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# Phosphorus Deficiency in Plants: Responses, Adaptive Mechanisms, and Signaling

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**Abstract**

Phosphorus (P) deficiency is a common nutritional factor limiting agricultural production around the globe. Application of phosphatic fertilizers is generally recommended to cope with P deficiency; however, low use efficiency of available P fertilizers both in calcareous and acid soils limits its viability and also had serious environmental concerns. Higher plants have adapted a number of mechanism to live with low available P in soil such as changes in root morphology and architecture, decreased growth rate, improved P uptake and utilization efficiency, and exudation of organic acids and enzymes to solubilize external inorganic and organic P compounds in the rhizosphere. Plant species and even cultivars widely differ in P efficiency because of differences in one or more of these mechanisms. Exploitation of these genetic variations among crop plants can sustain agricultural production. Understanding the mechanism involved in sensing P deficiency could facilitate selection, breeding, and genetic engineering approaches to improve crop production in P-stressed environments and could reduce dependence on nonrenewable inorganic P resources. In this chapter, we briefly reviewed the responses of P deficiency in higher plants, their adaptive mechanisms, and signaling pathways.

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## 7.1 Introduction

Phosphorus (P) is an essential macronutrient which constitutes about 0.2 % of plant's dry matter (Marschner 1995). Phosphorus is required during the process of energy generation and transfer, carbon metabolism, membrane synthesis, enzyme activation, and nitrogen fixation (Schachtman et al. 1998) and is a constituent of key biomolecules like nucleic acids, phospholipids, and adenosine triphosphate (ATP) (Marschner 1995). Limited P availability in soils is an important nutritional constraint to the growth of plant (Bates and Lynch 2000). Phosphorus is the least mobile nutrient under most soil conditions irrespective of total P contents in the soils (Hinsinger 2001; Schachtman et al. 1998). Soils can be classified into two major groups with respect to total P contents: soils containing inherently low-P contents like acrisols or sandy soils, and other group of the soils includes nitisols, acid andosols, or calcareous/alkaline soils that contain considerable amount of P, but major fraction is fixed with different soil constituents. In both type of soils, P concentration in soil solution is suboptimal and is generally in the range of 1–10 μM (Frossard et al. 2000; Mengel and Kirkby 1987; Ozanne 1980; Schachtman et al. 1998). Suboptimal P levels in soil solution can cause yield depressions up to 5–15 % of maximum crop yields (Shenoy and Kalagudi 2005). Application of P fertilizers is the most common practice to address the problem of low-P availability in agricultural soils (Ramaekers et al. 2010). However, this practice is confronted with daunting challenges of immobilization/precipitation of applied P with soil constituents, depletion of nonrenewable P sources, and high cost of P fertilizers (Vance et al. 2003). Available P in most of soils may constitute < 0.1 % of total soil P (Khan et al. 2009). In P-deficient soils, the use efficiency of applied P is very low and >80 % of applied P may be fixed on soil constituents or precipitation with Ca, Fe, and Al compounds and thus becomes unavailable to the plants (Gill et al. 1994; Trolove et al. 2003; Vance et al. 2003) or converted to organic forms (Holford 1997) and about 20 % or less of P applied is removed by the crop in the first year after its application. According to the US geological survey, globally, 22 million tonnes P extracts from natural sources annually (Gaxiola et al. 2011). Globally, P consumption is increasing about 3 % annually and natural reserves may be depleted in the near future (Cordell et al. 2009; Jasinski 2008).

Globally, the demand for P is increasing by 3–4 % (Maene 2007) and major demand is coming from Asian countries (Cordell et al. 2009). Modern agriculture is fully dependent on application of P fertilizers which are manufactured by using nonrenewable phosphate rock. The known reserves of phosphate rock are sufficient only of approximately 50–100 years (Smil 2000; Steen 1998). Strategies and management practices should be adopted to increase P use efficiency for sustaining agricultural production. This can be accomplished by breeding crops which are efficient in P acquisition or P use (Gill et al. 2004; Gill and Ahmad 2003), as presence of variability among different crop cultivars has been reported for P efficiency (El Bassam 1998; Kosar et al. 2002; Osborne and Rengel 2002; Ozturk et al. 2005; Singh Gahoonia and Nielsen 2004). An adaptation of cultivars which are efficient users of nutrients is an easy approach due to no additional costs and no major changes in cropping systems. Categorization of crop cultivars on the basis of growth and P uptake will be helpful in the identification of varieties which can be cultivated in different soils and selection of parents for recombination breeding to develop P-efficient cultivars (Gill et al. 2004). Efficiency of applied P fertilizers can be increased by growing crop species/varieties efficient in P absorption and utilization and thus reduce the environmental degradation as well as input cost.

## 7.2 Adaptations of Plants to P-Deficient Environment

Plants have a wide range of adaptive mechanisms under P-deficient conditions to absorb sufficient P to maintain metabolic activities and growth (Lambers et al. 2010; Rengel and Marschner 2005). Physiological mechanisms relating to P-deficiency tolerance by crop plants have been reported by many of the earlier scientists (Krasilnikoff et al. 2003; Singh Gahoonia and Nielsen 2004), and some of these adaptations are listed in Table 7.1. Plant adaptations can be grouped into two major categories (Rengel and Marschner 2005; Vance et al. 2003), viz., acquisition efficiency and utilization efficiency. Acquisition efficiency is the capacity to absorb sparingly soluble nutrients like P, while utilization efficiency is the capacity to produce a large amount of biomass per unit of nutrient absorbed. Strategies which aim at reducing P use include decreased growth rate, enhanced growth per unit of P absorbed, remobilization of internal P, modifications in metabolism of carbon and alternative respiratory pathways (Uhde-Stone et al. 2003), and modifications in the biosynthesis of membrane requiring less P (Lambers et al. 2006; Plaxton and Carswell 1999; Uhde-Stone et al. 2003; Wasaki et al. 2003).

Exudation of phosphatases, release of organic acids from roots (Dakora and Phillips 2002; Gahoonia et al. 2000; Johnson and Loeppert 2006; Singh Gahoonia and Nielsen 2004; Vance et al. 2003), enhanced root growth with altered root architecture (Bucher 2006; Raghothama and Karthikeyan 2005; Singh Gahoonia and Nielsen 2004), root hair development, and enhanced expression of $P_i$ transporters (Gilroy and Jones 2000) are responsible for enhanced P uptake.

Different plant species and genotypes within species differ in adaptive mechanisms for efficient P use. Intraspecific variations for P acquisition and utilization in several species are well documented (Aziz et al. 2006, 2011a; Gill et al. 2004; Lambers et al. 2010, 2011; Singh Gahoonia and Nielsen 2004). These variations may be attributed due to differences in relation to external critical levels of P; internal critical requirements; P uptake, transport, and utilization efficiencies; exudation pattern; root morphology; and expression of $P_i$ transporter genes (Aziz et al. 2006; Singh Gahoonia and Nielsen 2004). Specific traits/mechanisms responsible for P efficiency in higher plants are briefly reviewed below.

### 7.2.1 Architectural Adaptations

Root architecture, defined as the spatial configuration of plant roots, is important for absorption of relatively less mobile nutrients like P (Lynch 2007; Zhu et al. 2005). Architectural adaptations are related to the change in root branching, root length, and formation of root hairs (López-Bucio et al. 2002; Richardson and Simpson 2011; Trachsel et al. 2011). Plants differ in the mechanisms for absorption of P from deficient environments. Efficient plant genotypes may have adaptations to explore more soil by increasing surface area, transforming plant-unavailable forms of nutrients in available forms, and take up nutrients across the plasma membrane (Rengel 2001). Plant roots perform a range of functions in plants like anchorage and absorption of nutrients and water (Bertin et al. 2003; Lambers et al. 2006, 2010; López-Bucio et al. 2003). Thus, the changes in the root architecture could affect nutrient and water absorption by plants. Root architecture is affected by three major processes, viz., (1) cell division at the primary root meristem which determines growth by adding new cells to the root, (2) lateral root formation which improves exploration of soil by the roots, and (3) development of root hairs, thereby increasing the root surface area (López-Bucio et al. 2003). The rooting pattern of plants is mainly determined by

**Table 7.1** Plant adaptive mechanisms to cope with P deficiency in soil

| Trait | Efficient genotypes | Inefficient genotypes | References |
|---|---|---|---|
| P contents in harvested portion | Low | High | Marshall and Wardlaw (1973) and Richardson and Simpson (2011) |
| Internal critical P concentration | Low | High | Hammond et al. (2009), Lambers et al. (2011), and Ozturk et al. (2005) |
| Number of adventitious roots | More | Less | Bates and Lynch (2001), Gahoonia et al. (1999), Jungk (2001), Liao et al. (2001), Lynch and Brown (2008), Richardson and Simpson (2011), Trachsel et al. (2011), and Walk et al. (2006) |
| Root diameter | Fine | Course | |
| Root volume | High | Low | |
| Rooting density | High | Low | |
| Root architecture and root growth angle | More shallower roots exploring surface soil | Less shallower roots | |
| Root hairs | More and long | Less and short | |
| Root exudates | Higher amounts | Lower amounts | Lambers et al. (2010, 2011), Aziz et al. (2011a), Pearse et al. (2006a), Pang et al. (2010), Richardson and Simpson (2011), Gregorge et al. (2008), Ma et al. (2009) |
| Organic acids/anions | | | |
| Phosphatases | | | |
| Internal P utilization | High | Lower | Lambers et al. (2010), Aziz et al. (2006, 2011a), Hammond et al. (2009), and Ozturk et al. (2005) |
| P remobilization | Yes | No or minimum | Aziz et al. (2011b), Lambers et al. (2010), Akhtar et al. (2008), Nagarajan et al. (2011), Lovelock et al. (2006) |
| Specialized root structures | Cluster roots | No or very little cluster roots | Shane and Hans (2005), Pearse et al. (2007), and Lynch (2007) |

the plant species, soil structure, and their interaction (Bertin et al. 2003). The larger root system provides more surface area for nutrient absorption by increasing the contact with soil which plays an important role for P absorption (Aziz et al. 2011a; Gahoonia and Nielsen 1998; Lynch 2007; Römer and Schenk 1998).

Distribution of nutrients in soils is heterogeneous or patchy. In order to enhance nutrient uptake, plant roots have to exploit these nutrient patches. Asymmetrical development and exceptional flexibility in architectural patterns of roots enable plants to exploit soils and allow root proliferation in nutrient-rich zones (Lynch 1995). Depending upon the plant species and environmental conditions, the root systems vary widely in terms of root architecture, including number and size of root hairs (Lambers and Shane 2007; Lynch and Brown 2001; Shane et al. 2006).

Various root characteristics including root architecture, root diameter, root hairs, cluster roots (Bates and Lynch 2000; Hill et al. 2006; Singh Gahoonia and Nielsen 2004), symbiotic relationship with mycorrhiza, kinetics of P uptake, and rhizospheric processes (Aziz et al. 2011a; Hinsinger 2001; Pang et al. 2010; Ryan et al. 2009) cause variations in P uptake among the plant species/cultivars (Lynch and Brown 2001; Singh Gahoonia and Nielsen 2004). Response to P deficiency by plant roots involves changes in root architecture and the shift of biomass allocation from basal to adventitious roots in such a way to explore more topsoil or P-rich (Lambers and Shane 2007) sites for P acquisition (Liao et al. 2001, 2004; Lynch and Brown 2001). These adaptations include horizontal basal root growth, increased adventitious root formation, enhanced lateral root formation, and increased root hair density and length (Bonser et al. 1996; Liao et al. 2001; Lynch 2007). Topsoil foraging is strongly associated with P acquisition in low-P soils (Rubio et al. 2003; Zhu et al. 2005) due to low mobility of P in soil. Low P in the rooting zone favors the formation of lateral roots (López-Bucio et al. 2002; Lynch 2007). A large root surface area is achieved by a combination of reduced mean root diameter and elongation of relatively thinner roots (Fitter et al. 2002). Root diameter is very important in exploration of soil volume by roots as it determines the volume of soil that can be explored by the roots (Fitter 1991; Gahoonia et al. 2006). Plants with a smaller root diameter can explore more soil per unit of root surface area (Fitter et al. 1991) and can efficiently uptake P from limiting environments (Singh Gahoonia and Nielsen 2004).

Root hair enhances the ability of roots to explore the rhizosphere for P due to increased surface area for absorption (Hill et al. 2010; Ma et al. 2001b; Zhu et al. 2010). Root hairs constitute up to 77 % of the total root surface area and thus are the major point of contact between plants and the rhizosphere (Föhse et al. 1991; Gahoonia and Nielsen 1998). Under P deficiency, increased root hair density and length is well documented in legumes (Yan et al. 2004) and barley (Gahoonia and Nielsen 1998). Ma et al. (2001a) reported that root hair density in *Arabidopsis thaliana* was high under P deficiency. Oilseed rape was reported to contain large amount of P as compared to maize despite having less root and shoot biomass (Morel and Hinsinger 1999), and this could be due to long root hairs of oilseed rape compared to maize (Gahoonia and Nielsen 2004). Large differences in root morphology and distribution are present between genotypes of many plants (Bates and Lynch 2001; Krasilnikoff et al. 2003; Römer and Schenk 1998; Vance 2001). Root characteristics such as total root length, root hair length and density, and specific root length have been shown to vary considerably between genotypes of several species (Løes and Gahoonia 2004; Nielsen et al. 1997; Römer and Schenk 1998; Singh Gahoonia et al. 1997; Yan et al. 1995). Significant differences in P uptake in cereal cultivars grown on low-P soil were reported due to differences in length of root hairs of these cultivars (Singh Gahoonia et al. 1997). Similarly, genetic differences in P uptake in cowpea and in maize due to variation in root length and root hairs have been reported (Krasilnikoff et al. 2003).

Maize genotypes modified their root architecture in response to low P in the rooting medium (Zhu et al. 2005). Genotypes which performed better under P-deficient conditions develop shallow root systems to tap P accumulated in topsoil and have greater specific P absorption rate, tissue P contents, relative growth rate, and biomass accumulation than others (Zhu et al. 2005). Phosphorus availability regulates different aspects of root architecture like axial extension, root branching, basal root gravitropic, the relative distribution of basal root length, and adventitious roots (Liao et al. 2004; Miller et al. 2003; Ochoa et al. 2006).

These differences raise the possibility of selection and breeding of crop genotypes having extensive root systems to cope with P deficiency in soils. Earlier studies showed that root growth (root size, root weight, etc.) positively correlated with biomass production in different crops (Barraclough 1984; Gill and Ahmad 2003; Kosar et al. 2002; Olaleye et al. 2011).

### 7.2.2 Root Biomass

Preferred biomass partitioning towards the roots is one of the most important adaptive mechanisms of the plants under P-deficient conditions (Hermans et al. 2006; Mollier and Pellerin 1999). Plants allocate more assimilates towards those areas which are directly involved in nutrient acquisition (Marschner 1995). Difference in preferred biomass partitioning between roots and shoots of the plants grown under P-deficient and sufficient supplies could be ontogenetic (comparing the plants at different growth stages) rather than a truly plastic response (Kemp and Blair 1994; Niklas 1994). However, it is evident that P supply influences biomass partitioning directly independent of ontogeny (de Groot and Grubmüller 2001; Ryser et al. 1997). Mollier and Pellerin (1999) reported that root:shoot ratio of maize significantly increased in P-deficient plants as compared to those grown with sufficient P supply, and this could be due to preferential distribution of carbohydrates towards roots under P-deficient conditions. Phosphorus deficiency causes accumulation of carbohydrates in roots and thus increases the root:shoot ratio of the plants (Cakmak et al. 1994; Hermans et al. 2006).

### 7.2.3 Phosphorus Uptake

Phosphorus moves to the plant roots by diffusion due to its strong reactions with soil constituents (Hinsinger et al. 2006; Rahmatullah et al. 1994; Trolove et al. 2003). Plants absorb P ions actively across the plasmalemma against the concentration gradient between soil solution and roots (Schachtman et al. 1998) as concentration of orthophosphates is usually very low (Bieleski 1973; Schachtman et al. 1998).

Plant species and cultivars differ greatly in their growth responses to low-P supply in the rooting medium (Gill et al. 2004; Gill and Ahmad 2003; Veneklaas et al. 2012). Some plants can grow efficiently in low-P soils mainly because they can take enough P for their optimum growth. Genotypes that are more efficient in P acquisition from deficient conditions are generally considered better adaptable to P deficiency in soils and their impact on adaptations to P stress (Duncan and Baligar 1990; Liu et al. 2004; Osborne and Rengel 2002; Rengel and Marschner 2005). Variations in nutrient acquisition from the rooting medium are attributed to variations in root plasticity in response to nutrient status, differences in uptake along the roots, and plant growth rate (Gahoonia and Nielsen 2004; Krasilnikoff et al. 2003). These may include morphological features as well as the biochemical mechanisms responsible for the initial transfer of ions across root cell membranes (Bates and Lynch 2000; Schachtman et al. 1998; Vance et al. 2003).

Naturally, plants can accumulate P and other nutrients selectively and actively in their tissues (Marschner 1995). Uptake kinetics explains the relationship between concentration of nutrient in soil solution and its influx into the root, and it can be explained in terms of a modified Michaelis-Menten kinetics (Nielsen 1972). Later on, idea of dual phasic P transport system which operates at low or high nutrient concentration in external solution was proposed (Epstein and Leggett 1954), and uptake systems were classified as low- and high-affinity uptake systems. Two independent Michaelis-Menten-type systems have been proposed in the literature under varying levels of P supply. Ullrich-Eberius et al. (1984) reported two P uptake systems with significantly different $K_m$ values. The value of $K_m$ in both systems was higher under P depletion. High-affinity system is inducible and operates when external P concentration is very low (Clarkson and Scattergood 1982; Smith et al. 2000). As P concentration in the rhizosphere is very low (usually in $\mu M$ range), only high-affinity uptake system operates in soil (Raghothama 1999).

Buhse (1992) proposed that differences in influx at the same concentration in solution are related to the uptake kinetics parameters, $I_{max}$ (maximum uptake rate), $K_m$ (external concentration at which uptake rate is half of $I_{max}$), and $C_{min}$ (minimum concentration at which influx ceases). Several authors reported that large reductions in shoot P concentration were related to an increase in $I_{max}$ (Anghinoni and Barber 1980; Drew 1984). Jungk and Barber (1974) proposed that increased $I_{max}$ under low shoot P concentration may be due to new root development during starvation period or increased concentration gradient with root P contents. $I_{max}$ value should be adjusted according to P concentration in plant and possibly root radius (Anghinoni and Barber 1980). The $C_{min}$ value indicates the lowest external concentration below which plants are unable to take up P from solution. Plants able to take up P at very low concentration in the soil solution ($C_{min}$) would be more efficient in P acquisition. Differences in values of uptake kinetics among several crop cultivars are well reported (Asher and Loneragan 1967; Nielsen and Barber 1978; Nielsen and Schjørring 1983).

Molecular research has revealed that plants have both a low- and high-affinity P uptake system (Bieleski 1973; Muchhal and Raghothama 1999). High-affinity systems are induced at low-P conditions (Furihata et al. 1992), while low-affinity system appears to be constitutive in plants (Raghothama 1999). Multiple plasmalemma P transporters differentially express under varying P nutritional regimes (Epstein and Leggett 1954; Plaxton and Carswell 1999). The high-affinity transporter mRNA transcripts in roots increased under low external P concentration for increased capacity of roots for P uptake (Duncan and Carrow 1999; Shenoy and Kalagudi 2005). These high-affinity transporters play an important role in the P acquisition under P-deficient root environment.

Bhadoria et al. (2004) reported the existence of differences in P use efficiency in maize and groundnut grown in solution culture which were related to differences in uptake kinetics of the two species. These differences observed in solution culture were opposite to those observed in the field (Bhadoria et al. 2004) and were probably based on several other edaphic factors other than uptake kinetics. Gahoonia and Nielsen (2004) proposed that genotypes should be selected for high $I_{\max}$ values and root length and low for $C_{\min}$ and $K_{\mathrm{m}}$ values. Lower $C_{\min}$ values show the ability of plants to uptake P at low concentration in soil solution that could be important in future low-input sustainable agriculture systems particularly in developing countries. They further pointed out that the importance of uptake kinetics parameters of plants in the soil plant system is still to be investigated. As P is moved in soil through diffusion, uptake efficiency of plants is of minor importance in the P acquisition (Barber 1995) than different P acquisition traits such as root dry matter, root length, no. of root hairs, and root hair density. Barber and Mackay (1986) and Krannitz et al. (1991) also reported that differences among cultivars of a species in P uptake can be explained by differences in root growth.

### 7.2.4 Nutrient Translocation/Remobilization Within the Plant

Movement of nutrients within the plant body under deficient conditions is another mechanism adopted by plants to cope with deficiency. Salinas and Sánchez (1976) proposed that these differences in nutrient movements under varying levels of nutrient supply are adjustments to adapt to deficiency. The capability of plants for retranslocation of P from one plant part to another is an adaptive strategy used by some plants under low-P supply (Gill and Ahmad 2003).

Efficient redistribution and reutilization of nutrients from deficient or senescent plant parts could also cause variations in nutrient utilization. Adu-Gyamfi et al. (1989) observed increased rate of absorption and translocation of P to leaves under P deficiency. Several researchers have reported that relatively lower proportions of total P was retained in roots and stems and higher proportions were translocated to leaves under P deficiency in P-efficient cultivars than inefficient cultivars (Snapp and Lynch 1996).

In P-deficient plants, limited P supply to the shoots from the roots via the xylem is supported by enhanced remobilization and retranslocation of stored P in mature leaves to the younger leaves. This compartmentation of P in various plant organs is reported to be inducible under conditions of P deficiency (Gerloff and Gabelman 1983) and is under genetic influence (Schachtman et al. 1998). Internal P concentration at a critical location in plants plays a regulatory force for enhanced P uptake from the root medium under P deficiency (Drew and Saker 1984; Lefebvre and Glass 1982).

### 7.2.5 Phosphorus Utilization Efficiency

Nutrient utilization is defined as the amount of biomass produced per unit amount of nutrient absorbed (Fageria and Baligar 1997; Siddiqi and Glass 1981). It has been used to compare the efficiencies of nutrient utilization among various cultivars or species. PUE is the ability of crop cultivars to grow well under low available P concentrations. Plants efficient in nutrient utilization may enhance the efficiency of applied P.

Efficient P use within the cell is another adaptive strategy in many crop species. Nanamori et al.

(2004) reported significant differences in P use efficiency among forage grass and rice. Variations for P use efficiency among cultivars of wheat (Batten 1993; Kosar et al. 2002), barley (Römer and Schenk 1998), maize (Elliott and Læuchli 1985), rice (Aziz et al. 2006; Gill and Ahmad 2003), forage crops (Mugwira and Haque 1993), and several other crop species (Föhse et al. 1991).

Some physiological and metabolic P transformations may also take place in plants as a response to P deficiency including induction of phosphate scavenging and recycling enzymes, organic acid excretion (Duff et al. 1994), induction of metabolic phosphate recycling enzymes (Plaxton and Carswell 1999), alternative pathways of cytosolic glycolysis (Plaxton and Carswell 1999), increased tonoplast $H^+$-,pumping pyrophosphatase, and alternative pathways of electron transport (Gonzàlez-Meler et al. 2004).

Phosphorus use efficiency is of special interest to developing countries, especially having soils low in available P. Tailoring plants to adapt to conditions of low-P supply and yield more from each unit of applied P is considered an alternative for high-input agriculture. An overall high PUE of plants can be achieved through the combined effect of P uptake efficiency and P utilization efficiency (Römer and Schenk 1998). As both these traits are genetically heritable (Nielsen and Schjørring 1983), they should be included in genetic improvement programs through breeding (Gill et al. 2004). An adaptation of nutrient-efficient crop cultivars is relatively easy, since no additional costs are involved and no major changes in cropping systems are necessary. Currently breeders are working on the selection or development of responsive cultivars, but traits responsible for differences in PUE should be considered in breeding programs such as P acquisition, translocation, and internal utilization and would be considered in breeding programs for low-input sustainable agriculture systems (Gill et al. 2004; Ortiz-Monasterio et al. 2007).

Cultivars can be categorized based on P use efficiency as discussed by Aziz et al. (2006), Fageria and Baligar (1997, 1999), and Kosar et al. (2002) into four groups as (1) efficient and responsive, (2) efficient and nonresponsive, (3) inefficient but responsive, and (4) inefficient and nonresponsive (Kosar et al. 2002). Fageria and Baligar (1999) compared different growth and P uptake parameters of efficient and responsive cultivars with inefficient and nonresponsive cultivars. They concluded that greater P efficiency in wheat genotypes was due to P use efficiency rather than to differences in P concentration. Gardiner and Christensen (1990) also reported that greater P efficiency in wheat genotypes was due to greater use efficiency rather than variations in P uptake. Recently Gill et al. (2004) studied P use efficiency of 30 wheat genotypes. They reported significant differences among the genotypes for biomass, P efficiency, harvest index, and grain yield. They categorized wheat genotypes into nine groups by regressing dry matter yield (*X*-axis) and P uptake (*Y*-axis).

### 7.2.6 Organic Acid Efflux

Plant roots exude a variety of carbon (C) compounds (simple sugars, organic acids, amino acids, phenolics, enzymes, other proteins) and inorganic ions (protons, phosphate, other nutrients, etc.) into the rhizosphere (Crowley and Rengel 1999; Jones and Darrah 1995; Marschner 1995; Miller et al. 2001; Rengel 2001; Veneklaas et al. 2003). Root exudation influences significantly rhizosphere chemistry, soil microflora and fauna, and plant growth (Hinsinger 2001; Johnson et al. 1996; Mench et al. 1987; Vance et al. 2003) and is involved in nutrient acquisition (Neumann et al. 2000; Römheld and Marschner 1990). Root exudates are a major source of energy for microbial growth in soils (Bowen and Rovira 1999; Rengel and Marschner 2005; Uren and Reisenauer 1988).

Nature of root exudates varies significantly in response to environmental stress especially under nutrient deficiency, e.g., P, Fe, Zn, and Mn (Jones and Brassington 1998; Jones and Darrah 1995; Neumann and Martinoia 2002). Among these diverse C compounds, organic acids and sugars are important for the mineral nutrition of plants as well as for microbial growth in the rhizosphere (Jones and Darrah 1995; Mench et al. 1987).

Under P-deficient conditions, exudation of organic acids like acetic, aconitic, citric, malic, fumaric, lactic, oxalic, and succinic acids increases in many plant species (Grierson 1992). Organic acids help in increasing the availability of P and micronutrients because the organic anions can compete with Pi for complexation by Fe, Al, and Ca (Gerke et al. 2000; Hinsinger 2001; Römheld and Marschner 1990) and may hydrolyze organic P (Gerke et al. 2000; Gerke and Meyer 1995). Increased exudation of organic acids under P deficiency has consistently been reported in many plant species such as in white lupin (Johnson et al. 1996; Neumann et al. 2000; Neumann and Römheld 1999), alfalfa (Lipton et al. 1987), and oilseed rape (Hoffland et al. 1989, 1992).

Kihara et al. (2003) reported significant increase in citrate release by rice under P deficiency. Citric acid can enhance significantly mobilization of P from Ca compounds by reducing the pH (Dinkelaker and Marschner 1992). Increased secretions of malic and citric acid in root zone of *Brassica napus* L (Aziz et al. 2011a, b; Hoffland et al. 1989) P deficiency was highly effective in increasing P uptake from sparingly soluble rock P. On the other hand, Wouterlood et al. (2005) reported that carboxylate exudation in chickpea did not correlate with P availability. However, di- and tricarboxylic acids have the ability to increase P solubility also in P-fixing soils and hence strongly improve P acquisition of plants grown in soils low in available P.

Species and genotypes which are tolerant to P deficiency differ in exudation of root secretions responsible for P solubilization. Cieśliński et al. (1998), Neumann and Römheld (1999), and Pearse et al. (2006b) reported significant differences among 13 plant species for amount of organic anion release under P deficiency. The amounting of the exudates also varied significantly between species.

The activity of phytase and acid phosphatase increased in root exudates in various species and genotypes within species grown under low-P supply (Asmar 1997; Lambers et al. 2010; Li et al. 1997; Pearse et al. 2006a; White and Veneklaas 2012). The P-deficiency-tolerant genotypes of different crops had a greater activity of extracellular phosphatases in the rhizosphere soil than genotypes sensitive to P deficiency (Asmar et al. 1995; Gerke et al. 2000; Richardson and Simpson 2011).

## 7.3 Gene Expression Under Phosphorus Deficiency

Response to phosphate deficiency involves a set of morphological, biochemical, and physiological changes in metabolic expression, which enables the plants to adapt to P-limited environments. Manipulation of the gene expression under P-deficient conditions could improve the PUE of plants.

A series of genes is involved in the adaptations, through the regulation of P acquisition, internal remobilization, change in metabolism, and signal transduction to P deficiency (Fang et al. 2009). For example, the expression of genes encoding ribonucleases (RNS) and purple acid phosphatases (PAPs) is generally upregulated in plants raised in P-limited environments. Ribonucleases help the plants to release P from organic sources and make that plant available; RNS also help in mobilization of the organic P in soil for plant uptake (Bariola et al. 1994; Duff et al. 1994). Likewise, genes responsible for phosphate transporters (PTs) are the major P-deficiency-induced genes which are isolated and characterized from different plant species (Liu et al. 2001; Miller et al. 2001). Several split-root experiments indicated that P-deficiency-induced genes are regulated by P status of the plant and not the soil P concentration (Burleigh and Harrison 1999; Liu et al. 1998; Shane et al. 2003).

Phosphorus uptake1 (*Pup1*), a major quantitative trait locus (QTL), involved in tolerance of soil P deficiency is located on rice chromosome 12 (Shane et al. 2003). As highly branched root systems with long root hairs are helpful in improving PUE (Ramaekers et al. 2010), Pup1 stimulates the root growth (Gamuyao et al. 2012; Li et al. 2008), increases the P uptake (Wissuwa and Ae 2001), and increases grain yield substantially (Chin et al. 2010). Similarly, white lupin exhibits morphological and gene expression changes in P-deficient roots. Phosphate transporter (*LaPT1*) and secreted acid phosphatase (*LaSAP1*) promoter-reporter genes isolated from lupin showed significant induction in roots specifically in response to P deficiency when transformed into alfalfa.

The identification of transcriptive factors, regulatory signaling cascades, and genes associated with plant responses to P stress could be helpful for developing crops with improved P use efficiency. However, since several studies have assayed gene expression in plants under controlled environment, the outcomes of such experiments need to be confirmed under field conditions.

## 7.4 Signaling and P Deficiency

Plant growth and development is determined by environmental factors like temperature, light intensity, water, and essential nutrients. Plants allocate new biomass to the organs used for acquiring the scarce resources to adjust the ionic imbalance (Marschner 1995). Many studies have focused on the relationships between nutrition, plant growth, and development and have explained the mechanisms of ion transport and the biochemical pathways influenced by mineral scarcity (Hermans et al. 2006; Chandna et al. 2012; Hakeem et al. 2012a, b). Although understanding about the molecular and physiological processes involved in sensing, signaling, and allocation of deficient nutrients is poor, but with onset of microarray technologies to study gene expression, study of transcriptional changes associated with mineral imbalance has become easier (Hammond et al. 2004). Deficiency of P results in preferential allocation of carbohydrates towards the roots and thus increases root to shoot ratio. This also results in modification of photosynthesis, metabolism of sugar, and/or partitioning of carbohydrate between source and sink tissues (Sánchez-Calderón et al. 2006). The knowledge about how the plants sense P deficiency is growing rapidly, but a lot is still to be discovered in the near future. Phosphorus deficiency in plants triggers many transcriptional, biochemical, and physiological changes that ultimately help the plants absorb P from the soil or improve the P use efficiency (Amtmann et al. 2005; Hammond and White 2008). Plants have evolved various adaptive mechanisms to absorb P under P-stressed conditions which involve diverse developmental and biochemical processes. Different transcription factors that control response of plants under P starvation has been identified. The miRNAs are responsible for Pi homeostasis and signaling through the identification and characterization of PSR miRNAs under P-deficient conditions (Kuo and Chiou 2011). Understanding the mechanism involved in sensing P deficiency could facilitate selection, breeding, and genetic engineering approaches to improve crop production in P-stressed environments and could reduce dependence on nonrenewable inorganic P resources.

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