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Improving Phosphorus Use Efficiency by Agronomical and Genetic Means

¹Hamza Armghan Noushahi, ²Mubashar Hussain, ³Muhammad Bilal, ⁴Muhammad Arslan Salim, ⁵Fahad Idrees, ⁶Muhammad Jawad, ⁷Muhammad Rizwan, ⁷Bilal Atta and ⁸Khuram Tanveer

¹College of Plant Science and Technology, Huazhong Agricultural University, Wuhan, China
²Department of Plant Breeding and Genetics, University of Agriculture Faisalabad, Pakistan
³Department of Entomology, University of Agriculture Faisalabad, Pakistan
⁴Department of Agronomy, University of Agriculture Faisalabad, Pakistan
⁵National Key Laboratory of Crop Genetic Improvement, Huazhong Agricultural University, Wuhan, China
⁶National Institute of Food Science and Technology, University of Agriculture Faisalabad, Pakistan
⁷Rice Research Institute, Kala Shah Kaku, Lahore, Pakistan
⁸National Institute for Biotechnology and Genetic Engineering, Faisalabad, Pakistan

Abstract: Limitation to archives maximum crop productivity by phosphorus (P) is wide spread and will probably increase day by day. P use efficiency can be increased by improved uptake of phosphate from soil (P-acquisition efficiency) and by maximization of productivity per unit P-use efficiency. In this review we discussed how we can improve P-use efficiency, which can be achieved by plants that have overall limited P concentrations and by optimum distribution and redistribution of P in the plant to gain maximum growth and biomass related to harvestable plant parts by agronomic and genetic means. Improvements in P distribution within the plant may be possible by increased remobilization from tissues that no longer need it (e.g. senescing leaves) and reduced partitioning of P to developing grains. Phosphorus use efficiency can also be improved by adopting good agronomic method such as right amount of P fertilizer, at right time, in right place, to right crop. Such methods would prolong and increase the productive use of P in photosynthesis and have nutritional and environmental benefits. In very handy to the future research considering physiological, agronomical, metabolic, molecular biological, genetic and phylogenetic aspects of P-use efficiency is needed to allow best improvements to be done to overcome this issue.

Key words: Phosphorus Usage • Enhancing Efficiency • Genetic Means • Agronomic Means

INTRODUCTION

Phosphorus (P) is the key element for the synthesis of many biomolecules, including DNA, RNA and ATP [1], with no substitute as a building block of life. P is also frequently limiting for a variety of biota, including vascular plants, marine and freshwater phytoplankton, aquatic and terrestrial bacteria and herbivorous animals [2] thus, understanding how P limitation shapes ecological and evolutionary dynamics is a key step in linking levels of biological organization from genes to ecosystems. Phosphorus is one of the seventeen essential nutrients required for plant growth [3]. P is an important plant macronutrient, making up about 0.2% of a plant's dry weight. It is a component of key molecules such as nucleic acids, phospholipids and ATP and, consequently, plants cannot grow without a reliable supply of this nutrient. P is also involved in controlling key enzyme reactions and in the regulation of metabolic pathways [4]. It is the second essential macronutrient next to nitrogen which can limit crop growth. Plant dry weight may contain up to 0.5% phosphorus and this nutrient is involved in an array of process in plants such as in photosynthesis, respiration, in energy generation, in nucleic acid biosynthesis and as an integral component of several plant structures such as phospholipids [5]. Despite its

Corresponding Author: Mubashar Hussain, Department of Plant Breeding and Genetics, University of Agriculture Faisalabad, Pakistan. importance in plants growth and metabolism, phosphorus is the least accessible macro-nutrient and hence most frequently deficient nutrient in most agricultural soils because of its low availability and its poor recovery from the applied fertilizers. The low availability of phosphorus is due to the fact that it readily forms insoluble complexes with cation such as aluminum and iron under acidic soil condition and with calcium and magnesium under alkaline soil conditions whereas the poor P fertilizer recovery is due to the fact that the P applied in the form of fertilizers is mainly adsorbed by the soil and is not available for plants lacking specific adaptations. Moreover, global P reserves are being depleted at a higher rate and according to some estimates there will be no soil P reserve by the year 2050 [5, 6].

The early supply of Phosphorus to the crop is influenced by soil Phosphorus and Phosphorus application as well as by soil and environmental conditions that affect P phyto-availability and root growth. Roots absorb Phosphorus ions from the soil solution. The ability of the plant to absorb P will depend on the concentration of P ions in the soil solution at the root surface and the area of absorbing surface in contact with the solution. Mass flow and diffusion govern the movement of P ions in soil, with diffusion being of primary importance [7, 8]. After Nitrogen Phosphorus is the second most frequently limiting macronutrient for plant growth. This update focuses on Phosphorus in soil and its uptake by plants, transport across cell membranes and re-distribution within the plant. We will concentrate on P in higher plants, although broadly similar mechanisms have been shown to apply in algae and fungi. For this mycorrhiza are also important for plant Phosphorus acquisition, since fungal hyphae greatly increase the volume of soil that plant roots explore [9]. Soil P is found in different pools, such as organic and mineral P. It is important to emphasize that 20 to 80% of P in soils is found in the organic form, of which phatic acid (inositol hexa-phosphate) is usually a major component [10]. The remainder is found in the inorganic fraction containing 170 mineral forms of P [11]. Plant root geometry and morphology are important for maximizing P uptake, because root systems that have higher ratios of surface area to volume will more effectively explore a larger volume of soil [12]. Plants require adequate P from the very early stages of growth for optimum crop production [13]. Restricted early-season P supply frequently limits crop production and P fertilizer is commonly applied to ensure that sufficient P is available to optimize crop yield and maturity. Total soil P usually ranges from 100 to 2000 mg P kg⁻¹ soil representing approximately 350 to 7000 kg P ha⁻¹ in the surface 25 cm of the soil, although only a small portion of this P is immediately available for crop uptake [14].

Applications of fertilizer or manure P in excess of P removal with crop harvest have resulted in sharp soil-test P (STP) increases in many areas of the region during the last few decades [15]. The time of P application before planting a crop is not a critical issue for the predominant crops and soils of the region. This is because P has relatively low mobility in soils and the soils of the region have low to moderate capacity for retaining added P in unavailable forms. Therefore, P can be applied at planting time or in advance of planting without a significant loss of efficiency. Several studies in Iowa [16] have shown that annual or bi-annual P applications for corn-soybean rotations have approximately similar efficiency. The placement of P or K fertilizer below the depth typically achieved with broadcast or planter band application has been evaluated as a method of avoiding reduced nutrient availability due to stratification, particularly in no-till and ridge-till systems. While substantial evidence of nutrient stratification exists [17, 18], reports of significant detrimental effects on crop vield are few.

The importance of phosphorus (P) in the delivery of multiple ecosystem services has received increased attention [19, 20] highlighted the central role that sustainable P management plays in balancing different ES across the water-energy-food continuum [21]. proposed the Phosphorus Ecosystem Services Cascade as a conceptual framework to integrate sustainable P management with key ES processes and functions from soil to large river basin scale. Holistic approaches to farm nutrient management have recently been adopted to provide a greater focus on multiple ES. For instance, the fertilizer industry has adopted the 4R Nutrient Stewardship Strategy (Right Rate, Right Time, Right Place and Right Form) to promote more efficient use of fertilizer and reduce field scale nutrient export to water [22].

Role of Phosphorus in Soil: Phosphorus is a necessary plant nutrient to increase the production of agricultural crops and forest and it is also used for production of detergents and for some other industrial products [23]. Phosphorus is the eleventh most abundant element in the earth's crust. Its average concentration in this environment has been estimated to 0.1 percent by weight and is thus geochemically classed as a trace element. Only a fractional percentage of the total is concentrated

in deposits consisting mainly of phosphate minerals [24]. Phosphorus occurs in nature almost exclusively as phosphate, in all known minerals more specifically as orthophosphate with an ionic form of Pod3 -. The distribution of the different species of orthophosphate is pH-dependent. H, PO, - is the pre- dominant species that can be expected to take part in phosphate sorption in the pH range 4-6. At higher pH, as can be found in cultivated soils, the importance of HPOd2- may increase. Since the soil solution will contain several kinds of metallic cations capable of forming complexes with H, PO, - and HPOd2-, a part of the soil solution phosphorus will exist as soluble metallic- phosphate complexes. In some cases, the degree of complexion of solution phosphorus may be a significant part of the total soil solution phosphorus [25].

Plants growing in an ecosystem low in available P have to obtain P from adsorbed P, sparingly soluble P and organic P complexes. Many plants have developed elegant biochemical mechanisms to solubilize P from insoluble P complexes thereby increasing the pool of P available for uptake [26]. Organic anions such as citrate and malate are the major root exudates released, in response to P deficiency for mobilizing P for plant uptake [27]. The range of organic anions released is, however, dependent on the plant species. [27]. While most of the focus on nutrient efficiency is on phosphorus (P) efficiency is also of interest because it is one of the least available and least mobile mineral nutrients. First year recovery of applied fertilizer P ranges from less than 10% to as high as 30%. However, because fertilizer P is considered immobile in the soil and reaction (fixation and/or precipitation) with other soil minerals is relatively slow, long-term recovery of P by subsequent crops can be much higher [40].

Phosphorus Use Efficiency in Plants: There is an increasing awareness that there are limits to global rock phosphate reserves and that increasing the efficiency with which these reserves are used to produce crops is vital to maintain current agricultural productivity, or to even increase it [28]. PUE is the amount of total biomass, or yield that is produced per unit of P taken up [29] distinguished when relevant by subscripts, PUEt and PUEy, respectively. In the case of biomass, measurements are often restricted to aboveground plant parts. In grain crops, PUEy is the grain yield per unit of maximum aboveground plant P. In vegetative plants, the productive use of a unit of P taken up is determined by (a) the efficiency with which it is used in metabolism and growth and (b)the duration of its presence in living parts of the plant where it contributes to these processes.

Following [30], who formalized this concept,

PUEt = [Biomass production per unit P per unit time] * [P residence time]

Photosynthetic phosphorus-use efficiency (PPUEmax) is defined as the instantaneous light-saturated rate of leaf photosynthesis expressed per unit leaf P. Photosynthetic capacities (Amax, mass-based) of crop species are found at the high end of the leaf trait spectrum, associated with fast growth and low leaf mass per area (LMA) [31].

Phosphorus Use Efficiency Through Agronomical Means: Annual grain crops (cereals, oil seeds and pulses), which are the focus of this review, provide 58% of the dietary energy for the world's growing population [32]. Improving the efficiency of phosphorus (P) fertilizer use for crop growth requires enhanced P acquisition by plants from the soil (P-acquisition efficiency) and enhanced use of P in processes that lead to faster growth and greater allocation of biomass to the harvestable parts (internal P-use efficiency (PUE), As only 15-30% of applied fertilizer P is taken up by crops in the year of its application [33], potentially large gains in efficiency can be made by improving P acquisition. This aspect of P efficiency has received signi?cant attention and has been reviewed recently [34, 35], identifying promising opportunities for improved crop traits and agronomic measures. Aiming at increasing P uptake alone will benefit yields, but will also increase total amounts of P exported from the field. Increased P exports can cause considerable off-site environmental problems [36] and will need to be replaced with additional fertilizer to avoid soil P depletion in the long term.

Plant productivity relies on photosynthesis and the process relies on photosynthetic P-containing compounds. Thus, an efficient use of P in photosynthesis is a potentially important determinant of crop PUE. As a result of similar increases of Amax (mass-based) and P concentrations with decreasing (leaf mass per area) LMA, however, PPUE is not strongly correlated with LMA so fast-growing species, which tend to have low (leaf mass per area) LMA, do not necessarily have a high PPUE. For example, thin leaves of barley have a similarly high PPUE to the sclerophylls of the genus Banksia [37]. Barley achieves this with a high [P], whereas Banksia has very low [P], but barley apparently uses P sparingly in structural tissue and very efficiently in photosynthetic machinery [37]. Highest PPUE tends to be achieved by leaves with high rates of photosynthesis, high P concentration and low LMA, but such traits are associated with short leaf life-spans [38], implying a trade-off that will reduce the C return per unit P over the life of a leaf (PPUE leaf life). It is important to note, however, that there is considerable variation between species in both indices, indicating that other leaf traits in?uence the efficiency of P use in photosynthesis, such as shown for leaf N. [39] argue that future increases in crop yield potential will come from increased photosynthetic capacity. It will be important to achieve this along with increased PPUE [40].

Remobilization of P from senescing leaves is more variable than that of N. P-resorption efficiency (PRE; the percentage of mature leaf P that has been exported before death) can reach values as high as 90% [41]. Reports are now emerging of individual Pi transporter genes that are up-regulated at the transcript level in senescent tissues; this suggests that they have a role in Pi remobilization from old source to new sink tissues and are linked to ethylene signaling [42]. Further research on the molecular physiology of P remobilization may provide valuable insights leading to enhanced Pre-use in crop plants.

Limitation of crop yield by phosphorus (P) is wide spread and will probably increase in the future. Enhanced P efficiency can be achieved by improved uptake of phosphate from soil (P-acquisition efficiency) and by improved productivity per unit P taken up (P-use efficiency). P-use efficiency, which can be achieved by plants that have overall lower P concentrations and by optimal distribution and redistribution of P in the plant allowing maximum growth and biomass allocation to harvestable plant parts.

Phosphorus Use Efficiency Through Genetic Means: Around 70-90% of the P fertilizers is adsorbed and becomes 'locked' in various soil P compounds of low solubility without giving any immediate contribution to crop production, when P fertilizers are applied [43]. This suggests that P fertilization alone is not a cost-effective way of increasing crop productivity in many P limiting soils [44]. New crop varieties with improved root traits, able to unlock and absorb P from bound soil P resources may be of additional value for increasing the efficiency of fertilization [45]. Although the variety of differences in P uptake and their link to the size of root systems were reported many years ago breeding for efficient root systems has received little attention This is despite the fact that wide variation has indeed been reported in the ability of crop genotypes to perform and produce economic yields under P-limited soil conditions [46].

There is substantial genetic variation in traits associated with PUE within the crop plants that have been examined and within Arabidopsis, Prinzenberg et al. [47]. Analysis of this variation has led to the identification of numerous genetic loci that influence PUE. The ability to identify these quantitative trait loci (QTL) suggests that improvements in PUE may be gained through conventional or marker-assisted breeding programs, directed gene identification and genetic engineering, or a combination of these approaches. These traits include high total plant P content, large root systems, improved root architecture (increased lateral root production, improved topsoil foraging, greater root surface to volume ratio, greater root hair production and greater root : shoot ratio) and the exudation of phosphatases and organic acids into the rhizo sphere. Nevertheless, OTL that have the potential to influence internal PUE have been found in several crop species [48, 49]. However, internal PUE is generally lower in plants with high P-acquisition efficiency as a result of higher tissue P concentrations, making it difficult to disentangle OTL that affect agronomic PUE generally from QTL that may specifically influence internal PUE [50] proposed that identifying QTL for internal PUE requires studies where P acquisition and metabolically non-saturating among is equal cultivars. As an alternative, explicit quantification of tissue P pools would allow a more specific evaluation of genotypes and identification of QTL that are related to the efficiency of P use in nucleic acids, phospholipids and P-esters.

There is much scope for future mapping of QTL that influence internal PUE. Advanced methods of genetic analysis have not yet been used extensively in the area of plant P relations. Approaches such as genome-wide expression (transcriptome) QTL analyses [51] and genome-wide association studies [52] supported by such emergent technologies as next generation sequencing hold much promise to identify loci related to and controlling plant P relations, including internal PUE [53].

CONCLUSION

To increase phosphorus use efficiency, we must introduce organic fertilizers and reduce phosphorus waste to the soil, to enhance the nutritional value of yield. We have discussed developmental, agronomic and genetic means to increase PUE. In which we identified important aspects to increase PUE. The maximum PUE obtained through various mechanisms, according to genetic and environmental conditions which provided to crop. Efficiency of phosphorus will be at peek by improvements in P-acquisition efficiency and reducing the total flux of phosphorus on crop soil with the environment. Maximum yield gains of increased PUE are predicted for crops when they take up very less amount phosphorus from the soil rather soil phosphorus is in very minor amount. In productive land when we applied optimal conditions for crop growing is the best option for increasing PUE.

REFERENCES

- Huang, J., Z. Su and Y. Xu, 2005. The evolution of microbial phosphonate degradative pathways. Journal of Molecular Evolution, 61(5): 682-690.
- Elser, J.J., M.E. Bracken, E. Cleland, D.S. Gruner, W.S Harpole, H. Hillebrand and J.E Smith, 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecology Letters, 10(12): 1135-1142.
- 3. Raghothama, K.G. and A.S. Karthikeyan, 2005. Phosphate acquisition. Plant and Soil, 274: 37-49.
- Theodorou, M.E. and W.C. Plaxton, 1993. Metabolic adaptations of plant respiration to nutritional phosphate deprivation. Plant physiology, 101(2): 339-344.
- Vance, C.P., C. Uhde Stone and D.L. Allan, 2003. Phosphorus acquisition and use: critical adaptations by plants for securing a nonrenewable resource. New Phytologist, 157(3): 423-447.
- Cordell, D., A. Rosemarin, J.J. Schröder and A.L. Smit, 2011. Towards global phosphorus security: A systems framework for phosphorus recovery and reuse options. Chemosphere, 84(6): 747-758.
- Barber, S.A., J.M. Walker and E.H. Vasey, 1963. Mechanisms for movement of plant nutrients from soil and fertilizer to plant root. Journal of Agricultural and Food Chemistry, 11(3): 204-207.
- Barber, S.A., 1984. Soil nutrient bioavailability: A mechanistic approach. John Wiley & Sons Inc., New York, NY, pp: 398.
- Smith, S.E. and D.J. Read, 1997. Mycorrhizal Symbiosis. Academic Press, San Diego, CA. Richardson AE (1994) Soil microorganisms and phosphorus availability. Soil Biota, pp: 50-62.
- 10. Richardson, A.E., 1994. Soil microorganisms and phosphorus availability. Soil Biota, pp: 50-62.
- Holford, I.C.R., 1997. Soil phosphorus: its measurement and its uptake by plants. Soil Research, 35(2): 227-240.

- 12. Lynch, J., 1995. Root architecture and plant productivity. Plant Physiology, 109(1): 7.
- 13. Grant, C.A., D.N. Flaten, D.J. Tomasiewicz and S.C. Sheppard, 2001. The importance of early season phosphorus nutrition. Canadian Journal of Plant Science, 81(2): 211-224.
- Morel, C., 2002. Characterization of phytodisponibility of soil P by modeling the transfer of phosphate ions between soil and solution. Ability to conduct researches. INPL-ENSAIA Nancy, France.
- Fixen, P.E., T.W. Bruulsema, A.M. Johnson, R.I. Mikkelsen, T.S. Murrell and C.S. Snyder, 2005. Soil Test Levels in North America, 2005. Summary Update. PPI/PPIC/FAR Technical Bulletin 2005-1.
- Randall, G.W., T.K. Iragavarapu and S.D. Evans, 1997. Long-term P and K applications: I. Effect on soil test incline and decline rates and critical soil test levels. Journal of Production Agriculture, 10(4): 565-571.
- Robbins, S.G. and R.D. Voss, 1991. Phosphorus and potassium stratification in conservation tillage systems. Journal of Soil and Water Conservation, 46(4): 298-300.
- Rehm, G.W., A.J. Scobbie, G.W. Randall and J.A. Vetsch, 1995. Impact of fertilizer placement and tillage system on phosphorus distribution in soil. Soil Science Society of America Journal, 59(6): 1661-1665
- Doody, D.G., P.J.A. Withers, R.M. Dils, R.W. McDowell, V. Smith, Y.R. McElarney, M. Dunbar and D. Daly, 2005. Soil Science Society of America Journal, 59(6): 1661-1665.
- Jarvie, H.P., A.N. Sharpley, D. Flaten, P.J. Kleinman, A. Jenkins and T. Simmons, 2015. The pivotal role of phosphorus in a resilient water-energy-food security nexus. Journal of Environmental Quality, 44(4): 1049-1062.
- MacDonald, G.K., H.P. Jarvie, P.J. Withers, D.G. Doody, B.L. Keele, P.M. Haygarth and A.N. Sharpley, 2016. Guiding phosphorus stewardship for multiple ecosystem services. Ecosystem Health and Sustainability, 2(12): e01251.
- Bruulsema, T., J. Lemunyon and B. Herz, 2009. Know your fertilizer rights. Crops and Soils, 42(2): 13-18.
- McClellan, G.H. and T.P. Hignett, 2009. Some economic and technical factors affecting use of phosphate raw materials. In Ciba Foundation Symposium, (No. 57, pp: 49-73).
- 24. Smil, V., 2000. Phosphorus in the environment: natural flows and human interferences. Annual Review of Energy and the Environment, 25(1): 53-88.

- Berkheiser, V.E., J.J. Street, P.S.C. Rao, T.L. Yuan and B.G. Ellis, 1980. Partitioning of inorganic orthophosphate in soil-water systems. Critical Reviews in Environmental Science and Technology, 10(3): 179-224.
- 26. Raghothama, K. G and A.S. DKarthikeyan, 2005. Phosphate acquisition. Plant and Soil, 274(1-2).
- Dechassa, N. and M.K. Schenk, 2004. Exudation of organic anions by roots of cabbage, carrot and potato as influenced by environmental factors and plant age. Journal of Plant Nutrition and Soil Science, 167(5): 623-629.
- Cordell, D., J.O. Drangert and S. White, 2009. The story of phosphorus: global food security and food for thought. Global Environmental Change, 19(2), 292-305.
- 29. Berendse, F. and R. Aerts, 1987. Nitrogen-useefficiency: a Biologically Meaningful Definition.
- Lambers, H.A.N.S. and H. Poorter, 1992. Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. In Advances in Ecological Research, 23: 187-261). Academic Press.
- 31. FAO, 2010. Fao statistical yearbook 2010. [WWW document] URL http://www. Fao.Org/economic/ess/ess-publications/ess-yearbook/ess-yearbook 2010/yearbook2010-consumption/en/.In [accessed 12 December 2011].
- Syers, J.K., A.E. Johnston and D. Curtin, 2008. Efficiency of soil and fertilizer phosphorus use. FAO Fertilizer and Plant Nutrition Bulletin, 18(108).
- Wang, X., J. Shen and H. Liao, 2010. Acquisition or utilization, which is more critical for enhancing phosphorus efficiency in modern crops?. Plant Science, 179(4): 302-306.
- Richardson, A.E., J.P. Lynch, P.R. Ryan, E. Delhaize, F.A. Smith, S.E. Smith and A. Oberson, 2011. Plant and microbial strategies to improve the phosphorus efficiency of agriculture. Plant and soil, 349(1-2): 121-156.
- Childers, D. L., J. Corman, M. Edwards and J.J. Elser, 2011. Sustainability challenges of phosphorus and food: solutions from closing the human phosphorus cycle. Bioscience, 61(2): 117-124.
- 36. Lambers, H., P.M. Finnegan, E. Laliberté, S.J. Pearse, M.H. Ryan, M.W. Shane and E.J. Veneklaas, 2011. Phosphorus nutrition of Proteaceae in severely phosphorus-impoverished soils: are there lessons to be learned for future crops? Plant Physiology, 156(3): 1058-1066.

- Wright, I.J., P.B. Reich, M. Westoby, D. Ackerly, Z. Baruch, F. Bongers and J. Flexas, 2004. The worldwide leaf economics spectrum. Nature, 428(6985): 821.
- Zhu, X.G., S.P. Long and D.R. Ort, 2010. Improving photosynthetic efficiency for greater yield. Annual Review of Plant Biology, 61: 235-261.
- 39. Roberts, T.L., 2008. Improving nutrient use efficiency. Turkish Journal of Agriculture and Forestry, 32(3): 177-182.
- Aerts, R. and F.S. Chapin III, 2000. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. In Advances in Ecological Research, 30: 1-67. Academic Press.
- 41. Nagarajan, V.K., A. Jain, M.D. Poling, A.J. Lewis, K.G. Raghothama and A.P. Smith, 2011. Arabidopsis Pht1; 5 mobilizes phosphate between source and sink organs and influences the interaction between phosphate homeostasis and ethylene signaling. Plant Physiology, pp: 111.
- Veneklaas, E.J., H. Lambers, J. Bragg, P.M. Finnegan, C.E. Lovelock, W.C. Plaxton and J.A. Raven, 2012. Opportunities for improving phosphorus-use efficiency in crop plants. New Phytologist, 195(2): 306-320.
- Holford, I.C.R., 1997. Soil phosphorus: its measurement and its uptake by plants. Soil Research, 35(2): 227-240.
- Tilman, D., K.G. Cassman, P.A. Matson, R. Naylor and S. Polasky, 2002. Agricultural sustainability and intensive production practices. Nature, 418(6898): 671.
- 45. Abelson, P.H., 2015. A potential phosphate crisis.
- Clark, R.B., 1990. Physiology of cereals for mineral nutrient uptake, use and efficiency. Crops as Enhancers of Nutrient Use, pp: 131-209.
- 47. Prinzenberg, A.E., H. Barbier, D.E. Salt, B. Stich and M. Reymond, 2010. Relationships between growth, growth response to nutrient supply and ion content using a recombinant inbred line population in Arabidopsis. Plant Physiology, 154(3): 1361-1371.
- Vance, C.P., 2010. Quantitative trait loci, epigenetics, sugars and microRNAs: quaternaries in phosphate acquisition and use. Plant Physiology, 154(2): 582-588.
- 49. White, P.J. and E.J. Veneklaas, 2012. Nature and nurture: the importance of seed phosphorus content. Plant and Soil, 357(1-2): 1-8.

- 50. Rose, T.J., M.T. Rose, J. Pariasca Tanaka, S. Heuer and M. Wissuwa, 2011. The frustration with utilization: why have improvements in internal phosphorus utilization efficiency in crops remained so elusive? Frontiers in Plant Science, 2: 73.
- 51. Hammond, J.P., S. Mayes, H.C. Bowen, N.S. Graham, R.M. Hayden, C.G. Love and G.J. King, 2011. Regulatory hotspots are associated with plant gene expression under varying soil phosphorus (P) supply in Brassica rapa. Plant Physiology, pp: 111.
- 52. George, T.S., L.K. Brown, A.C. Newton, P.D. Hallett, B.H. Sun, W.T. Thomas and P.J. White, 2011. Impact of soil tillage on the robustness of the genetic component of variation in phosphorus (P) use efficiency in barley (*Hordeum vulgare* L.). Plant and Soil, 339(1-2): 113-123.
- Morrell, P.L., E.S. Buckler and J. Ross-Ibarra, 2012. Crop genomics: advances and applications. Nature Reviews CGenetics, 13(2): 85.