

# **Recent Advances in CROP PHYSIOLOGY**

**VOLUME 2**

## The Editor

---



**Dr. Amrit Lal Singh**, Principal Scientist, Plant Physiology at the Directorate of Groundnut Research, Junagadh, Gujarat obtained his M.Sc. (Botany) from BHU, Varanasi and Ph.D. in Botany from Utkal University, Bhubaneswar. During his Ph.D. Dr. Singh worked on the biological nitrogen fixation by *Azolla* and blue green algal biofertilizers and demonstrated their use in rice. Dr. Singh, joined ICAR as an ARS Scientist in Plant Physiology, at DGR in Jan. 1985, upgraded to Senior and Principal Scientists and even as Director of DGR. Last 35 years he has been working on the various aspects of crop physiology. He is the life member of more than a dozen of scientific societies and published more than 150 research papers, 25 reviews and book chapters, and several technology bulletins. He is Fellow of the Indian Society for Plant Physiology (ISPP), New Delhi and Indian Society for Oilseeds Research, DOR, Hyderabad, and recipient of the J.J. Chinoy Gold medal award 2011 of the ISPP, New Delhi. Dr. Singh served as a Vice-President (2012) of the ISPP New Delhi, visited China, Japan, Tanzania, Turkey and USA and has worked as Referee/Reviewer of the Annals of Applied Biology, UK, Australian J. of Crop Science, Journal of Plant Nutrition, USA and Journal of Plant Nutrition and Soil Science, Germany.

# **Recent Advances in CROP PHYSIOLOGY**

**VOLUME 2**

— Editor —

**Dr. Amrit Lal Singh**

*Principal Scientist,*

*Plant Physiology*

*Directorate of Groundnut Research,*

*Junagadh, Gujarat*

**2015**

**Daya Publishing House®**

*A Division of*

**Astral International Pvt. Ltd.**

**New Delhi – 110 002**

© 2015 EDITOR

*Publisher's Note:*

*Every possible effort has been made to ensure that the information contained in this book is accurate at the time of going to press, and the publisher and author cannot accept responsibility for any errors or omissions, however caused. No responsibility for loss or damage occasioned to any person acting, or refraining from action, as a result of the material in this publication can be accepted by the editor, the publisher or the author. The Publisher is not associated with any product or vendor mentioned in the book. The contents of this work are intended to further general scientific research, understanding and discussion only. Readers should consult with a specialist where appropriate.*

*Every effort has been made to trace the owners of copyright material used in this book, if any. The author and the publisher will be grateful for any omission brought to their notice for acknowledgement in the future editions of the book.*

*All Rights reserved under International Copyright Conventions. No part of this publication may be reproduced, stored in a retrieval system, or transmitted in any form or by any means, electronic, mechanical, photocopying, recording or otherwise without the prior written consent of the publisher and the copyright owner.*

**Cataloging in Publication Data–DK**

Courtesy: D.K. Agencies (P) Ltd. <docinfo@dkagencies.com>

**Recent advances in crop physiology** / editor, Dr. Amrit Lal Singh.  
volume 2 cm

Includes bibliographical references and index.

ISBN 978-93-5124-678-7 (Volume 2)

ISBN 978-93-5124-277-2 (Series)

ISBN 978-93-5130-744-0 (International Edition)

1. Crops–Physiology. 2. Crops–Physiology–India. I. Singh, Amrit Lal, editor.

DDC 571.2 23

*Published by* : **Daya Publishing House®**  
A Division of  
**Astral International Pvt. Ltd.**  
– ISO 9001:2008 Certified Company –  
4760-61/23, Ansari Road, Darya Ganj  
New Delhi-110 002  
Ph. 011-43549197, 23278134  
E-mail: info@astralint.com  
Website: www.astralint.com

*Laser Typesetting* : **Classic Computer Services, Delhi - 110 035**

*Printed at* : **Thomson Press India Limited**

PRINTED IN INDIA

---

# Foreword

---

Agriculture plays a pivotal role for food and nutritional security, and in alleviation of poverty. But, agriculture sector has been confronted with numerous challenges linked to food and energy crisis, climate change and natural resources. With beginning of 21<sup>st</sup> century, India is being recognized as the global power in the key economic sectors with high economic growth, but its slow growth in agriculture sector is major concerns for the future food and nutritional security, as one-third of the country's population lives below poverty line, and about 80 per cent of our land mass is highly vulnerable to drought and floods. Indian agriculture, with only 9 per cent of world's arable land, contribute 8 per cent to global agricultural gross domestic product to support 18 per cent of the world population. Also, India has nearly 8 per cent of the world's biodiversity and many of these are crucial for livelihood security of poor and vulnerable population. Thus, acceleration of agricultural growth along with natural resources conservation is of supreme importance.

As the Global food demand is expected to be doubled by 2050, world must learn to produce more food with less land, less water and less labour by devising more efficient and profitable production systems that are resilient to climate change. Thus, more than ever, we need to produce more food with less land. Also looking to the demand of 2050 all the institutions and agricultural universities need to redesign their research and teaching programmes for harnessing power of science and bringing excellence in agricultural research and education that ensures food, nutrition and livelihood security for all.

The ICAR with the help of SAUs has brought green revolution in agriculture in India through its research and technology development in past and its subsequent efforts have enabled the country to increase the production of food grains by 4-fold, horticultural crops by 6-fold since 1950-51 which made a visible impact on the national food and nutritional security. Using cutting edge technologies, there is

tremendous development in agriculture during the last two decades and it is hoped that with ingenuity, determination and innovative partnerships among everyone working in the agricultural sector, we can meet the food needs of 9 billion people by 2050 without irreparably harming our planet. However, all these informations are scattered and need to be compiled and circulated widely.

This series on "Recent Advances in Crop Physiology" is a timely effort in this direction, which will act as a reference for directly implementing the available technologies and to help the researchers for planning their future research programme.

*Swapan Kumar Datta*

---

# Preface

---

*“Food security exists when all people, at all times, have physical, social and economic access to sufficient safe and nutritious food that meets their dietary needs and food preferences for an active and healthy life.”*

Global food demand is expected to be doubled by 2050, while production environment and natural resources are shrinking and deteriorating. World cereal production has gone 2525 million tonnes (mt) during 2013-14 and is expected to be 2535 mt in 2014-15. Same time, world cereal utilization which was 2416 mt in 2013-14 is put 2464 mt in 2014-15. To feed the world in 2050, yields on maize, rice, wheat, and soybeans will have to rise by 60-110 per cent, but the present projections show an increase of only 40-65 per cent and most rice and wheat had very low rates of increase in crop yields. In other places, the trajectories of population growth and food production are heading in different directions. The rice, is the central to existence in many nations, feeds the world, and provides more calories to humans than any other food, and more than a billion people depend on rice cultivation for their livelihoods. Changes in the price and availability of rice have caused social unrest in developing countries and in 2008, when rice prices tripled, 100 million people were pushed into poverty. About 90 per cent of the world’s rice is grown in Asia, on more than 200 million small scale farms (about 1 acre), where additionally 8-10 m t of rice need to be produced every year to keep prices affordable with population increase. However, the International Food Policy Research Institute estimates that by 2050 rice prices may increase 35 per cent because of yield losses due to climate change.

Malnutrition in form of under nutrition, micronutrient deficiencies and obesity imposes unacceptably high economic costs and improving nutrition requires a multisectoral approach that begins with food and agriculture. A total of 842 million people in 2011-13, or around one in eight people in the world, are estimated to be suffering from chronic hunger, regularly not getting enough food for an active life.

The agriculture play its fundamental role in producing food and its processing, storage, transport and consumption contribute to the eradication of malnutrition. Because of better agriculture the total number of undernourished during 2013 has fallen by 17 percent since 1990–92. Agricultural policies and research must continue to support productivity growth for staple foods with greater attention to nutrient-dense foods and more sustainable production systems. Traditional and modern supply chains can enhance the availability of a variety of nutritious foods and reduce nutrient waste and losses.

Recently the Intergovernmental Panel on Climate Change (IPCC) predicted that global food production due to climate change will decline 2 per cent per decade for the remainder of this century compared to food production without climate change even as food demand increases 14 per cent per decade. In 2007, the panel was hopeful that gains in agricultural productivity would more than make up for losses due to climate change. But later research revealed in greater detail the impacts of climate change on sensitive crops and raised questions about how much elevated carbon dioxide levels could increase productivity.

The organic material decays without oxygen, in water-logged rice paddies, soil microbes generate methane, a greenhouse gas with 25 times more warming potential than CO<sub>2</sub>. In India, rice methane emission accounts for about 10 per cent of the nation's total greenhouse gas (GHG) emissions. Also, nitrous oxide emissions from rice grown under dryer and aerated conditions, can be as significant as methane emissions which has about 300 times more warming potential than CO<sub>2</sub>. It has not yet been estimated what percentage of nitrous oxide emissions come from rice cultivation in India, and other rice growing regions in Asia.

If we are unable to double yields on existing cultivated lands, due to food insecurity pressure, we are likely to clear more land for agriculture leaving environmental concerns and efficiency measures a side. This will have a ripple effect, putting additional pressure on already stressed water resources and wildlife habitat, accelerates climate change. This cycle, left unchecked, can only end with farmers competing for increasingly scarce water and arable land in the face of ever more extreme weather – from floods to droughts – brought on by climate change.

These colliding trends indicate that the world must learn to produce more food with less land, less water and less labour by devising, climate resilient more efficient and profitable production systems. Thus, more than ever, we need to produce more food with less land. Farmers must seek out crop production technologies that will be highly productive and have a smaller impact on water quality and quantity, climate and habitat. To do this, we have the tools and technologies that reduce the need for inputs like fertilizer, pesticides and herbicides; innovative irrigation methods that reduce water demand; and methods that reduce greenhouse gas emissions. Using improved technologies, there has been tremendous development in agriculture and productivity during the last two decades and it is hoped that with ingenuity, determination and innovative partnerships among everyone working in the agricultural sector, we can meet the food needs of 9 billion people by 2050 without irreparably harming our planet on which we all depend. However, all these



informations are scattered and need to be compiled and circulated widely. This series on Recent Advances in Crop Physiology is an effort in this direction, which will act as a reference to the farmers for directly implementing the technologies and also to help the researchers for planning their future research to improve crop productivity.

This second volume of *'Recent Advances in Crop Physiology'* encompasses 13 chapters written by the experts in the field describing production physiology, drought and salinity stresses, nutrient efficiencies particularly P and N, radiotracer and their use in mineral nutrition, nutritional quality of potato and wheat and role of bioregulators in increasing productivity through amelioration of abiotic stressed. Abiotic stresses are the major factors limiting crop productivity worldwide. The chapter one on 'Drought management in pulses and their diversification under new niches' and chapter seven on 'Can water deficit be useful in potato? – Some issues', widely covers the physiological behavior of these crops under water stresses and how best the water stress could be managed to increase productivity and quality of pulses and potato in India. Chapter eight on 'Bioregulators ameliorate water deficit stress in wheat' is an effort on water stress management through bioregulators and new molecules altogether a different approach.

There are plenty of acid soils and the soil salinity problem is increasing in India and worldwide due to faulty irrigation and drainage practices. A comprehensive chapter three on 'Salinity Management in Vertisols: Physiological Implications' and chapter six on 'Physiological basis of Iron toxicity and its management in crops' takes care of soil and crop management in saline soil and iron- toxicity in crops in acid soils and provide a guidelines how to manage these crops under these stresses. The nutrients and fertilizers are the driving force in increasing the productivity of any crop, but in recent years there is an indiscriminate use of nitrogen and phosphorus inspite of the fact that there is limited P sources on the planet. The use of nutrient efficient crop varieties are the best alternative for managing both deficiencies and excess of these nutrients and in chapter two on 'Role of phosphorus efficient genotypes in increasing crop production' and chapter 12 on 'Nitrogen-use efficiency and productivity of wheat crop' discuss these issues in depth with solutions.

The precise study of mineral nutrition in crop plants require use of radiotracer and hence chapter 10 on the 'Radiotracer use in understanding mineral nutrition of crop plants' is fully devoted on the same.

India is emerging as an export hub of several horticultural crops and chapter four on 'Physiological basis for maximizing yield potentials in coffee' extensively covers the major hurdles and list the ways to increase production and quality of coffee for domestic consumption as well as export. Similarly the chapter five on 'Bioregulators improve the productivity and quality of Indian table grapes' list the best practices and use of bioregulators to increase the productivity of indian grapes.

The forest cover majority of the geographical areas of India and world and play an important role in the climate management and environmental protection, but there are no systematic studies on the productivity of forest. The chapter nine on 'Phenology and productivity of forest flora of Gujarat' is an effort in this direction to highlight the issues how the phenological studies can help to increase forest

productivity of Gujarat and reduce the carbon dioxide concentrations on earth through carbon sequestration by forest plant species.

Finally, seed, which is the primary requirement for enhancing crop productivity, plays a vital role in ensuring food security, and a chapter on 'Quality seed- a mega factor in enhancing crop productivity' are well composed by the renowned scientists in the field.

I would like to express my gratitude to all the stalwarts of agriculture and plant biology from various disciplines who has contributed in enhancing agricultural production. Thanks are also due to all the staffs of plant physiology at DGR Junagadh for their help in the various ways. Finally, I would like to express my sincere thanks to Mr. Prateek Mittal for coming forward to take up the responsibility of publishing the series and Mr. Anil mittal and the staff of Astral International (P) Ltd, New Delhi for their care and diligence in producing the book timely.

*Dr. Amrit Lal Singh*

---

# Contents

---

<i>Foreword</i>	<i>v</i>
<i>Preface</i>	<i>vii</i>
<b>1. Drought Management in Pulses and their Diversification under New Niches</b>	<b>1</b>
<i>P.S. Basu and Jagdish Singh</i>	
<b>2. Role of Phosphorus Efficient Genotypes in Increasing Crop Production</b>	<b>19</b>
<i>B.C. Ajay, A.L. Singh, Narendra Kumar, M.C. Dagla, S.K. Bera and R. Abdul Fiyaz</i>	
<b>3. Salinity Management in Vertisols: Physiological Implications</b>	<b>51</b>
<i>G. Gururaja Rao</i>	
<b>4. Physiological Basis for Maximizing Yield Potentials in Coffee</b>	<b>107</b>
<i>Chandra Gupt Anand and P. Prathima</i>	
<b>5. Bioregulators Improve the Productivity and Quality of Indian Table Grapes</b>	<b>173</b>
<i>S.D. Ramteke</i>	
<b>6. Physiological Basis of Iron Toxicity and its Management in Crops</b>	<b>203</b>
<i>K.K. Baruah and Ashmita Bharali</i>	
<b>7. Can Water Deficit be Useful in Potato?—Some Issues</b>	<b>225</b>
<i>Devendra Kumar and J.S. Minhas</i>	

---

<b>8. Bioregulators Ameliorate Water Deficit Stress in Wheat</b>	<b>237</b>
<i>Sushmita and Pravin Prakash</i>	
<b>9. Phenology and Productivity of Forest Flora of Gujarat</b>	<b>261</b>
<i>R.N. Nakar, B.A. Jadeja and A.L. Singh</i>	
<b>10. Radiotracer Use in Understanding Mineral Nutrition of Crop Plants</b>	<b>295</b>
<i>Bhupinder Singh, Prashant Kumar Hanjagi, Manoj Shrivastava, Achchelal Yadav, Sumedha Ahuja and Rinki</i>	
<b>11. Nutritional Quality of Wheat</b>	<b>315</b>
<i>Sewa Ram</i>	
<b>12. Nitrogen-use Efficiency and Productivity of Wheat Crop</b>	<b>337</b>
<i>C. Gireesh, B.C. Ajay, R. Abdul Fiyaz, K.T. Ramya and C. Mahadevaiah</i>	
<b>13. Quality Seed: A Mega Factor in Enhancing Crop Productivity</b>	<b>357</b>
<i>J.S. Chauhan, A.L. Singh, S. Rajendra Prasad and Satinder Pal</i>	
<i>Previous Volume Content</i>	<b>427</b>
<i>Index</i>	<b>429</b>

---

## Chapter 2

# Role of Phosphorus Efficient Genotypes in Increasing Crop Production

*B.C. Ajay<sup>1\*</sup>, A.L. Singh<sup>1</sup>, Narendra Kumar<sup>1</sup>, M.C. Dagla<sup>1</sup>,  
S.K. Bera<sup>1</sup> and R. Abdul Fiyaz<sup>2</sup>*

*<sup>1</sup>ICAR-Directorate of Groundnut Research,  
PB 5, Junagadh – 362 001, Gujarat, India*

*<sup>2</sup>ICAR-Directorate of Rice Research, Rajendranagar, Hyderabad*

---

### 1. Introduction

Today, agricultural sector supports food to nearly 7 billion people in the world; of this nearly 4.5 billion people are living in Asia where the food scarcity, which was repeatedly claimed due to increasing population, has been evaded by the tremendous progress of agricultural technology particularly in India and China during the past four decades (FAO, 2013; Singh, 2014). The world population is predicted to become nearly 10 billion in next 20-25 years, of this more than 60 per cent people will be living in Asia with only 50 per cent of the world production. Thus food shortage may become an important problem in future in Asia where optimization of mineral nutrition holds a key to optimize crop production (Singh and Mann, 2012).

Phosphorus (P) is one of the important element required for crop growth and development and is often applied in the form of fertilizers for obtaining high productivity. The phosphorus fertilizers is derived from inorganic minerals such as phosphate rock and around 90 per cent of the phosphate rock extracted globally is for

---

\* Corresponding Author: E-mail: [ajaygpb@nrcg.res.in](mailto:ajaygpb@nrcg.res.in)

food production and the remainder is for industrial purposes (Jasinski, 2006). These phosphate rock reserves are distributed in very few countries around the world (Table 2.1). Morocco who controls western Sahara's reserves holds 75 per cent of world's phosphate rock reserves. Importing Western Saharan P rock via Moroccan authorities is condemned by the UN and has recently been boycotted by several Scandinavian firms (Corell, 2002). Phosphate rock is a non-renewable resource that takes 10-15 million years to form from seabed to uplift and weathering, and current known reserves are likely to be depleted in 50-100 years (Jainski, 2006). It is expected that global P requirement will reach its peak by 2040 (Cordell *et al.*, 2009). Like oil and other natural resources P has no substitute in agriculture and as an element can't be manufactured or synthesized. Hence it becomes very important to conserve and efficiently use these limited natural resources.

**Table 2.1: Phosphate Rock Reserve Estimates around the World**

Country	Reserves (million metric tons)	Share (per cent) of World Total
Moroco and Western Sahara	50000	74.9
China	3700	5.5
Algeria	2200	3.3
Syria	1800	2.7
South Africa	1500	2.2
Jordan	1300	1.9
Russia	1300	1.9
United states	1100	1.6
Australia	870	1.3
Peru	820	1.2
Iraq	430	0.6
Brazil	270	0.4
Kazakhstan	260	0.4
Saudia Arabia	211	0.3
Israel	130	0.2
Egypt	100	0.1
Tunisia	100	0.1
Senegal	50	0.1
India	35	0.1
Other countries	582	0.9
World total	16758	

Data: U.S. Geological Survey, Mineral Commodity Summary 2014.

Several agronomic practices have been proposed for efficient phosphorus utilization in agriculture system but are cost affected. The development of P-efficient cultivars is regarded as efficient strategy to mitigate the problem of phosphorus

limitation. Release of P-efficient genotypes for both high and low input farming systems would reduce the production cost of P fertilizer application in both acidic and calcareous soils (Singh and Basu, 2005a, b), minimize environmental pollution and contribute to the maintenance of P reserve globally (Cakmak, 2002; Vance *et al.*, 2003). Development of P-efficient genotypes with a great ability to grow and yield in -deficient soil is therefore an important goal in plant breeding (Rengel, 1999; Hash *et al.*, 2002; Wissuwa *et al.*, 2002; Yan *et al.*, 1992, 2004).

## 2. Role of P in Crop Production and its Widespread Deficiency

The phosphorus, known to be a constituent of nucleic acid, phytin and phospholipids in plants is the second most important nutrient for crop growth and development. It plays important role in energy storage and transfer within cells, speeds up root development, facilitates greater N uptake and results in higher grain protein yields. Phosphorus is essential for the formation of chlorophyll and absorption of potassium which is an essential part of life, cell division and development of meristematic tissues, helps in the seed development and maturity of plant and phosphorus has got specific role in nodule formation as a component of ATP and ADP involved in the energy transformations, driving most of the biochemical reactions including respiration and photosynthesis (Marschner, 1995; Singh, 2004; Singh and Basu, 2005a; Singh *et al.*, 2004). Thus high P supply is required for realising high yields (Clark, 1990; Singh and Basu, 2005a). However phosphorous availability in calcareous and low pH soils is very less as it forms complexes with calcium and aluminium making it unavailable to the plants (Singh, 2000, Singh *et al.*, 2004). Hence phosphorus is regarded as most limiting nutrient for plant growth. It is estimated that P availability to plant roots is limited in two thirds of the cultivated soil in the world (Batjes, 1997; Singh, 2004).

While studying the effects of P deficiency on plant growth in a wide range of species of various ecological habitats Atkinson (1973) described three common features of P-deficiency (a) Leaves are the first organs to be affected and their growth reduced most severely, (b) Root growth is the least affected, root/shoot ratio increased with time but increase is proportionate and greater in deficient plants, (c) Leaf development is delayed. Hence it is considered as one of the essential nutrient for plant growth and development.

In order to maintain P availability to the plants external application of phosphorus is required. But concerns are being expressed that due to limited P resources, lasting only a few decades, lack of P fertilizers may become a serious problem in the future (Mucchal *et al.*, 1996). Annually 17.5 million tons of phosphate rock is mined (Cordell *et al.*, 2009) however, these P reserves are finite resources and are concentrated in few places like Morocco and China which together hold 70 per cent of world's reserves (Rosamarin, 2004). Cordell *et al.* (2009) suggested that we may experience "peak" in P supply as early as 2033 a point at which global supply cannot keep pace with demand for P. As the demand increases cost of P fertiliser increase and in long term it affects sustainability and economic viability of agriculture. Thus, these finite P reserves should be used judiciously by adopting suitable crop husbandry practices and by developing P efficient crop varieties.

In most of the crops and in almost all soils right from acidic ferrosols to neutral to acidic andosols and in calcareous soils phosphorus deficiency is a widespread problem. Ferrosols with low pH and Andisols with wider range of pH exhibit a high P fixing capacity. In natural soils, the level of soluble orthophosphate (Pi) is often below many of the minor elements (Epstein, 1972). Tropical soils also frequently have high capacities for P fixation and may require heavy P fertilization to achieve economic yields. Excess of P fertilizer application not only increases the costs to farmers but also creates serious problem of nutrient pollution. Phosphorus is added to the soil as phosphatic fertilizer from where plants acquire their P in soluble ionic forms  $\text{HPO}_4^{2-}$  and  $\text{H}_2\text{PO}_4^-$ . The low P availability to leguminous crops, having nodules responsible for N fixation has a high P requirement (Vance, 2001). The fixation of P in the soil converts most often applied P into insoluble form. Some work has been done to understand the factor associated with P-efficiency in plants (Gerloff and Gabelman, 1983; Blair, 1993). Understanding the P-efficiency at physiological and molecular level (Goldstein, 1991) should assist in developing and refining selection criteria for plant improvement programs.

### 3. Defining P Efficiency

Several definitions have been proposed for nutrient use efficiency and accordingly criterions used by these definitions also vary. Moll *et al.* (1982) defined N and P use efficiency as grain yield per unit of nutrient supplied (from the soil and/or fertilizer). Fohse *et al.* (1998) defined P efficiency as the ability of plant to produce its certain percentage of its maximum yield at a certain level of soil P. *i.e.* P content in soil required to produce 80 per cent of maximum yield. These definitions may include absolute yield and amount of P absorbed under P-limited conditions, relative shoot dry weight, P acquisition and utilisation efficiency, rate of P absorbed per unit of root weight or root length, relative reduction in shoot dry weight etc. It is of the opinion that relative P-efficiency indices like relative shoot dry weight, would take into account both the acquisition and P utilisation efficiencies (Rengel, 1999).

#### 3.1. P Stress Factor (PSF)

P-stress factor (PSF) is a tolerance index of cultivars under P-starvation. PSF indicates relative reduction in SDM due to P-stress and cultivars exhibiting low PSF values are considered more P-tolerant under P-deprivation (Akhtar *et al.*, 2007). P stress factor (PSF) takes into account shoot dry weight (SDW) under P-deficiency and p-sufficiency conditions and measures relative reduction (per cent) in SDW under P-deficiency conditions (Iqbal *et al.*, 2001). It determines the responsive and nonresponsive behaviour of a crop towards a nutrient. In general, varieties showing smaller PSF values are preferred in screening programs, because they show lesser decrease in SDW production with decreased nutrient supply in root medium (Iqbal *et al.*, 2001).

#### 3.2. P-Efficiency (PE)

Similarly Sepher *et al.* (2009) used another relative P-efficiency (PE) index *i.e.* relative shoot dry weight (shoot dry weight under P-/shoot dry weight under P+). Genotypes with PE value close unity are regarded as efficient.



### 3.3. Agronomic P Use Efficiency (APE)

Another relative P efficiency index used is “Agronomic P use efficiency (APE)” which is calculated as increase in yield per unit of added P fertilizer. APE will account both the acquisition and P utilisation efficiencies (Hammond *et al.*, 2009). Preferably reduction in yield per unit of P applied under P deficit conditions among genotypes should be low. Hence for a genotype to be efficient lower APE values are preferred.

### 3.4. P Use Efficiency (PUE)

It is defined as the kg of grain yield produced per kg of soil available P. PUE depends on ability of genotype to acquire P from soil and the way it is being utilised in the plant. Hence PUE is obtained by multiplying two variables *viz.* P acquisition efficiency (PAE) and P internal utilisation efficiency (PUTIL). PAE is defined as the amount of phosphorus accumulated in plant per unit of P available in soil. PUTIL is defined as the grain yield produced per unit of P in plant.

### 3.5. P Efficiency Index (PEI)

Pan *et al.* (2008) used principal component analysis to calculate PEI. This method not only simplifies parameters into several important principal components but also provides relative weights of different principal components. Higher the PEI more efficient is the genotype (Pan *et al.*, 2008).

The practices proposed for efficient phosphorus utilisation in agricultural system and development of P-efficient cultivars has been regarded as efficient strategy to mitigate the problem of P limitation. Considerable work has been done to understand the complex factor associated with P-efficiency in plants (Gerloff and Gabelman, 1983; Blair, 1993). Understanding P-efficiency at physiological and molecular level (Goldstein, 1991) should assist in developing and refining selection criteria for plant improvement programs. Various other definitions of P-efficiency are listed in Table 2.2. Ranking genotypes for nutrient efficiency can vary according to definition used (McLachlan, 1976; Blair and Cordero, 1978 and Blair, 1993).

### 3.6. P Efficiency and Response

Genotypes may be classified in two different ways based on efficiency of genotype (Efficient and In-efficient) and based on its response to applied fertilizer (responders and non-responders). Responsive plants would increase uptake and yield as nutrient supply increases whereas P-efficient plants would produce high yields at low levels of P (Randall, 1995). P-efficient plants depending on their responsiveness may or may-not respond to applied nutrients. Hence combining responsiveness and efficiency in one genotype becomes important. By combining both responsiveness and efficiency Blair (1993) proposed four response classes (Figure 2.1).

In order to identify suitable criteria to classify genotypes as “efficient or in-efficient” or “responders and non-responders” all available definitions of phosphorus use efficiency were classified into two groups: efficiency and responders. Definitions listed under “efficiency” will classify genotypes into “efficient” or “in-efficient”.

Table 2.2: Definitions of Phosphorus Use Efficiency to Identify P Efficient Genotypes

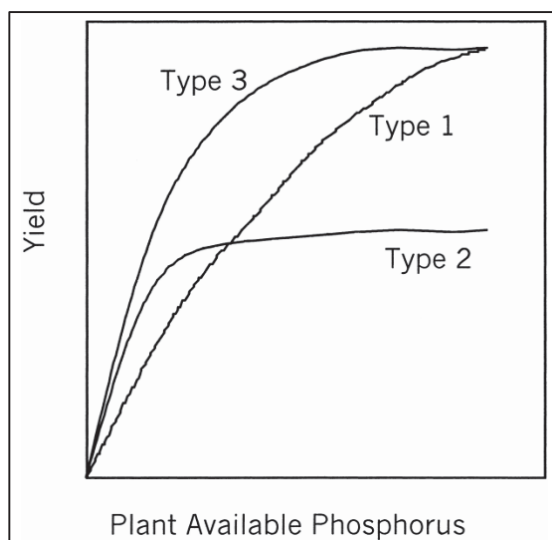
Name	Abbreviation	Description	Formula	Authors
Phosphorus acquisition efficiency	PAE	kg P in the plant kg <sup>-1</sup> of soil available P	Pt/Ps	Parentoni and Junior, 2008
Phosphorus uptake efficiency	PUPE	P in plant/P in soil	Pt/Ps	Kakar <i>et al.</i> , 2002
Root P absorption efficiency	RPAE	Capacity of root to absorb P from soil	Pt/RDW	Gerloff and Gabelman, 1983
Root efficiency ratio	RER	Shoot P uptake/Root dry matter	Pso/RDW	Jones <i>et al.</i> , 1989
P utilisation efficiency	PUtE	Organ P content/Plant P content	Sto/Pt	Sepehr <i>et al.</i> , 2009
P efficiency ratio	PER	Yield/amount of P in the plant (tissue P concentration)	Gr/Pt or Sto/Pt	White <i>et al.</i> , 2005; White and Hammond, 2008
Relative P uptake	RP	Organ P content/Plant P content	Gr/Pt or Sto/Pt	Grant and Matthews, 1996
physiological P efficiency index	PPEI	Grain yield/Total P uptake	Gr/Pt	Yaseen and Malhi, 2009
P internal utilisation efficiency	PUtE	kg of grain produced per kg of P in the plant	Gr/Pt	Parentoni and Junior, 2008
Phosphorus utilisation efficiency	PUtE	Yield/P in plant	Gr/Pt	Kakar <i>et al.</i> , 2001
Whole Phosphorus utilisation efficiency	WPUE	The efficiency of plant to utilize the absorbed P within the plant	(Gr+Sto)/Pt	Gerloff and Gabelman, 1983
Phosphorus biological yield efficiency ratio	PBER	Rate of whole plant weight and total phosphorus content	(Gr+Sto)/Pt	Su <i>et al.</i> , 2006
P efficiency ratio	PER	Biological yield/Total P uptake	(Gr+Sto)/Pt	Yaseen and Malhi, 2009
Physiological P use efficiency	PPUE	dry weight/P content	Sto/Pso or Gr/Pgo	Gerloff and Gablemen, 1983
Phosphorus efficiency ratio	PER	Yield/tissue P concentration at a given P concentration	Gr/GPc	White <i>et al.</i> , 2005; White and Hammond, 2008
Phosphorus utilisation index	PUI	Shoot dry matter/shoot P content	Sto/Pso	Jones, 1989
Quotient of P utilisation	QUt	Shoot dry matter/shoot P content	Sto/Pso	Siddiqi and Glass, 1981
Shoot Phosphorus utilisation efficiency	SPUe	kg of grain dry matter per kg of P in the grain	Gr/Pg	Parentoni and Junior, 2008
Phosphorus harvest index	PHI	Above ground biomass/total P content in shoot	Sto/Pso	Su <i>et al.</i> , 2006
		P uptake in grain/Total P uptake * 100	Pgo/Pt	Jones <i>et al.</i> , 1989
		Shoot P content/Total P content	Pso/Pt	Siddiqi and Glass, 1981

Contd...

Table 2.2–Contd...

Name	Abbreviation	Description	Formula	Authors
Phosphorus use efficiency	PUE	Gr/ps Yield/P in soil	Gr/Ps	Parentoni and Junior, 2008
Fertilizer P uptake efficiency	FPUpE	(P in fertilised plants – P in control plants)/ P applied	$[(Pt_{high} - Pt_{low}) / P_{applied}]$	Kakar <i>et al.</i> , 2001 Kakar <i>et al.</i> , 2002
P acquisition efficiency	PACE	Increase in plant P content per unit of added P fertilizer	$Pso_{low} / Pso_{high}$ $(Pgo_{high} - Pgo_{low}) / \Delta Papp$ or $(Pso_{high} - Pso_{low}) / \Delta Papp$	Sepehr <i>et al.</i> , 2009 White <i>et al.</i> , 2005; White and Hammond, 2008
P response efficiency	PRE	Yield responses/difference between amounts of P supplied	$(Sto_{high} - Sto_{low}) / \Delta Papp$ or $(Gr_{high} - Gr_{low}) / \Delta Papp$	Pang <i>et al.</i> , 2010
P efficiency	PE	$Sto_{low} / Sto_{high}$	$Sto_{low} / Sto_{high}$	Sepehr <i>et al.</i> , 2009
Fertilizer P Utilisation efficiency	FPUtE	$[(Yield_{high} - yield_{low}) / (Pt_{high} - Pt_{low})]$	$[(Gr_{high} - Gr_{low}) / (Pt_{high} - Pt_{low})]$	Kakar <i>et al.</i> , 2002
P utilization efficiency	PUtE	Increase in yield per unit increase in plant P content	$(Sto_{high} - Sto_{low}) / (Pso_{high} - Pso_{low})$	White and Hammond, 2008
Fertilizer P Use efficiency	FPUE	$[(Yield_{high} - yield_{low}) / P_{applied}]$	$[(Yield_{high} - yield_{low}) / P_{app}]$	Kakar <i>et al.</i> , 2002
Agronomic P use efficiency	APE	Increase in yield per unit of added P fertilizer	$(Sto_{high} - Sto_{low}) / \Delta Papp$ or $(Gr_{high} - Gr_{low}) / \Delta Papp$	White <i>et al.</i> , 2005; White and Hammond, 2008
P efficiency index	PEI	$PEI = \sum_{i=1}^n PCI \times RW_i$		Pan <i>et al.</i> , 2008

Papp: Applied phosphorus; Pgo: Grain/kernel P content; Pso: Shoot P content; Pgc: Grain/kernel P concentration; Pt: Total P content; Ps: P concentration in soil; Gr: Grain/kernel dry weight; Sto: Shoot dry weight; RDW: Root dry weight.



**Figure 2.1: Four Classes in Response to P (Blair, 1993): 1) Inefficient responder (type 1); Efficient non-responder (type 2); 3) Efficient responder (type 3); and 4) Inefficient non-responder (not shown).**

**Type I- Inefficient responder:** These genotypes give low yield when nutrient availability is less, but increases their yield as the nutrient availability increases. Thus their ability to respond to applied fertilizer could be used in breeding to develop new efficient responders.

**Type II- Efficient non-responder:** These genotypes are capable of giving high yield even when nutrient availability is less, but do not respond with increased yield under high input conditions. These can be used in breeding to develop new efficient responding lines.

**Type III- Efficient responders:** These genotypes show high yield at low level of nutrient supply and their yield level increases as nutrient supply increases. Identifying efficient responders would be an ideal breeding programme for nutrient use efficiency.

**Type IV- Inefficient non-responders:** These genotypes give low yield irrespective of nutrient availability.

### 3.7 P Uptake and Utilisation Efficiencies

In order to understand superior performance of efficient genotypes over inefficient genotypes it is important to study their P-uptake and P-utilisation separately. Hence, Parentoni and Junior (2008) obtained P use efficiency by multiplying the means of “uptake” and “utilisation”. To study P-uptake pattern four definitions are available which consider rate of P-content of whole plant or P- content in shoot over P available from soil or root dry weight. To further complicate the matter four different acronyms are used for each definition. The P-utilisation pattern explained using 15 different types of definitions in literature, accordingly the criterion used to explain utilisation efficiency also varies and ranking of genotypes for nutrient efficiency also varies according to definition used (McLachlan, 1976; Blair and Cordero, 1978 and Blair, 1993). Thus there is a need of common universal definition to explain utilisation pattern of P in plant.

Most of the available definitions of P-utilisation consider either grain yield or shoot weight over P-content of whole plant. Few other definitions consider grain yield or shoot weight over P content in grain or shoot respectively to explain P-utilisation efficiency. Three definitions proposed by Gerloff and Gabelman, 1983, Su *et al.* (2006) and Yaseen and Malhi (2009) consider both grain yield and shoot biomass weight over P-content of whole plant but with different acronyms (*viz.* PUE, WPUE and PBER). Rose and Wissuwa (2012) are of the view that for valid comparison of genotypes and to improve physiological mechanisms, internal P-use efficiency should be defined as biomass produced per unit of P accumulated in tissue and further this PUE has to be dissected into components such as “shoot PUE”, “root PUE” and “grain PUE”. “Root PUE” has been defined as P accumulation per unit of dry matter which may be misleading because P uptake from soil depends on volume of soil explored which in turn depends on root length and its surface area. Hence “root PUE” should be interpreted as root surface area per mg P (Rose and Matthews, 2012). In maize P-efficient genotype had lower root P concentration and high root surface area than P in-efficient genotype. Definitions proposed by Gerloff and Gabelman (1983), Su *et al.* (2006) and Yaseen and Malhi (2009) consider only grain and shoot weight and lack root surface area for calculating “root PUE”. Adding root surface area to the above proposed formula PUE can be written as:

$$PUtE = (Gr+Sto+RSA)/Pt$$

To study the physiological mechanisms of PUE this formula could be dissected out as:

$$PUtEg = Gr/Pt \text{ (P utilisation efficiency of grain)}$$

$$PUtEs = Sto/Pt \text{ (P utilisation efficiency of shoot)}$$

$$PUtEr = RSA/Pt \text{ (P utilisation efficiency of root), RSA is root surface area.}$$

$$PUtE = PUtEg + PUtEs + PUtEr$$

Parentoni and Junior (2008) obtained PUE by multiplying the means of PUtE and PUpE.  $PUE = PUpE * PUtE$

$$= (Pt/Ps) * (Gr+Sto+RSA)/Pt$$

$$PUE = (Gr+Sto+RSA)/Ps$$

This definition would facilitate in improving PUE of shoot, grain and root individually. Interpreting root PUE on the basis of root biomass per unit of P may be misleading because soil explored by roots for P acquisition depends on root length (or surface area) rather than on root biomass (Rose and Matthews, 2012).

In order to identify genotypes responsive to fertilizer application i.e. “responders” and “non-responders” several definitions are available. Classification of genotypes as efficient and responders using formulas proposed here would help in identifying four classes of genotypes as proposed by Blair (1993).

As there were no well-defined selection criteria for P-efficiency in groundnut, an effort was made in our laboratory (Singh and Basu 2005b) by growing the crop under control and P fertilized condition and recording the relative pod and haulm yields (RPY, RHY) and relative P uptake by groundnut genotypes calculated as:

Relative yield =  $100 \times \text{Yield in P-unfertilized plot} / \text{Yield of P-fertilized plot}$ .

The groundnut genotypes were sorted based on their high pod and haulm yields, per cent P contents in leaves at 60 DAE, P uptake by Pod, total P uptake by Plant, both under P-fertilized and P-unfertilized conditions, separately as well as combined. The genotypes having high values of these parameters were categorized as P-efficient and the one having low values were categorized as the P-inefficient one.

The data on various parameters, shows genotypic differences under both P-fertilized and P-unfertilized conditions. These genotypic differences were more pronounced on pod yields, P concentrations and uptake. With the data on these parameters, when the groundnut genotypes were arranged in the descending order, no single genotypes could top the list on the basis of all these parameters. However, certain genotypes were common in the top ten in most of the parameters assessed and showed their higher values. In a similar fashion a few genotypes were common in bottom ten showing lower values of these parameters. Accordingly, for demarcating P-efficient and P-inefficient genotypes, the average values of these parameters from top 20, and bottom 20, were taken into consideration. However such study need to be conducted over the years and, only the genotypes fulfilling majority of the criteria during most of the years need to be categorized as P-efficient and P-inefficient.

Among the various parameters, high pod yield followed by high P uptake were the most important for identifying P-efficient genotypes, the relative pod yield and relative P-uptake further strengthen these parameters (Singh, 2004; Singh and Basu, 2005a, b).

#### 4. Mechanisms of PUE

The P-efficient plants can employ a number of potential adaptive mechanisms for better growth on low-P soils.

##### 4.1 Root Morphology and Architecture

Root hair formation, growth of primary root and lateral root formation are particularly sensitive to changes in the internal and external concentration of nutrients increases absorptive area and soil volume explored. Wang *et al.* (2004) found that root hair density, average root hair length and root hair length per unit root, varied among different genetic materials and that these variations were highly associated with P status.

Root architecture: Indicates the extent to which soil volume is explored and includes, lateral root branching, length and growth angle of basal roots and root growth plasticity. Plants with shallow root architecture have higher P-efficiency attributed to higher nutrient availability in topsoil.

The high P availability in top soil causes shallower growth angles of axial roots, enhanced adventitious rooting, and greater dispersion of lateral roots are associated with foraging of P from top soil and thus P acquisition. Variation in root growth angle among bean contributed 600 per cent increase in P acquisition and 300 per cent increase in yield (Bonser *et al.*, 1996; Liao *et al.*, 2001). The root growth angle (RGA) is influenced by basal roots which appear in distinct nodes/whorls. Basal root whorl

number (BRWN) varies among genotypes from one to four (16 basal roots). Shallow basal RGA are found in topmost whorls whereas lower whorls produce steeper basal RGA. The RGA has been successfully used for breeding varieties for low fertility soils (Lynch, 2007). In dicots adventitious roots grow from subterranean portion of hypocotyls horizontally through the top soil and are associated with P acquisition in low P soils. Metabolic cost of soil exploration by these roots is also less.

## 4.2 Symbiosis

### 4.2.1. Rhizobium

P addition has considerable impact on rhizobium symbiosis and biological N<sub>2</sub> fixation by increasing nodule formation and nitrogenase activity on the upper parts of the roots (Kuang *et al.*, 2005). The shallow root systems increase P-uptake efficiency and facilitate biological N<sub>2</sub> fixation. Improved N status with resulting enhanced root growth might be the mechanism by which soybean P uptake was increased in plants inoculated with the effective rhizobium strains on low-P acid soils.

### 4.2.2. Azolla and Blue Green Algae

The blue green algae (BGA) inside Azolla fixes atmospheric nitrogen in symbiotic association. Azolla encompasses a BGA *Anabaena azollae* inside its leaf where fertilizer P application either as foliar spray or in split doses increases the growth of azolla and BGA and nitrogen fixation and finally the growth and productivity of rice and fertility of rice field (Singh and Singh, 1990; Singh *et al.*, 1988).

### 4.2.3. Mycorrhizae

Mycorrhizal fungi can increase phosphorus availability by exuding various organic acids themselves, freeing phosphates in the same manner as those exuded from plant roots. Under low P conditions, plants often have higher mycorrhizal infection rate and contribute more to P uptake (Singh and Chaudhari, 1996). Plant growth response to arbuscular mycorrhizae (AM) associations (*i.e.* the 'mycorrhizal growth response', MGR) varies widely among plant species and even varieties.

Colonization by these beneficial fungi improved access of phosphorus by extending the crop's root system with mycorrhizal hyphae (Bucher, 1971), indirectly increasing the root surface area for nutrient absorption and crop growth. Mycorrhizal hyphae work to improve nutrient acquisition by increasing their affinity for phosphorus ions and decreasing the concentration gradient required for more energy efficient absorption (Shenoy and Kalagudi, 2005). Additionally, biodiversity of AM fungi is greater in low-input production systems compared to high-input, likely due to the availability of nutrients making microbial symbiotic relationships obsolete and energy expensive to the crop (Oehl *et al.*, 2004).

### 4.2.4. Root Exudates

Root apices exude a variety of organic acids, which can influence plant nutrition and provide an easily degradable nutrient source for soil microorganisms (Rengel and Marschner, 2005). The roots under phosphorus deficiency exude citrate, malate, and oxalate organic acids which are the most effective at mobilizing soil phosphorus

(Hinsinger, 2001; Ryan *et al.*, 2001). These organic acids release unavailable phosphorus from bound minerals, allowing for the chelation of  $\text{Al}^{3+}$ ,  $\text{Fe}^{3+}$ , and  $\text{Ca}^{2+}$  consequently freeing phosphorus and helping to alleviate P stress (Marschner, 1995; Singh, 2000; 2008). Differences in the exudation of organic acids can be seen between crops under P-deficiency or not (Neumann and Romheld, 1999; Yan *et al.*, 2002). In addition to improving access of previously unavailable phosphate via rhizosphere acidification, exuded carboxylates promote microbial growth, and potentially exploit beneficial microbial relationships that correlate with P bioavailability (Rengel and Marschner, 2005). Thus beneficial relationships between crops and mycorrhizal fungi improve availability and uptake of phosphorus (Li *et al.*, 2010).

### 4.3 Activation of High-Affinity Phosphate (Pi) Transporters

The inorganic phosphate (Pi) concentration within the plant cells is approximately  $>10$  mM ( $>3$  g  $\text{kg}^{-1}$ , on a biomass dry-weight basis), and yet the concentration in the soil solution is typically  $<10$   $\mu\text{M}$  (Bielecki, 1973; Marschner, 1995). Due to low concentration of soluble form of P and slow rate of diffusion plants have evolved several mechanisms to increase Pi uptake from soil and among them high-affinity Pi transporters (PTs) are assumed to be the predominant role in Pi acquisition by plant roots (Marschner, 1995; Raghothama, 1999). The genes encoding these PTs were first identified in Arabidopsis (Muchhal *et al.*, 1996) followed by identification of similar such genes from other plant species including cereals, legumes and solanaceous species (Chen *et al.*, 2007; Chiou *et al.*, 2001; Glassop *et al.*, 2005; Harrison *et al.*, 2002; Javot *et al.*, 2007a; Leggewie *et al.*, 1997; Liu *et al.*, 1998a,b; Maeda *et al.*, 2006; Mitsukawa *et al.*, 1997; Mudge *et al.*, 2002; Nagy *et al.*, 2005; Paszkowski *et al.*, 2002; Rae *et al.*, 2003; Smith *et al.*, 1997; Xu *et al.*, 2007).

Most of these plant PTs belong to Pht1 family of genes and are believed to be made of 12 transmembrane (TM) domains (Saier, 2000), containing two partially duplicated subdomains of six TM segments (Lagerstedt *et al.*, 2004). Most of these genes expressed predominantly in roots induced by low-Pi supply or by AM fungi (Bucher, 2007) and few of them also expressed in other plant parts such as stem, leaves, cotyledons, tubers and flowers (Karthikeyan *et al.*, 2002; Mudge *et al.*, 2002). Analysis of the Arabidopsis genome has revealed that there are nine genes in the Pht1 family (Mudge *et al.*, 2002), whereas in barley at least eight members have been identified (Rae *et al.*, 2003).

In vascular plants, at least two forms of PTs are known and they are classified based on the Pi absorption kinetics and affinity to target Pi *i.e.*, high-affinity PTs,  $K_m$  (Pi) = 3–7  $\mu\text{M}$ ; low-affinity PTs  $K_m$  (Pi) = 50–330  $\mu\text{M}$  (Furihata *et al.*, 1992; McPharlin and Bielecki, 1987; Ullrich-Eberius *et al.*, 1984). The high- and low-affinity PTs belong to Pht1 and Pht2 families, respectively (Bucher *et al.*, 2001). The members of Pht1 family are induced under P deficiency often exclusively in the root (Daram *et al.*, 1998; Liu *et al.*, 1998b; Rae *et al.*, 2003). On the contrary, the members of Pht2 family are mostly expressed constitutively in the aerial parts of the plant (Daram *et al.*, 1999; Rae *et al.*, 2003). High-affinity PTs are involved in regulating Pi uptake and transcriptional control of PTs activity (Muchhal and Raghothama, 1999; Raghothama and Karthikeyan, 2005) and post-transcriptional regulatory mechanisms (Bucher *et al.*, 2001). Hence, high-affinity PTs have been suggested as potential targets for improving



Pi uptake (Mitsukawa *et al.*, 1997; Rae *et al.*, 2003; Vance *et al.*, 2003). Studies have indicated that plasma membrane H<sup>+</sup>-ATPase is also involved in P uptake (Shen *et al.*, 2006).

#### 4.4. Secretion of Organic Acids and Phosphatases into the Rhizosphere

A major portion of Pi in soil may be present in organic forms. Organic P complexes such as phytic acid may contribute to significant portions (20–80 per cent) of P in soil (Jungk *et al.*, 1993; Richardson, 1994). The organic P complexes need to be broken down by enzymatic activity before the inorganic Pi is released into the rhizosphere (Raghothama and Karthikeyan, 2005). Inoculation of food crops with plant growth-promoting rhizobacteria (PGPR) or mycorrhizae can directly increase plant available P via mechanisms of solubilization and mineralization of fixed P from inorganic and organic forms (Rengel and Marschner, 2005; Hodge *et al.*, 2009). Mechanisms include the release of organic acids, protons and phosphatases into the rhizosphere. Bacteria from the genera *Pseudomonas* and *Bacillus* and fungi, primarily *Penicillium* and *Aspergillus* are among the most powerful P solubilizers.

Another mechanism which indirectly leads to increased P acquisition by plants is the production of phytohormones (mainly auxins) by rhizobacteria that stimulate root growth (Richardson, 2001; Jacobsen *et al.*, 2005; Richardson *et al.*, 2009a). Inoculation with *Azospirillum*, known to produce substantial amounts of indole-3-acetic-acid (IAA), increases the length and density of root hairs as well as the appearance and elongation rates of lateral roots in many plant species (Fallik *et al.*, 1994) which increases the surface area for absorption of P.

### 5. Strategies to Improve P Use Efficiency

In order to improve phosphorus use efficiency (PUE) it is important to understand the source through which P is obtained, its movement in the soil and different ways in which it is deposited in the soil. When the fertilizer is added, phosphate ions are readily available as plant-available P in soil solution. These Pi ions may get adsorbed on to the soil surface or may be lost through leaching. Phosphate ions after entering plant and animal system get exported in different forms. In order to maintain yield levels, it is important that, P removed from the soil is replaced back to maintain the balance. Simpson *et al.* (2011) gave P balance efficiency formula as,

$$P_{\text{fertilizer}} = P_{\text{export}} + P_{\text{erosion/leaching}} + P_{\text{waste disposal}} + P_{\text{soil accum}}$$

where,

$P_{\text{export}}$  = removal of P in products,  $P_{\text{erosion/leaching}}$  = P lost by leaching, runoff or soil movement,  $P_{\text{waste disposal}}$  = P accumulated in small areas of farms as a result of uneven dispersal of animal excreta rendering the P less available and  $P_{\text{soil accum}}$  = P accumulating as sparingly-available phosphate or organic P compounds that are slowly mineralised.

#### 5.1. Improving P Use Efficiency by Minimizing Losses

P fertilizer efficiency can only be achieved when P loss through erosion is reduced, uniform distribution of excreta reducing P fixation in soils. This could be achieved by interventions of fertilizer, agronomic, microbial and plant based technologies.

### 5.1.1. P Export Loss through Farm Products

The amount of P applied to soil can be reduced by modified deliver products with low P content leading to low P export. In this system P absorbed from soil is less; hence quantity of P fertilizer applied may also be reduced. This is an ideal system for low P fixing soils but leads to accumulation of applied P in moderate to high P fixing soils. Hence in high P fixing soils if P loss by export is reduced it is counteracted by accumulation of unavailable forms of P in soils.

### 5.1.2. P Loss through Erosion, Runoff and Leaching

For P to cause an environmental problem there must be a source of P (*i.e.*, high soil levels, manure or fertilizer applications, etc.) and P must be transported to a sensitive location (*i.e.*, leaching, runoff, erosion, etc.) (Gburek *et al.*, 2000). A high P source with little opportunity for transport, while it may be a waste of a resource, may not constitute an environmental threat. Likewise, a situation where there is a high potential for transport, but no source of P to move, is also of little threat.

P losses from agricultural fields vary with soil type. In soils with high P fixing ability loss is only 0.4 -5 per cent of applied P, (McCaskill and Cayley, 2000; Ridley *et al.*, 2003; Melland *et al.*, 2008), but on soils with low P fixing capacity losses could range from 40 -90 per cent of applied P (Ozanne *et al.*, 1961; Lewis *et al.*, 1987). P lost from agricultural fields is entering water bodies and is causing serious environmental problems. In agricultural fields P is lost through erosion; runoff and leaching which could be avoided to improve P efficiency using following strategies (Chambers *et al.*, 2000; Uusi-Kamppa *et al.*, 2000):

- ☆ Appropriate forms and placement of obilized,
- ☆ Appropriate timing of obilized in relation to rain and crop growth,
- ☆ Use of soil amendments to reduce nutrient transport,
- ☆ Use of buffer strips and fencing of waterways to capture obilized nutrients and avoid direct contamination,
- ☆ Location of field access points,
- ☆ Attention to cultivation methods
- ☆ Use of minimum tillage and attention to ground cover
- ☆ Conservation tillage and crop residue management
- ☆ Terracing
- ☆ Contour tillage
- ☆ Cover crops

## 5.2 Agronomic Interventions to Improve P Availability to Plants

### 5.2.1. Microbial Activity and Organic P Cycling

The rate of mineralization of fixed form of P in soil increases the P balance efficiency of our farming system. Organic manure increases microbial activity in soils. This inturn will increase organic P mineralization in soil. But recovery of P

from organic manure was affected when plant available P is high in soil solution. Low uptake of residual P from manure also indicates that, yield response of plant is due to the use of residual P reserves of soil than plant available residual P.

Organic P mineralisation and microbial P pool could be enhanced under different farming systems. Grass-legume and grass only pastures have demonstrated that organic P and microbial activity can increase plant available P in soils (Oberson *et al.*, 1999). Thus managing interactions of residues with soil will also slow down P sorption reaction and P held in microbial biomass is also protected temporarily from absorption.

### 5.2.2. Minimising Inefficiencies and Constraints Associated with Yield

#### *Reducing Constraints to Yield*

P availability also influences yield indirectly through various yield constraints like root growth affected by soil acidity, root diseases, soil compaction and others which in turn affect nutrient uptake and finally yield. Alleviating these constraints will improve P export and P balance efficiency. In general, P fertilizers are applied in excess of requirement to overcome several other constraints and relieving these constraints can increase are relieved P-use efficiency. For example in acid soils when Aluminium ( $Al^{3+}$ ) concentration in soil solution increases it will affect root elongation and which in turn affects water and nutrient uptake and finally P uptake. The recovery or amelioration of Al-toxicity through the use of lime increased the P availability.

#### *Targeted Use of P-Fertilizer*

In efficient farming systems there is accumulation of sparingly available phosphate, losses due to leaching, erosion and runoff, and accumulations due to uneven distribution of excreta will continue to increase beyond critical P level. In these farming systems when soil P is in excess of critical P, lower P inputs and short term cessation of fertilizer is a viable option (Butkitt *et al.*, 2010).

#### *Uneven Dispersal of Excreta*

Grazing animals deposit excreta in camps, in shade or close to water bodies and thus results in poor P balance efficiency. For example sheep on low slope areas deposits 25 to 47 per cent of dung in 5 to 15 per cent of area. Over long period of time this uneven disposal of excreta may lead to accumulation of P in small areas and thus making it unavailable for plant growth.

#### *Precision Agriculture*

Inefficient P utilisation can also occur due to productivity gradients which may arise due to topography, botanical composition, soil type and depth even when fertiliser is applied uniformly. As the price of fertiliser increases its application as per the fertility or productivity gradient is expected to give economic benefits (Hackney, 2009). Differential fertilizer application would be easy in areas where there are large and easily identified differences, but complex productivity patterns can be identified using ground level, airborne or space borne canopy reflectance sensing devices (Trotter *et al.*, 2010). GPS technology can also be used to develop productivity maps for variable rate fertiliser application.

These agronomic practices would help avoid inefficient use of P-fertilizer and bring farming systems to P balance efficiency. The productive farming systems under low soil P concentrations would be economically efficient and environment friendly also.

### 5.3 Genetic Interventions to Improve P Availability to Plants

The P uptake has been found to be multigenic with involvement of additive, dominance and epistatic effects (Duncan and Carrow, 1999). Several genes for P uptake and transportation have been identified, cloned and characterized. QTL mapping has been well conducted with P efficiency in Arabidopsis (Ma *et al.*, 2001), rice (Shimizu *et al.*, 2004), maize (Zhu *et al.*, 2006), wheat (Su *et al.*, 2006) and common bean (Beebe *et al.*, 2006). Expression of genes imparting tolerance to Pi starvation have been identified in soybean (Guo, 2008), rice (Wissuwa, 2005), Arabidopsis (Hammond *et al.*, 2003) and in other crops.

When external-P level drops low to micro-molar concentration, the high affinity transporter mRNA transcripts in roots increase leading to enhanced capacity of roots for P uptake. The inorganic P starvation is known to enhance synthesis of these carrier systems, resulting in better PUE (Duncan and Carrow, 1999). The high-affinity transporters are expressed in the cells in close contact with soil solution (*e.g.* epidermal cells with their associated root hairs and outer layer of cortex) and play an important role in acquisition of P. The low-affinity transporters are active in vascular loading and unloading, *i.e.*, in internal distribution and re-mobilization of acquired P in millimolar concentration range (Smith, 2001). The *Pht1* and *Pht2* families of genes are the two well characterized gene families of P transporters in plants. Three major classes of P transporters with partially overlapping specificities and genes for them have been identified (Duncan and Carrow, 1999). Genes for the four major P metabolic enzymes have been identified. The cytosolic GAPDH is coded by the nuclear gene *GapC*, whereas the chloroplastic GAPDH is encoded by the nuclear genes *GapA* and *GapB*. The nuclear *GapN* encodes the cytosolic GAPDH (Valverde *et al.*, 1999).

### 5.4. Low P-Farming Systems

#### 5.4.1. Prior Fertilizer Application

Prior application of phosphate lowers the P sorption capacity of soil and increases the availability of subsequent fertilizer application (Bolland and Baker, 1998; Bolland and Allen, 2003; Burkitt *et al.*, 2008). This has got significance in soils where large quantity of fertilizer is added to soil. Bolland and Becker (1998) in a study applied P fertilizer at different rates starting from 0 kg/ha to 599 kg/ha only once 20 years ago and after 20 years he applied fresh fertilizer at different rates for wheat. He observed that the initial P-fertilizer applied increased effectiveness of freshly applied fertilizer in increasing yield.

#### 5.4.2. P mobilisation by Soil Microorganisms

Microorganisms can enhance P mobilisation capacity of plants by increased root growth, alteration in sorption equilibria: Results in release of orthophosphate ion into soil solution and increase mobility of organic P and solubilising and

mineralisation of sparingly available forms of P (both organic and inorganic P). Microorganisms decompose organic matter in soil, mineralise organic P and later are incorporated into microbial biomass. Increased microbial activity is observed as P in soil solution decreases (when P is not added or P limiting soils or when P is added) when organic matter (C and N) is added. Hence microorganisms also compete with plants for available P from soil solution and make it temporarily unavailable. This is an important mechanism for regulating P supply as it avoids reaction of P in soil solution with soil particles.

#### **Mineralization of Organic P**

Organic P has to be mineralised by phosphatases (plant or microbial origin) before it can be utilised by microorganisms or plants. Phosphatase activity increases when there is a deficiency of P as a part of P starvation response. When soil suspensions were treated with phosphatases orthophosphate was released (George *et al.*, 2007). Bunemann (2008) reported that 60 per cent of the total organic P may be hydrolyzed by phosphatases with highest amounts being released by phytases (monoester phosphatases active against phytate). Grasses and Legumes grown in media inoculated with soil microorganisms showed increased utilisation of phytate P (Richardson *et al.*, 2001). Genetically modified plant with their ability to release extracellular fungal phytase was able to acquire P directly from phytate. The organic acids chelate cations like Fe and Al bound to P, compete with P for reaction sites on cations and thus release P. Thus organic acids also help by preventing Al from entering into plant.

#### **Solubilisation of Inorganic P**

The bacteria (*e.g. Actinomycetes, Pseudomonas, and Bacillus spp.*) and fungi (*e.g. Aspergillus and Penicillium spp.*) acidify growth media, release organic anions like citrate, gluconate, oxalate and succinate. Amount of P solubilised depend on type of inorganic P present like Ca, iron, aluminium phosphates and other sources of rock phosphate. Inoculation of plants with P solubilising microorganisms' results in improved growth and P nutrition. These P solubilisers include *Pseudomonas, Bacillus, Penicillium* and *Aspergillus* (Richardson *et al.*, 2009). The plant growth promoting rhizobacteria (PGPR) or mycorrhizae solubilise and mineralise fixed form of phosphorus by releasing organic acids or phosphatases. The *Azospirillum* produces phytohormones like auxin (Indole – 3 acetic acid) which increases root hair length and density (Fallik *et al.*, 1994).

#### **5.4.3. Slow Release Fertilizer**

When plants efficiency for P uptake is increased it would lower total soil P content. To avoid total exhaustion of P from soil slow release fertilizer like rock phosphate may be added. In low P fixing soils this strategy prevents leaching loss where as in P fixing soils it will prevent P fixation. Hence slow release fertiliser along with P use efficient lines will ensure that added P-fertilizer is utilised efficiently.

#### **5.4.4. Application of Silica**

Application of Silica or silicate in the form of rice-husk ash or calcium silicate increase P availability for the plant by competing with phosphate ion for adsorption

sites within the soils. But some soils may not respond to silicate application further silicon sources must be water soluble.

#### 5.4.5. Space and Timing of Fertiliser Application

When Plant available P is high in soil, then external application of P may not have any effect on yield. P can also be applied when soil is near to critical soil P level.

#### 5.4.6. Application of Fertilizer Close to Seeds

Small quantity of fertilizer may be placed close to seed instead of broadcasting without affecting yield (Van der Eijk, 2006). Since applied phosphorus is in the vicinity of seedlings major quantity is available for plants uptake and only smaller quantity is fixed in the soil. This will also increase P-use efficiency.

## 6. Phosphorus Use Efficient Varieties

Several Phosphorus use efficient varieties have been released in several crops globally and examples of such varieties are listed in Table 2.3.

**Table 2.3: Phosphorus Use Efficient Cultivars/Breeding Materials Reported in Various Crops**

<i>Sl.No.</i>	<i>Crop</i>	<i>Varieties</i>	<i>Reference</i>
1	Wheat	Lovrin	Su <i>et al.</i> , 2006
		81 (85) 5-3-3-3, Ji 87-4617	Chun-Jian <i>et al.</i> , 2003
		rye Bevy, rye PC00361	Osborne and Rengel, 2002a
		Egret and Durati	Osborne and Rengel, 2002b
		BR10, CPAC89128, and NL459	Fageria and Baligar, 2008
2	Common bean	G19833	Yan <i>et al.</i> , 1995a,b
		Milenio, BAT477, and A785	Mourice and Tryphone, 2009
		BAT477	L'taief <i>et al.</i> , 2012
3	<i>Brassica napus</i>	Eyou Changjia.	Yang <i>et al.</i> , 2011
		RIL 102	Yao <i>et al.</i> , 2011
4	Maize	Mo17	Kaepler <i>et al.</i> , 2000
		082	Chen <i>et al.</i> , 2008
		NY821	Reiter <i>et al.</i> , 1991
		Mutant 99038	Li <i>et al.</i> , 2007b
		L3, 228-3	Parentoni <i>et al.</i> , 2008, 2010
		CB-2, DP × Tromba, HV313 × DEM, Macho III-04, and CIMMYT-1	Bayuelo-Jiménez and Ochoa-Cadavid, 2014
5	Rice	Kasalath	Wissuwa and Ae, 2001
		Zhangzao 18	Li <i>et al.</i> , 2010
		99112	Zai-Hua <i>et al.</i> , 2006
		BRA032048, BRA042094, BRA02601, BRA032051, RA032033, BRA052015, BRA042156, BRA01600, BRA01506, BRA052023 and BRA042160	Fageria <i>et al.</i> , 2014

Contd...

**Table 2.3–Contd...**

Sl.No.	Crop	Varieties	Reference
6.	Arabidopsis	C24, Co, Cal	Narang <i>et al.</i> , 2000
7.	Soybean	Nannong 94-156	Zhang <i>et al.</i> , 2009
		BX10	Zhao <i>et al.</i> , 2004
		IAC-1, IAC-2, IAC-4, IAC-5, IAC-6, IAC-9, Sta. Rosa and UFV-1	Furlani <i>et al.</i> , 2002
8.	Groundnut	SAMNUT 10 and 21	Gabasawa and Yusuf, 2013
		ICGV 86590, ICG 14475, Mutant 68, ICGV 92188	Amit <i>et al.</i> , 2009
		GG5, FeESG 10, SP 250A	Singh and Basu, 2005
9.	Cowpea	IT90K-277-2	Singh, 1999
10.	Potato	CGN 17903 and CIP 384321.3	Balemi and Schenk, 2009
11.	Black gram	DBS-7, DBS-13	Shridevi <i>et al.</i> , 2009.

## Conclusion and Future Prospects for PUE

The P deficiency is most wide spread problem of most of the crop worldwide, where fertilization is of utmost important. However the world P reserves are limited and shrinking. Under such circumstances the role of P efficient genotypes is of utmost importance. All efforts are needed to find out the P efficient and P responsive genotypes for each and every crop.

The nutrient efficiency is the ability of a system to convert inputs into desired outputs, or to minimize the conversion of inputs into waste. The supply or availability of the mineral nutrient is the input and plant growth and yield are the outputs. Thus the efficiency is the relationship of output to inputs and expressed as simple ratio, such as kg yield per kg fertilizer or kg dry weight per g of nutrient supply. However this efficiency depends upon the uptake efficiency (uptake of nutrient per unit supply of nutrients) and utilization efficiency (dry matter production per unit of nutrient taken up). The nutrient responsiveness is the capacity of a plant to increase uptake and yield as nutrient supply increases. The responsive plants are most desirable in fertilized high-input systems, while the nutrient efficient plants, which produce high yields at low levels of nutrients, are most valuable in low-fertility situations.

Breeding for P use efficient lines differs between low P soils and high P fixing soils. In low input agro-ecosystem or in soils with low P content where erosion losses are more, phosphorus availability is more in top soils. Hence in these conditions cultivars with shallow roots would cover the soil surface enabling it to use the available phosphorus and reduce its loss through erosion. Also, plants' internal P use efficiency also can be improved which is defined as capacity to produce a large amount of organic matter per unit of P taken up. These P efficient plants show higher growth potential under same amount of P added.

Luckily in India the peanut varieties released through multi-locational testing under All India Coordinated Research Project on Groundnut (AICRP-G) are as P-

efficient as phosphorus fertility status of the most of the soils where these are evaluated are moderate in majority of states. However, if the responsiveness and efficiency are combined in one genotype through breeding program or achieve through natural selection, it is the best and this is high time to put efforts in this direction in the present day modern agriculture.

## References

- Amit K, Kusuma P, Gowda MVC. 2009. Genotypic variation for root traits in groundnut germplasm under phosphorus stress conditions. *SAT ejournal* 7: 1-4.
- Araújo AP, Plassard C, Drevon JJ. 2008. Phosphatase and phytase activities in nodules of common bean genotypes at different levels of phosphorus supply. *Plant Soil* 312: 129–138.
- Atkinson, D., 1973. Some general effects of phosphorus deficiency on growth and development. *New Phytology*, 72: 101-111.
- Balemi T, Schenk MK. 2009. Genotypic difference of potato in carbon budgeting as a mechanism of phosphorus utilization efficiency. *Plant Soil* 322: 91–99.
- Bariola P A, Howard C J, Taylor C P, Verburg M T, Jaglan V D and Green P J 1994 The Arabidopsis ribonuclease gene RNS1 is tightly controlled in response to phosphate limitation. *Plant J.* 6: 673–685.
- Batjes N H 1997. A world data set of derived soil properties by FAO-UNESCO soil unit for global modeling. *Soil Use Manage* 13: 9–16.
- Bayuelo-Jiménez JS, Ochoa-Cadavid I. 2014. Phosphorus acquisition and internal utilization efficiency among maize landraces from the central Mexican highlands. *Field Crops Research* 156 (2014) 123–134.
- Beebe SE, Rojas-Pierce M, Yan X, Blair MW, Pedraza F, Munoz F, Tohme J, Lynch JP (2006). Quantitative trait loci for root architecture traits correlated with phosphorus acquisition in common bean. *Crop Sci* 46: 413–423.
- Bieleski, R.L. (1973). Phosphate pools, phosphate transport, and phosphate availability. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 24, 225–252.
- Blair G J 1993. In *Genetic aspects of mineral nutrition*. Eds. P J Randall, E Haize, R A Richards and R Munson. pp 205-213. Kluwer Academic Publishers, Dordrecht, Netherlands.
- Blair G J and Cordero S. (1978). The phosphorus efficiency of three annual legumes. *Plant Soil* 50: 387-398.
- Bolland MDA, Allen DG (2003). Phosphorus sorption by sandy soils from Western Australia: effect of previously sorbed P on P buffer capacity and single-point P sorption indices. *Aust J Soil Res* 41: 1369–1388.
- Bolland MDA, Baker MJ (1998). Phosphate applied to soil increases the effectiveness of subsequent applications of phosphate for growing wheat shoots. *Aust J Exp Agr* 38: 865–869.



- Bonser AM, Lynch J, Snapp S (1996). Effect of phosphorus deficiency on growth angle of basal roots in *Phaseolus vulgaris*. *New Phytol* 132: 281–288.
- Bucher M, Rausch C, Daram P (2001). Molecular and biochemical mechanisms of phosphorus uptake into plants. *J Plant Nutr Soil Sci* 164: 209–217.
- Bucher, M. (2007). Functional biology of plant phosphate uptake at root and mycorrhiza interfaces. *New Phytol.* 173, 11–26. Chen *et al.*, 2007.
- Bünemann EK (2008). Enzyme additions as a tool to assess the potential bioavailability of organically bound nutrients. *Soil Biol Biochem* 40: 2116–2129.
- Burkitt LL, Donaghy DJ, Smethurst PJ (2010). Low rates of phosphorus fertiliser applied strategically throughout the growing season under rain-fed conditions did not affect dry matter production of perennial ryegrass (*Lolium perenne* L.). *Crop Pasture Sci* 61: 353–362.
- Cakmak I (2002). Plant nutrition research: priorities to meet human needs for food in sustainable ways. *Plant Soil* 247: 3–24.
- Chambers BJ, Garwood TWD and Unwin RJ. (2000). Controlling soil water erosion and phosphorus losses from arable land in England and Wales. *Journal of Environmental Quality* 29: 145-150.
- Chen J, Xu L, Cai Y, Xu J. 2008. QTL mapping of phosphorus efficiency and relative biologic characteristics in maize (*Zea mays* L.) at two sites. *Plant Soil* 313: 251–266.
- Chiou, T.J., Liu, H. and Harrison, M.J. (2001). The spatial expression patterns of a phosphate transporter (MtPT1) from *Medicago truncatula* indicate a role in phosphate transport at the root/soil interface. *Plant J.* 25, 281–293.
- Chun-Jian L, Xin P, Fu-Suo Z. 2003. Comparison of response of phosphorus-efficient wheat varieties to phosphorus-deficient stress. *Acta Botanica Sinica.* 45: 936.
- Clark RB 1990. In *Crops as enhancers of nutrient use*. Eds. VC Baligar and R R Duncan. pp. 131-209. Academic Press, Inc., San Diego, CA.
- Cordell D, Drangert J-O, White S. 2009. The story of phosphorus: global food security and food for thought. *Global Environmental Change* 19: 292–305.
- Corell, H. (2002). Letter dated 29 January 2002 from the Under-Secretary-General for Legal Affairs, the Legal Counsel, addressed to the President of the Security Council. United National Security Council, Under-Secretary- General for Legal Affairs The Legal Counsel.
- Dan Zhang D, Cheng H, Geng L, Kan G, Cui S, Meng Q, Gai J. Yu D. 2009. Detection of quantitative trait loci for phosphorus deficiency tolerance at soybean seedling stage.
- Daram P, Brunner S, Persson BL, Amrhein N, Bucher M (1998). Functional analysis and cell-specific expression of a phosphate transporter from tomato. *Planta* 206: 225–233.

- Duan GL, Zhou Y, Tong YP, Mukhopadhyay R, Rosen BP, Zhu YG (2007). A CDC25 homologue from rice functions as an arsenate reductase. *New Phytol* 174: 311–321.
- Duncan RR, Carrow RN. 1999. Turfgrass molecular genetic improvements for abiotic/edaphic stress resistance. *Advances in Agronomy* 67, 233–305.
- Epstein, E. (1972). *Mineral Nutrition of Plants: Principles and Perspectives*. John Wiley and Sons, New York.
- Fageria NK and Baligar VC. 2008. Phosphorus-use efficiency in wheat genotypes. *Journal of Plant Nutrition* 22: 331-340.
- Fageria NK, de Moraes OP, dos Santos AB and Vasconcelos MJ. 2014. Phosphorus use efficiency in upland rice genotypes under field conditions. *Journal of Plant Nutrition*, 37: 633–642.
- Fallik, E., Sarig, S., Okon, Y., 1994. Morphology and physiology of plant roots associated with *Azospirillum*. In: Okon, Y. (Ed.), *Azospirillum/plant associations*. CRC Press, Boca Raton, pp. 77-86.
- Faye I, Diouf O, Guisse A, Se'ne M, and Diallo N. 2006. Characterizing Root Responses to Low Phosphorus in Pearl Millet [*Pennisetum glaucum* (L.) R. Br.]. *Agron. J.* 98: 1187–1194.
- Fohse, D., N. Claassen and A. Jung (1998). Phosphorus efficiency of plants. I. External and internal P requirements and P uptake efficiency of different plant species. *Plant Soil*, 110: 101-109.
- Furihata T, Suzuki M, Sakurai H (1992). Kinetic characterization of two phosphate uptake systems with different affinities in suspension-cultured *Catharanthus roseus* protoplast. *Plant Cell Physiol* 33: 1151–1157.
- Furlani AMC, Furlani PR, Tanaka RT, Mascarenhas HAA, Delgado MDP. 2002. Variability of soybean germplasm in relation to phosphorus uptake and use efficiency. *Scientia Agricola* 59: 529-536.
- Gabasawa AI, Yusuf AA. 2013. Genotypic variations in phosphorus use efficiency and yield of some groundnut cultivars grown on an Alfisol at Samaru, Nigeria. *Journal of Soil Science and Environmental Management* 4(3): 54-61.
- Gburek W J, Sharpley A N, Heathwaite A L, and Folmar G J. 2000. Phosphorus management at the watershed scale: a modification of the phosphorus index. *J. Environ. Qual.* 29, 130–144.
- George TS, Gregory PJ, Simpson RJ, Richardson AE (2007). Differential interactions of *Aspergillus niger* and *Peniophora lycii* phytases with soil particles affects the hydrolysis of inositol phosphates. *Soil Biol. Biochem* 39: 793-803.
- Gerloff, G.C. and W.H. Gabelman. 1983. Genetic basis of inorganic plant nutrition. Vol. 15B. pp. 453-476. In: A. Lauchli and R.L. Bielecki (eds.), *Encyclopedia of Plant Physiology*, New Series. Springer-Verlag, New York, NY.
- Gill H.S., Singh A, Sethia S.K, Behl R.K. 2004. Phosphorus uptake and use efficiency in different varieties of bread wheat (*Triticum aestivum* L). *Archives of Agronomy and Soil Science* 50: 563-572.

- Glassop, D., Smith, S.E. and Smith, F.W. (2005). Cereal phosphate transporters associated with the mycorrhizal pathway of phosphate uptake into roots. *Planta*, 222, 688–698.
- Goldstein, A.H. 1991. Plant cells selected for resistance to phosphate starvation show enhanced P use efficiency. *Theoretical and Applied Genetics* 82: 191-194.
- Grant RS, Matthews MA (1996). The influence of phosphorus availability and rootstock on root system characteristics, phosphorus uptake, phosphorus partitioning and growth efficiency. *Am. J. Enol. Vitic.* 47: 403-409.
- Guo B, Jin Y, Wussler C, Blancaflor EB, Motes CM, Versaw WK. 2008. Functional analysis of the Arabidopsis PHT4 family of intracellular phosphate transporters. *New Phytologist* 177, 889–898.
- Hammond JP, Broadley MR, White PJ, King GJ, Bowen HC, Hayden R, Meacham MC, Mead A, Overs T, Spracklen WP and Greenwood DJ. 2009. Shoot yield drives phosphorus use efficiency in *Brassica oleracea* and correlates with root architecture traits. *Journal of Experimental Botany* 60: 1953-1968.
- Hammond, J. P., Bennett, M. J., Bowen, H. C., Broadley, M. R., Eastwood, D. C., May, S. T., Rahn, C., Swarup, R., Woolaway, K. E., and White, P. J. (2003). Changes in gene expression in Arabidopsis shoots during phosphate starvation and the potential for developing smart plants. *Plant Physiol.* 132, 578–596.
- Hash C T, Schaffert R E and Peacock J M 2002. Prospects for using conventional techniques and molecular biological tools to enhance performance of ‘orphan’ crop plants on soils low in available phosphorus. *Plant Soil* 245, 135–146.
- Hinsinger, P. 2001. Bioavailability of soil inorganic P in the rhizosphere as affected by root-induced chemical changes: A review. *Plant Soil* 237, 173-195.
- Hodge, A., Berta, G., Doussan, C., Merchan, F., Crespi, M., 2009. Plant root growth, architecture and function. *Plant Soil* 321, 153-187.
- Isral, D. W., 1987. Investigations of the role of the phosphorus in symbiotic nitrogen fixation. *Plant Physiol.*, 84 : 835-840.
- Jacobsen, I., Leggett, M.E., Richardson, A.E., 2005. Rhizosphere microorganisms and plant phosphorus uptake. In: Sims, J.T. and Sharpley, A.N. (Eds.), *Phosphorus, agriculture and the environment*. Soil Sci. Soc. America, Madison, pp. 437-494.
- Jasinski, S.M., 2006. Phosphate Rock, Statistics and Information. US Geological Survey.
- Javot, H., Penmetsa, R.V., Terzaghi, N., Cook, D.R. and Harrison, M.J. (2007a). A *Medicago truncatula* phosphate transporter indispensable for the arbuscular mycorrhizal symbiosis. *Proc. Natl Acad. Sci. USA*, 104, 1720–1725.
- Johnson JF, Allan DL, Vance CP, Weiblen G. 1996a. Root carbon dioxide fixation by phosphorus-deficient *Lupinus albus*, Contribution to organic acid exudation by proteoid roots. *Plant Physiology* 112: 19–30.
- Jones, G. P. D., Blair, G. J., and Jessop, R. S. (1989). Phosphorus efficiency in wheat: A useful selection criterion? *Field Crop Res.* 21, 257–264.

- Jungk A, Seeling B and Gerke J 1993. Mobilization of different phosphate fractions in the rhizosphere. *Plant Soil* 155/156: 91–94.
- Kaeppler SM, Parke JL, Mueller SM, Senior L, Stuber C and Tracy WF 2000. Variation among maize inbred lines and detection of quantitative trait loci for growth at low P and responsiveness to arbuscular mycorrhizal fungi. *Crop Sci.* 40, 358–364.
- Kakar, K. M., Tariq, M., Taj, F. H., and Nawab, K. (2002). Phosphorus use efficiency of soybean as affected by phosphorus application and inoculation. *Pak. J. Agron.* 1, 49–50.
- Karthikeyan, A.S., Varadarajan, D.K., Mukatira, U.T., D’Urzo, M.P., Damsz, B. and Raghothama, K.G. (2002). Regulated expression of Arabidopsis phosphate transporters. *Plant Physiol.* 130, 221–233.
- Kuang R, Liao H, Yan X, Dong Y. 2005. Phosphorus and nitrogen interactions in field-grown soybean as related to genetic attributes of root morphological and nodular traits. *Journal of Integrative Plant Biology* 47: 549-559.
- LLtaief B, Sifi B, Zaman-Allah M, Horres R, Molina C, Beebe S, Winter P, Kahl G, Drevon J. and Lachaâl M. 2012. Genotypic variability for tolerance to salinity and phosphorus deficiency among N<sub>2</sub>-dependent recombinant inbred lines of Common Bean (*Phaseolus vulgaris*). *African Journal of Microbiology Research* 6(20): 4205-4213.
- Leggewie, G., Willmitzer, L. and Riesmeier, J.W. (1997). Two cDNAs from potato are able to complement a phosphate uptake-deficient yeast mutant: identification of phosphate transporters from higher plants. *Plant Cell*, 9, 381–392.
- Lewis DC, Clarke AL, Hall WB (1987). Accumulation of plant nutrients and changes in soil properties of sandy soils under fertilised pastures in south-eastern South Australia. I. Phosphorus. *Aust J Soil Res* 25: 193–202.
- Li L, Liu C, Lian X. 2010. Gene expression profiles in rice roots under low phosphorus stress. *Plant Mol Biol* 72: 423–432.
- Li, K., Xu, Z., Zhang, K., Yang, A. and Zhang, J. (2007b). Efficient production and characterization for maize inbred lines with low phosphorus tolerance. *Plant Sci.* 172, 255–264.
- Li, L., Liu, C., Lian, X. 2010. Gene expression profiles in rice roots under low phosphorus stress. *Plant Mol. Biol.* 72, 423-432.
- Liao H, Ge Z, Yan X. 2001a. Ideal root architecture for phosphorus acquisition of plants under water and phosphorus coupled stresses: from simulation to application. *Chinese Science Bulletin* 46: 1346–1351.
- Liu L, Liao H, Wang X, Yan X. 2008. Regulation effect of soil P availability on mycorrhizal infection in relation to root architecture and P efficiency of Glycine max. *Chinese Journal of Applied Ecology* 19: 564–568.
- Liu, C.M., Muchhal, U.S., Uthappa, M., Kononowicz, A.K. and Raghothama, K.G. (1998a). Tomato phosphate transporter genes are differentially regulated in plant tissues by phosphorus. *Plant Physiol.* 116, 91–99.

- Liu, H., Trieu, A.T., Blaylock, L.A. and Harrison, M.J. (1998b). Cloning and characterization of two phosphate transporters from *Medicago truncatula* roots: regulation in response to phosphate and to colonization by arbuscular mycorrhizal (AM) fungi. *Mol. Plant Microbe Interact.* 11, 14–22.
- Lynch J (1995). Root architecture and plant productivity. *Plant Physiol* 109: 7–13.
- Lynch J. 2007. Roots of the second green revolution. *Australian Journal of Botany* 55, 493–512.
- Ma Z, Walk TC, Marcus A, Lynch JP (2001). Morphological synergism in root hair length, density, initiation and geometry for phosphorus acquisition in *Arabidopsis thaliana*: A modeling approach. *Plant Soil* 236: 221–235.
- Maeda, D., Ashida, K., Iguchi, K., Chechetka, S.A., Hijikata, A., Okusako, Y., Deguchi, Y., Izui, K. and Hata, S. (2006). Knockdown of an arbuscular mycorrhiza-inducible phosphate transporter gene of *Lotus japonicus* suppresses mutualistic symbiosis. *Plant Cell Physiol.* 47, 807–817.
- Marschner, H. (1995). *Mineral Nutrition of Higher Plants*. London: Academic Press.
- McCaskill MR, Cayley JWD (2000). Soil audit of a long-term phosphate experiment in South-Western Victoria: total phosphorus, sulfur, nitrogen and major cations. *Aust J Agr Res* 51: 737–748.
- McLachlan KD 1976. Comparative phosphorus responses in plants to a range of available phosphorus situations. *Aust. J. Agric. Res.* 27: 323-341.
- McPharlin J, Bielecki R (1987). Phosphate uptake by *Spirodela* and *Lemna* during early phosphate deficiency. *Aust J Plant Physiol* 14: 561–572.
- Melland AR, McCaskill MR, White RE, Chapman DF (2008). Loss of phosphorus and nitrogen in runoff and subsurface drainage from high and low input pastures grazed by sheep in Australia. *Aust J Soil Res* 46: 161–172.
- Mitsukawa N, Okamura S, Shirano Y, Sato S, Kato T, Harashima S, Shibata D (1997). Overexpression of an *Arabidopsis thaliana* high-affinity phosphate transporter gene in tobacco cultured cells enhances cell growth under phosphate-limited conditions. *Proc Natl Acad Sci USA* 94: 7098–7102.
- Moll RH, Kamprath EJ, Jackson WA (1982). Analysis and interpretation of factors which contribute to efficiency of nitrogen utilization. *Agron. J.* 74: 562-564.
- Mourice SK and Tryphone GM. 2009. Evaluation of Common Bean (*Phaseolus vulgaris* L.) Genotypes for Adaptation to Low Phosphorus. *ISRN Agronomy* 2012 doi: 10.5402/2012/309614.
- Muchhal US, Pardo JM, Raghothama KG (1996). Phosphate transporters from the higher plant *Arabidopsis thaliana*. *Proc Natl Acad Sci USA* 93: 10519–10523.
- Muchhal US, Raghothama KG (1999). Transcriptional regulation of plant phosphate transporters. *Proc Natl Acad Sci USA* 96: 5868–5872.
- Mudge, S.R., Rae, A.L., Diatloff, E. and Smith, F.W. (2002). Expression analysis suggests novel roles for members of the Pht1 family of phosphate transporters in *Arabidopsis*. *Plant J.* 31, 341–353.

- Nadeem M, Mollier A, Morel C, Vives A, Prud'homme L, Pellerin S (2011a). Relative contribution of seed phosphorus reserves and exogenous phosphorus uptake to maize (*Zea mays* L.) nutrition during early growth stages. *Plant Soil* 346: 231–244.
- Nagy, R., Karandashov, V., Chague, W., Kalinkevich, K., Tamasloukht, M., Xu, G.H., Jakobsen, I., Levy, A.A., Amrhein, N. and Bucher, M. (2005). The characterization of novel mycorrhiza-specific phosphate transporters from *Lycopersicon esculentum* and *Solanum tuberosum* uncovers functional redundancy in symbiotic phosphate transport in solanaceous species. *Plant J.* 42, 236–250.
- Narang RA, Bruene A, Altmann T. 2000. Analysis of Phosphate Acquisition Efficiency in Different Arabidopsis Accessions. *Plant Physiology* 124: 1786-1799.
- Neumann, G.; Romheld, V. 1999. Root excretion of carboxylic acids and protons in phosphorus-deficient plants. *Plant Soil*, 211, 121-130.
- Oberson A, Friensen D K, Tiessen H, Morel C and Stahel W 1999. Phosphorous status and cycling in native savanna and improved pastures on an acid low-P. *Colombian Oxisol*. 77–88.
- Oehl, F.; Sieverding, E.; Mader, P.; Dubois, D.; Ineichen, K.; Boller, T.; Wiemken, A. 2004. Impact of long-term conventional and organic farming on the diversity of arbuscular mycorrhizal fungi. *Oecologia*, 138, 574-583.
- Osborne LD. and Rengel Z. 2002a. Genotypic differences in wheat for uptake and utilisation of P from iron phosphate. *Australian Journal of Agricultural Research* 53 (7) 837 – 844.
- Osborne LD. and Rengel Z. 2002b. Screening cereals for genotypic variation in efficiency of phosphorus uptake and utilization. *Australian Journal of Agricultural Res* 53 (3) 295 - 303.
- Ozanne PG, Kirton DJ, Shaw TC (1961). The loss of phosphorus from sandy soils. *Aust J Agr Res* 11: 927–924.
- Pan XW, Li WB, Zhang QY, Li YH, Liu MS. Assessment on Phosphorus Efficiency Characteristics of Soybean Genotypes in Phosphorus-Deficient Soils. *Agricultural Sciences in China* 7(8): 958-969.
- Pang J, Tibbett M, Denton MD, Lambers H, Siddique KHM, Bolland MDA, Revell CK. (2010). Variation in seedling growth of 11 perennial legumes in response to phosphorus supply. *Plant Soil* 328: 133–143.
- Parentoni, S.N., C.L. Souza Junior, V.M.C. Alves, E.E.G. Gama, A.M. Coelho, A.C. de Oliveira, C.T. Guimaraes, M.J.V. Vasconcelos, C.A.P. Pacheco, W.F. Meirelles, J.V. Magalhaes, L.J.M. Guimarães, A.R. da Silva, F.F. Mendes, and R.E. Schaffert. 2010. Inheritance and breeding strategies for phosphorus efficiency in tropical maize (*Zea mays* L.). *Maydica* 55: 1–15.
- Parentoni, S.N., C.L. Souza Junior. 2008. Phosphorus acquisition and internal utilization efficiency in tropical maize genotypes. *Pesq. agropec. bras., Brasília*, 43: 893-901.

- Park MR, Baek SH, de los Reyes BG, Yun SJ. 2007. Overexpression of a high-affinity phosphate transporter gene from tobacco (NtPT1) enhances phosphate uptake and accumulation in transgenic rice plants. *Plant Soil* 292: 259–269.
- Paszkowski, U., Kroken, S., Roux, C. and Briggs, S.P. (2002). Rice phosphate transporters include an evolutionarily divergent gene specifically activated in arbuscular mycorrhizal symbiosis. *Proc. Natl Acad. Sci. USA*, 99, 13324–13329.
- Pathak H. 2010. Trend of fertility status of Indian soils. *Current Advances in Agricultural Sciences* 2(1): 10-12.
- Rae, A.L., Cybinski, D.H., Jarmey, J.M. and Smith, F.W. (2003). Characterization of two phosphate transporters from barley; evidence for diverse function and kinetic properties among members of the Pht1 family. *Plant Mol. Biol.* 53, 27–36.
- Raghothama KG (1999). Phosphate acquisition. *Ann Rev Plant Physiol Plant Mol Biol* 50: 665–693.
- Raghothama KG, Karthikeyan AS (2005). Phosphate acquisition. *Plant Soil* 274: 37–49.
- Randall, PJ. 1995. Genotypic differences in phosphorus uptake. In: C. Johansen, K.K. Lee, K.K. Sharma, G.V. Subbarao, E.A. Kueneman eds. *Genetic Manipulation of crop Plants to Enhance Integrated Nutrient Management in Cropping Systems - 1. Phosphorus*. Patancheru, India: ICRISAT, pp. 31-47.
- Reiter, R. S., Coors, J. G., Sussman, M. R. *et al.*, 1991. Genetics analysis of tolerance to low-phosphorus stress in maize using RFLP, *Theor. Appl. Genet.*, 82: 561.
- Rengel Z, Marschner P (2005). Nutrient availability and management in the rhizosphere: Exploiting genotypic differences. *New Phytol* 168: 305–312.
- Rengel Z. 1999. Physiological mechanisms underlying differential nutrient efficiency of crop genotypes. In: Rengel Z, ed, *Mineral Nutrition of Crops: Fundamental Mechanisms and Implications*. Haworth Press, New York. pp. 227-265.
- Richardson AE 1994. Soil microorganisms and phosphorus availability. *Soil Biota*, 50–62.
- Richardson AE, Barea JM, McNeill AN, Combaret CP (2009). Acquisition of phosphorus and nitrogen in the rhizosphere and plant growth promotion by microorganisms. *Plant Soil* 321: 305–339.
- Richardson AE, Hadobas PA, Hayes JE (2001). Extracellular secretion of *Aspergillus* phytase from *Arabidopsis* roots enables plants to obtain phosphorus from phytate. *Plant J* 25: 641–649.
- Ridley AM, Christy BP, White RE, McLean T, Green R (2003). North-east Victoria SGS National Experiment site: water and nutrient losses from grazing systems on contrasting soil types and levels of inputs. *Aust J Exp Agr* 43: 799–815.
- Rose TJ and Matthews W. 2012. Chapter five – Rethinking Internal Phosphorus Utilization Efficiency: A New Approach Is Needed to Improve PUE in Grain Crops. *Advances in Agronomy* 116: 185-217.

- Rosmarin, A. (2004). The Precarious Geopolitics of Phosphorous Down to Earth (Science and Environment Fortnightly), (June 30, 2004): p. 27-31.
- Ryan, P.R.; Delhaize, E.; Jones, D.L. 2001. Function and mechanism of organic anion exudation from plant roots. *Annu. Rev. Plant Physiol. Plant Mol. Biol.*, 52, 527-560.
- Saier, M.H. (2000). Families of transmembrane transporters selective for amino acids and their derivatives. *Microbiol. Sgm*, 146, 1775– 1795.
- Schachtman DP, Reid RJ, Ayling SM (1998). Phosphorus uptake by plants: from soil to cell. *Plant Physiol* 116: 447–453.
- Sepehr, E., Malakouti, M. J., Kholdebarin, B., Samadi, A., and Karimian, N. (2009). Genotypic variation in P efficiency of selected Iranian cereals in greenhouse experiment. *Int. J. Plant Prod.*, 3: 17–28.
- Shen H, Chen J, Wang Z, Yang C, Sasaki T, Yamamoto Y, Matsumoto H, Yan X (2006). Root plasma membrane H<sup>+</sup>-ATPase is involved in the adaptation of soybean to phosphorus starvation. *J Expt Bot* 57: 1353–1362.
- Shenoy, V.V.; Kalagudi, G.M. 2005. Enhancing plant phosphorus use efficiency for sustainable cropping. *Biotechnol. Adv.* 23, 501-513.
- Shimizu A, Kato K, Komatsu A, Motomura K, Ikehashi H. 2008. Genetic analysis of root elongation induced by phosphorus deficiency in rice (*Oryza sativa* L.): Fine QTL mapping and multivariate analysis of related traits. *Theor Appl Genet* 117: 987–996.
- Shimizu A, Yanagihara S, Kawasaki S, Ikehashi H (2004). Phosphorus deficiency-induced root elongation and its QTL in rice (*Oryza sativa* L.). *Theor Appl Genet* 109: 1361–1368.
- Shridevi AJ, Kajjidoni ST, Koti RV. 2009. Genotypic variation for root traits to phosphorus deficiency in blackgram (*Vigna mungo* L. Hepper). *Karnataka J. Agric. Sci.*, 22(5): 946-950.
- Siddiqui, M.Y. and A.D.M. Glass, 1981. Utilization index: A modified approach to the estimation and comparison of nutrient utilization efficiency in plants. *J. Plant Nutr.*, 4: 289–302.
- Singh A.L. 1999. Mineral Nutrition of Groundnut. In: *Advances in Plant Physiology* (Ed. A. Hemantranjan), Vol II pp. 161-200. Scientific Publishers (India), Jodhpur, India.
- Singh, A.L. 2000. Mechanism of Tolerance and Crop Production in acid Soils. In: *Advances in Plant Physiology* Vol. III Plant Physiology, Biochemistry and Plant Molecular Biology in 2000 (Ed. A. Hemantranjan), pp. 353-394. Scientific Publishers (India), Jodhpur, India.
- Singh, A.L. 2004. Mineral nutrient requirement, their disorders and remedies in Groundnut. pp. 137-159. In: *Groundnut Research in India* (Eds. M.S. Basu and N. B. Singh) National Research Center for Groundnut (ICAR), Junagadh, India.



- Singh, A.L. 2006. Macronutrient stresses and their management in crop plants. In: *Advances in Plant Physiology* (Ed. P.C. Trivedi), pp.198-234. I.K. International Publishing House Pvt. Ltd. New Delhi, India.
- Singh, A.L. 2008. Mineral Stresses and Crop Productivity. In *International Symposium on Natural Resource management in Agriculture*. Dec 19-20 2008, Agricultural Research Station, RAU, Durgapura, Jaipur. pp. 9-23. Invited Lead paper.
- Singh, A.L. 2014. Role of nutrient efficient crop genotypes in modern agriculture. In: Proc National Conference of Plant Physiology (NCP 2014) on “Frontiers of Plant Physiology Research: Food Security and Environmental Challenges” 23-25 Nov 2014, Odisha University of Agriculture and Technology, Bhubaneswar, India pp. 135-142.
- Singh A.L. and M.S. Basu 2005a. Integrated Nutrient Management in Groundnut: A Farmer’s Manual. National Research center for groundnut, Junagadh, India. 54 p.
- Singh, A. L., and M. S. Basu. 2005b. Screening and selection of P efficient genotypes for calcareous soils in India. In: Plant nutrition for food security, human health and environmental protection (Eds C.J. Li *et al.*), pp. 1004-1005 (Plant and Soil Series). Proceedings 15th International Plant Nutrition Colloquium, China Agricultural University, Beijing, China 14-19 Sept. 2005. Tsinghua Univ. Press Beijing, China.
- Singh, A. L., Basu, M. S. and Singh, N. B. (2004). Mineral Disorders of Groundnut. National Research Center for Groundnut (ICAR), Junagadh, India p. 85.
- Singh A.L. and V. Chaudhari 1996. Use of zincated and boronated super phosphate and mycorrhizae in groundnut in calcareous soil. *J. Oilseed Research*, 13: 61-65.
- Singh, A.L. and V. Chaudhari 1996. Interaction of sulphur with phosphorus and potassium in groundnut nutrition in calcareous soil. *Indian Journal of Plant Physiology* (New Series), 1: 21-27.
- Singh, A.L. and V. Chaudhari 2006. Macronutrient requirement of groundnut: Effects on the growth and yield components. *Indian J. Plant Physiology*, 11: 401-409.
- Singh, A.L. and V. Chaudhari 2007. Macronutrient requirement of groundnut: Effects on uptake of macronutrients. *Indian J. Plant Physiology*, 12: 72-77.
- Singh, A.L. and Anita Mann 2012. Recent Advances in Plant Nutrition. In: Proc National Seminar of Plant Physiology on “Physiological and molecular approaches for development of climatic resilient crops” 12-14 Dec. 2012, ANGRAU, Hyderabad, India pp. 6-22.
- Singh, A.L. and P.K. Singh 1990. Phosphorus fertilization and the growth and N<sub>2</sub>-fixation of Azolla and blue-green algae in rice field. *Indian J. Plant Physiol.* 33: 21-26.
- Singh, A.L., P.K. Singh and Pushp Lata 1988. Effect of split application of phosphorus fertilizer on the growth of Azolla and low land rice. *Nutrient Cycling in Agroecosystems (Fertilizer Research)*, 16: 109-117.

- Singh, A.L., Vidya Chaudhari and V.G. Koradia 1991. Foliar nutrition of Nitrogen and Phosphorous in groundnut. In: *Physiological Strategies For Crop Improvement: Proceeding of the International Conference of Plant Physiology* (Eds. D.N. Tyagi, B. Bose, A. Hemantranjan and T. Meghabati Devi), pp. 129-133. B.H.U., Varanasi, India.
- Singh BB (1999). Improved drought tolerant cowpea varieties for the Sahel. Project II. Cowpea cereal system improvement for the savannas, p. 36. International Institute of Tropical Agriculture, Ibadan, Nigeria. Annual Report.
- Smith, F.W., Ealing, P.M., Dong, B. and Delhaize, E. (1997). The cloning of two Arabidopsis genes belonging to a phosphate transporter family. *Plant J.* 11, 83–92.
- Smith, FW. 2001. S and P transport systems in plants. *Plant Soil* 232: 109–118.
- Su, J. Y., Xiao, Y., Li, M., Liu, Q., Li, B., Tong, Y., Jia, J., and Li, Z. (2006). Mapping QTLs for phosphorus-deficiency tolerance at wheat seedling stage. *Plant Soil* 281, 25–36.
- Teng W, Deng Y, Chen XP, Xu XF, Chen RY, Lv Y, Zhao YY, Zhao XQ, He X, Li B, Tong YP, Zhang FS, Li ZS. 2013. Characterization of root response to phosphorus supply from morphology to gene analysis in field-grown wheat. *Journal of Experimental Botany* 64: 1403-1411.
- Trotter MG, Lamb DW, Donald GE, Schneider DA (2010). Evaluating an active optical sensor for quantifying and mapping green herbage mass and growth in a perennial grass pasture. *Crop Pasture Sci* 61: 389–398.
- Ullrich-Eberius CI, Novacky A, van Bel A (1984). Phosphate uptake in Lemna gibba G1: energetics and kinetics. *Planta* 161: 46–52.
- Uusi-Kamppa J, Braskerud B, Jansson H, Syversen N, Uusitalo R. 2000. Buffer zones and constructed wetlands as fillers for agricultural phosphorus. *Journal of Environmental Quality* 29: 151-158.
- Valverde F, Losada M, Serrano A. 1999. Engineering a central metabolic pathway: glycolysis with no net phosphorylation in an *Escherichia coli* gap mutant complemented with a plant Gap N gene. *FEBS Lett* 449: 153–8.
- van der Eijk, D., Janssen, B.H. and Oenema, O. 2006. Initial and residual effects of fertilizer phosphorus on soil phosphorus and maize yields on phosphorus fixing soils. A case study in south-west Kenya. *Agr. Ecosyst. Environ.*, 116(1–2): 104–120.
- Vance CP, Uhde-Stone C, Allan DL (2003). Phosphorus acquisition and use: critical adaptation by plants for securing a non-renewable resource. *New Phytol* 157: 423–447.
- Vance, C. P 2001. Symbiotic nitrogen fixation and phosphorus acquisition. Plant nutrition in a world of declining renewable resources. *Plant Physiol* 127: 390-397.

- Wang LH, Duan GL, Williams PN, Zhu YG. 2008. Influences of phosphorus starvation on OsACR2.1 expression and arsenic metabolism in rice seedlings. *Plant Soil* 313: 129–139.
- Wang S, Basten CJ, Zeng Z-B. 2004. Windows QTL Cartographer 2.0. Department of Statistics, North Carolina State University. Raleigh, NC, USA.
- Wang X, Wang Y, Tian J, Lim B, Yan X, Liao H. 2009. Over expressing AtPAP15 enhances phosphorus efficiency in soybean. *Plant Physiol* 151: 233–240.
- White PJ, Broadley MR, Greenwood DJ, Hammond JP. 2005. Genetic modifications to improve phosphorus acquisition by roots. Proceedings 568. York, UK: International Fertiliser Society.
- White, P. J., and Hammond, J. P. (2008). Phosphorus nutrition of terrestrial plants. In *“The Ecophysiology of Plant–Phosphorus Interactions”* (P. J. White and J. P. Hammond, Eds.), pp. 51–81. Springer, The Netherlands.
- Wissuwa M (2005). Combining a modelling with a genetic approach in establishing associations between genetic and physiological effects in relation to phosphorus uptake. *Plant Soil* 269: 57–68.
- Wissuwa M, Ae N. 2001. Further characterization of two QTLs that increase phosphorus uptake of rice (*Oryza sativa* L.) under phosphorus deficiency. *Plant and Soil* 237: 275–286.
- Wissuwa M, Wegner J, Ae N, Yano M (2002). Substitution mapping of Pup1: a major QTL increasing phosphorus uptake of rice from a phosphorus-deficient soil. *Theor Appl Genet* 105: 890–897.
- Wissuwa, M., Gamat, G., and Ismail, A. (2005). Is root growth under phosphorus deficiency affected by source or sink limitations? *J. Exp. Bot.* 56, 1943–1950.
- Xu, G.H., Chague, V., Melamed-Bessudo, C., Kapulnik, Y., Jain, A., Raghothama, K.G., Levy, A.A. and Silber, A. (2007). Functional characterization of LePT4: a phosphate transporter in tomato with mycorrhiza-enhanced expression. *J. Exp. Bot.* 58, 2491– 2501.
- Yan X, Beebe S E and Lynch J P 1995a. Genetic variation for P efficiency of common bean in contrasting soil types: II. Yield response. *Crop Sci.* 35, 1094–1099.
- Yan X, Liao H, Beebe SE, Blair MW, Lynch JP (2004). QTL mapping of root hair and acid exudation traits and their relationship to phosphorus uptake in common bean. *Plant Soil* 265: 17–29.
- Yan X, Lynch J P and Beebe S E 1995b. Genetic variation for P efficiency of common bean in contrasting soil types: I. Vegetative response. *Crop Sci.* 35, 1086–1093.
- Yan, F., Zhu, Y.Y., Muller, C., Zorb, C., Schubert, S. 2002. Adaptation of H<sup>+</sup>-pumping and plasma membrane H<sup>+</sup> ATPase activity in proteoid roots of white lupin under phosphate deficiency. *Plant Physiol.* 129, 50-63.
- Yang M, Ding G, Shi L, Xu F, Meng J. 2011. Detection of QTL for phosphorus efficiency at vegetative stage in *Brassica napus*. *Plant Soil* (2011) 339: 97–111.

- Yao Y, Sun H, Xu F, Zhang H, Liu S. 2011. Comparative proteome analysis of metabolic changes by low phosphorus stress in two *Brassica napus* genotypes. *Planta* 233: 523–537.
- Yaseen, M., and Malhi, S. S. (2009a). Variation in yield, phosphorus uptake, and physiological efficiency of wheat genotypes at adequate and stress phosphorus levels in soil. *Commun. Soil Sci. Plant Anal.* 40, 3104–3120.
- Yaseen, M., and Malhi, S. S. (2009b). Differential growth response of wheat genotypes to ammonium phosphate and rock phosphate phosphorus sources. *J. Plant Nutr.* 32, 410–432.
- Yoshida S, Forno DA, Cook JH, Gomez KA (1976). Laboratory manual for physiological studies of rice. International Rice Research Institute, Manila, pp 61–67.
- Yun SJ and Keppler SM. 2001. Induction of maize acid phosphatase activities under phosphorus starvation. *Plant and Soil* 237: 109–115,.
- Zai-hua G, Ping D, Li-Yuan H, Cai-Guo X. 2006. Genetic Analysis of Agricultural Traits in Rice Related to Phosphorus Efficiency. *Acta Genetica Sinica*, 33: 634–641.
- Zhao J, Fu J, Liao H, He Y, Nian H, Hu Y, Qiu L, Dong Y, Yan X. 2004. Characterisation of root architecture in an applied core collection for phosphorus efficiency of soybean germplasm. *Chinese Science Bulletin* 49, 1611–1620.
- Zhu JM, Kaeppler SM, Lynch JP (2006) Mapping of QTLs for lateral root branching and length in maize (*Zea mays* L.) under differential phosphorus supply. *Theor Appl Genet* 111((4): 688–695.
- Zhu, J., and Lynch, J. P. (2004). The contribution of lateral rooting to phosphorus acquisition efficiency in maize (*Zea mays*) seedlings. *Funct. Plant Biol.* 31, 949–958.