits and processes affecting the components of this simple model for improving the P-use efficiency of crops, with a particular focus on root architectural traits for enhancing P-acquisition efficiency (PAE) and hence Nut<sub>accum</sub>. As field-grown crops commonly encounter a combination of various abiotic stresses, the potentially negative effects of root architectural traits for improved P acquisition on crop water uptake are also considered.

Given that P efficiency at whole-plant level is a complex multi-genic trait governed by interactions between genetic, environmental, and management factors ( $G \times E \times M$ ), we then highlight the potential and limitations of root architectural and crop simulation models for evaluating the utility of root adaptive traits for P uptake and crop yield. Furthermore, the application of crop models for assessing the long-term impacts of P-efficient genotypes on soil P dynamics and productivity of cropping systems under current and future climatic conditions is addressed. We then present the components of an interdisciplinary research framework for exploiting genetic diversity in root traits for developing new P-efficient crop varieties and cropping systems in order to (i) lower the critical soil-P levels for optimum crop yields, thereby allowing crop production at lower soil-P loads, (ii) improve the internal P-cycling and crop productivity in low-input and organic cropping systems, (iii) reduce the inefficient use of P fertilisers in fertilised and intensive systems, (iv) improve the environmental sustainability of cropping systems by reducing the potential risk of soil-P losses to water bodies.

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#### 1. Introduction

Phosphorus (P) is an essential and unsubstitutable mineral nutrient for plant growth and development. Consequently, crop production relies on continuous input of large amounts of P in form of mineral fertilisers. Phosphorus fertilisers are manufactured from phosphate rock (PR), a finite resource controlled by a handful of countries. Only four countries, i.e. China, Morocco, United States, and Russia, account for more than two-third of the world

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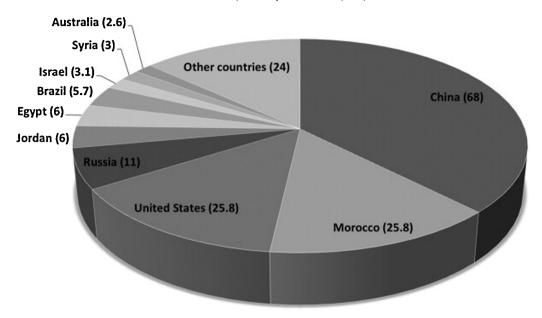


Fig. 1. World production of phosphate rock by country in thousand metric tonnes.

Source: Jasinski (2011).

PR production (181 Mt in 2010) (Jasinski, 2011) (Fig. 1). Recent estimates suggest that the global commercial PR reserves will be depleted in 50 to maximum 400 years (Cordell et al., 2009; Dawson and Hilton, 2011; Jasinski, 2011).

The non-renewable nature of PR together with the imbalance in spatial distribution of PR reserves and the associated geopolitical tensions raise serious concerns about the future security of P supply. In fact, the P importing nations are extremely vulnerable to supply disruptions, price volatility, and other market forces, as witnessed in 2008, when the PR prices spiked by 800% (Schröder et al., 2011). Despite being a finite natural resource, P use in the pathway from "mine to fork" is very inefficient: only one-fifth of the P mined in the world is consumed by humans as food (Schröder et al., 2011). Therefore, there is a pressing need to significantly reduce P losses in order to avert a future P crisis. Developing crop genotypes with enhanced P-use efficiency (PUE) will make a key contribution to sustainable use of P resources (Lynch, 2007; Manschadi et al., 2013).

Nutrient-use efficiency (NutUE) is commonly defined as the crop yield per unit of nutrient supply from soil and fertiliser. In cereal, grain legume, and oilseed crops, NutUE can be considered as the product of two subcomponents: (i) nutrient-acquisition efficiency (NutAE; total nutrient in the above-ground plant organs at maturity per unit of nutrient supply), and (ii) nutrient-utilisation efficiency (NutUtE; crop seed yield per unit of nutrient taken up) (Moll et al., 1982; Barraclough et al., 2010; Wang et al., 2010a).

In the context of crop production, the NutUtE component, or the internal efficiency with which the absorbed nutrient is utilised to produce yield, can be expressed as the ratio of per-unitarea seed yield ( $Y_{\rm seed}$ , kg  $ha^{-1}$ ) to total accumulated nutrient in the above-ground plant parts at physiological maturity (Nutaccum, kg Nut  $ha^{-1}$ ). The crop  $Y_{\rm seed}$  can be considered as the result of total above-ground plant dry mass (DM $_{\rm plant}$ , kg  $ha^{-1}$ ) and seed harvest index (HI, fraction of total accumulated DM in the plant that is allocated to the seed), while Nutaccum is the product of DM $_{\rm plant}$  and plant nutrient concentration (%Nut $_{\rm plant}$ ). Thus, NutUtE can be simplified as the ratio between seed HI and %Nut $_{\rm plant}$  (Ciampitti and Vyn, 2012):

$$NutUtE = \frac{Y_{seed}}{Nut_{accum}} = \frac{DM_{plant} \times HI}{DM_{plant} \times \%Nut_{plant}} = \frac{HI}{\%Nut_{plant}}$$
(1)

For a more agronomically meaningful analysis, NutUtE can be partitioned into two components,  $Y_{seed}$  divided by the accumulated nutrient in the seed (Nut $_{seed}$ , kg Nut ha $^{-1}$ ) and the nutrient harvest index (NutHI, the fraction of total accumulated nutrient in the plant that is allocated to the seed) (Sadras, 2006). As  $Y_{seed}$ /Nut $_{seed}$  is the inverse of seed nutrient concentration (%Nut $_{seed}$ ), crop NutUtE can be calculated as:

$$NutUtE = \frac{Y_{seed}}{Nut_{seed}} \times NutHI = \frac{1}{\% Nut_{seed}} \times NutHI = \frac{NutHI}{\% Nut_{seed}} \qquad (2)$$

Relating NutUtE to the nutrient allocation efficiency (or partitioning) from vegetative parts to the seed (NutHI) and the seed nutrient concentration (%Nut<sub>seed</sub>) provides an appropriate physiological framework for exploring the opportunities for improving NutUE, seed nutritional quality, and yield of crop plants on a perunit-area basis. Sinclair and Rufty (2012) proposed a simple model for quantitative analysis of the physiological factors affecting the use efficiency of nitrogen (N) in crop plants, which can also be applied to P. This model describes the maximum nutrient-limited crop yield (Y<sub>seed</sub>) as a function of total accumulated nutrient in the plant (Nut<sub>accum</sub>), nutrient harvest index (NutHI), and seed nutrient concentration (%Nut<sub>seed</sub>):

$$Y_{seed} = Nut_{accum} \times \frac{NutHI}{\%Nut_{seed}}$$
 (3)

Eqs. (2) and (3) suggest that crop yield is directly related to the plant capacity for nutrient uptake and storage (Nutaccum) and the allocation efficiency of accumulated nutrients to the seed (NutHI). In other words, genotypic selection for increasing  $\boldsymbol{Y}_{\text{seed}}$  and NutUE could be focused on increasing Nut<sub>accum</sub> and NutHI and/or reducing %Nut<sub>seed</sub>. For N, breeding for reduced %Nut<sub>seed</sub> is constrained by commercial demands for high seed protein content in many crops. In fact, the results of recent retrospective analyses of the effects of breeding efforts during the past few decades on N-use efficiency (NUE) of wheat (Triticum aestivum L.), barley (Hordeum vulgare L.), and maize (Zea mays L.) clearly indicate that improvements in NUE of modern crop varieties have primarily been the result of a reduction in grain N concentration and to a minor degree with gains in nitrogen harvest index (Calderini et al., 1995; Barraclough et al., 2010; Gaju et al., 2011; Bingham et al., 2012; Ciampitti and Vyn, 2012; Sadras and Lawson, 2013). The N harvest indices of

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