Update on White Lupin Cluster Root Acclimation to Phosphorus Deficiency

Lingyun Cheng, Bruna Bucciarelli, Jianbo Shen, Deborah Allan, and Carroll P. Vance*

Department of Plant Nutrition, China Agricultural University, Key Laboratory of Plant-Soil Interactions, Beijing 100193, People's Republic of China (L.C., J.S.); Department of Agronomy and Plant Genetics (L.C., B.B., C.P.V.) and Department of Soil, Water, and Climate (D.A.), University of Minnesota, St. Paul, Minnesota 55108; and United States Department of Agriculture Agricultural Research Service, St. Paul, Minnesota 55108 (B.B., C.P.V.)

Phosphorus (P) is one of 17 essential elements (nutrients) required for plant growth (Tiessen, 2008; Cordell et al., 2009). Although bound P is quite abundant in many soils, it is largely unavailable for uptake. As such, P is frequently the most limiting element for plant growth and development. Crop yield on 40% to 60% of the world's arable land is limited by P availability. Mined rock phosphate is the primary source of P fertilizer. Approximately 90% of all mined rock phosphate is used for agriculture (Tiessen, 2008; Cordell et al., 2009). However, rock phosphate is a nonrenewable resource (Steen, 1998; Cordell et al., 2009), and easily mined, high-quality rock phosphate sources are projected to be depleted within 30 to 50 years (Steen, 1998; Tiessen, 2008; Cordell et al., 2009). Peak P production is projected to occur in 2035 to 2040 (Cordell et al., 2009). In addition, the world's major reserves of rock phosphate are located in geographical areas where uncertain political issues could limit access to the world's P resources. Sustainable management of P in agriculture requires that plant biologists discover mechanisms that enhance P acquisition and exploit these adaptations to make plants more efficient at acquiring P, develop P-efficient germplasm, and advance crop management schemes that increase soil P availability.

Cluster roots (Fig. 1), extremely specialized tertiary lateral root structures, are an important adaptive strategy of plants to cope with nutrient-poor, P-depleted soils (Dinkelaker et al., 1995; Neumann and Martinoia, 2002; Vance et al., 2003; Lambers et al., 2006). They are produced on plants from a diverse range of families (Dinkelaker et al., 1995; Watt and Evans, 1999; Shane and Lambers, 2005). White lupin (*Lupinus albus*) forms cluster roots in response to P starvation. Cluster roots are characterized as concentrated zones of tertiary lateral roots emerging in waves from secondary roots. Root hair density appears to be greater in mature cluster root zones than typical lateral roots. Such an adaptation leads to a striking increase in root surface area available for P uptake from the rhizosphere (Keerthisinghe et al., 1998; Neumann et al., 1999). Cluster root development and function involve a highly synchronous series of molecular and biochemical processes, including highly enhanced lateral root initiation, increased root hair formation, root exudation of organic acid chelators (citrate and malate), modified carbon assimilation, release of enzymes (acid phosphatase, ferric chelate reductases) into the rhizosphere, and more efficient uptake of P from the rhizosphere (Dinkelaker et al., 1989; Neumann et al., 1999; Watt and Evans, 1999; Liu et al., 2001, 2005; Miller et al., 2001; Uhde-Stone et al., 2003a, 2005; Wasaki et al., 2003). Advances have recently been made in understanding the molecular and biochemical events surrounding cluster root formation and function. As a crop, white lupin is a practical alternative to evaluate acclimation to P deficiency, particularly as related to cluster-rooted species (Johnson et al., 1996; Keerthisinghe et al., 1998; Watt and Evans, 1999; Neumann and Martinoia, 2002).

P SIGNALING: SYSTEMIC VERSUS LOCAL

Cluster root system development is highly plastic and affected by the deficiency of several nutrients. Among these factors, P deficiency appears to be the most important element determining cluster root formation in white lupin (Gardner et al., 1983; Dinkelaker et al., 1995; Johnson et al., 1996). Both local (external P) and systemic (internal P) signaling have been implicated as factors influencing cluster root formation. Reciprocal grafting studies between white lupin and narrow leaf lupin (*Lupinus angustifolius*), which does not form cluster roots, have shown that the root genotype dictates cluster root development when P is limiting. These results support the hypothesis that both local and systemic signaling regulates cluster root formation. Application of P through foliar feeding of white lupin and split-root systems (Marschner et al., 1987; Gilbert et al., 1997; Shane et al., 2003; Li et al., 2008) has conclusively shown that increasing internal P concentration results in reduced cluster root formation and exudation of organic acids and protons. They further confirmed that the critical internal P concentration for cluster root development was 2 to 3 mg P g^{-1} dry weight.

* Corresponding author; e-mail carroll.vance@ars.usda.gov.
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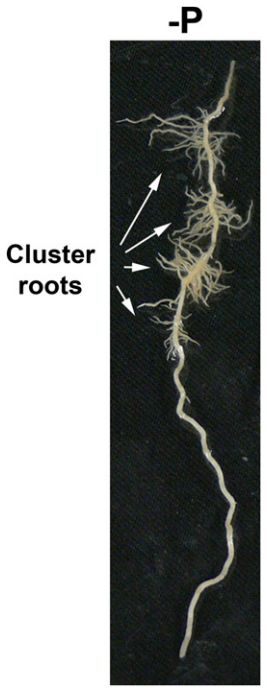

Figure 1. White lupin P deficiency cluster roots emerge as waves of tertiary lateral roots along the axis of secondary roots.

Similar to the classic studies of Drew (1975), Shu et al. (2007) demonstrated that availability of local root P (external) in soil patches can induce cluster root formation and proton extrusion. Local P sensing by the root is well known in Arabidopsis (*Arabidopsis thaliana*). Root contact with low P blocks growth of the primary root and stimulates lateral root formation (López-Bucio et al., 2003; Ticconi et al., 2004; Reymond et al., 2006). Liu et al. (2005) and Tesfaye et al. (2007) have shown that localized root contact with high P quickly reduces P deficiency-induced gene expression in white lupin cluster roots. An Arabidopsis mutant, *P deficiency response2* (*pdr2*), which encodes a P_5-type ATPase, displays altered root architecture and hypersensitivity to low P due to the disruption of local P sensing (Ticconi et al., 2004, 2009). PDR2 was further found to function in the endoplasmic reticulum and to be required for proper expression of SCARECROW (SCR). SCR belongs to the GRAS family of transcription factors and key regulators of root patterning (Petricka and Benfey, 2008). SCR protein was markedly reduced in the *pdr2* mutant within 1 d after transferring to P-free medium; however, this reduction can be rescued by increasing SCR gene dosage (Ticconi et al., 2009). Evidence suggested that PDR2 is imperative for maintaining SCR protein during P starvation. White lupin *SCRs* (*LaSCR1* and *LaSCR2*) have been isolated and recently characterized (Sbabou et al., 2010). Consistent with the localization of *SCR* genes in all the species examined to date (Pysh et al., 1999; Sassa et al., 2001; Kamiya et al., 2003; Laajanen et al., 2007), the expression of *LaSCR* genes has been localized to the root endodermis and quiescent center and seems to be closely related to cluster root development rather than to the P status of the plant. Suppression of *LaSCR1* transcripts in transgenic lupin roots resulted in reduced cluster root numbers, implying a role for *LaSCR1* in maintaining root growth in white lupin (Sbabou et al., 2010).

Also in Arabidopsis, three low-phosphate root quantitative trait loci (*LPR1–LPR3*) involved in root growth response to low P have been mapped in recombinant inbred lines derived from the Bayreuth and Shahdara wild accessions (Reymond et al., 2006). Map-based cloning showed that *LPR1* encodes a multicopper oxidase. The quantitative trait locus trait was explained by the different patterns of *LPR1* expression in the root tip, specifically in the root cap (Svistoonoff et al., 2007). Through an agar plate compartmented root-growth experiment, the authors further showed that physical contact of the primary root tip with low-P medium is necessary and sufficient to arrest root growth. We have found an EST having high similarity to the Arabidopsis *LPR1* in a white lupin P deficiency-induced cluster root cDNA library. It appears to be highly up-regulated in root tips of P-starved plants when compared with other cluster root developmental stages (L. Cheng and C. Vance, unpublished data). It will be informative to determine whether lupin *LPR1* shows the same conserved function as Arabidopsis *LPR1* in sensing external P.

It is noteworthy that white lupin is an excellent system in which to evaluate signal transduction compounds transported in phloem and xylem sap (Atkins and Smith, 2007). Recent analysis of white lupin phloem has identified 86 proteins and 609 unique transcripts transported in sap (Rodriguez-Medina et al., 2011). Signal transduction proteins and mRNAs constituted 2% and 5%, respectively, of the compounds found in phloem sap. In addition, 330 small RNAs, several of which are implicated in signal transduction, were detected in phloem sap. The ease with which white lupin xylem and phloem sap can be collected provides a unique tool to use in evaluating the transport of signal transduction components in plants grown under abiotic and/or biotic stress.

HORMONES ARE INVOLVED IN LUPIN CLUSTER ROOT DEVELOPMENT

Because white lupin cluster root development involves the synchronized initiation and growth of a large number of tertiary lateral roots in distinct wave-like patterns originating lateral roots, it would not be surprising that hormone balance plays a role in this P-adaptive process (Gilbert et al., 2000; Neumann et al., 2000; Skene and James, 2000). Many of the hormonally controlled developmental responses occurring in P-stressed Arabidopsis that give rise to modified root architecture appear also to be involved in cluster root formation. Substantial support for the role of auxin in

cluster root formation comes from observations showing that exogenous application of auxin to P-sufficient white lupin stimulates cluster roots, thereby mimicking P deficiency-induced cluster root induction (Gilbert et al., 2000; Skene and James, 2000). Moreover, white lupin roots impaired for endogenous auxin transport by being grown in the presence of the auxin transport inhibitor *N*-1-naphthylphthalamic acid failed to form induced cluster roots under P deficiency (Gilbert et al., 2000). Many genes involved in auxin synthesis and signaling are abundantly expressed in developing cluster roots of white lupin (Uhde-Stone et al., 2003b; Vance et al., 2003; Yamagishi et al., 2011). These data clearly show that a significant component of P-induced cluster root formation is due to auxin synthesis and transport. We have initiated studies to evaluate auxin signaling in cluster root development by transforming them with the auxin reporter construct DR5-GUS (Ulmasov et al., 1997). In addition, we have isolated an *IAA7/axr2* gene and transformed white lupin roots with an *IAA7/axr2*:GUS reporter (Fig. 2). The *IAA7/axr2* reporter was highly active in P-stressed cluster roots relative to P-sufficient roots. In comparison, the DR5 reporter was active over a greater range of cluster root development in P-stressed plants as compared with P-sufficient ones (data not shown). These studies, similar to those in Arabidopsis, suggest that P-deficient cluster roots have increased sensitivity to auxin.

Although microRNA (miRNA) involvement in P stress is addressed elsewhere, it is worthwhile to note that Zhu et al. (2010) evaluated the expression of miRNAs in P-stressed lupin. As expected, miR399 had enhanced expression in P-stressed plants. However, in relation to auxin, the authors found that the lupin NAC domain-containing *NAC1* gene, the target for miR164, was up-regulated in tissues under P deficiency while miR164 had reduced expression. Transcripts of miR164 mediate the cleavage of *NAC1* transcripts to direct auxin-dependent signaling for lateral root formation (Xie et al., 2000, 2002; Guo et al., 2005; Zhu et al., 2010). In Arabidopsis, NAC1 acts as a transcriptional activator to transmit auxin signals for lateral root development. *NAC1* mRNA accumulates mainly in roots, with greatest expression at lateral root initiation sites. In addition, there is a positive correlation between *NAC1* mRNA levels and lateral root numbers (Xie et al., 2000). Guo et al. (2005) found that transgenic Arabidopsis overexpressing miR164, which targets *NAC1* for degradation, exhibited reduced lateral roots, whereas mutants having reduced miR164 accumulated higher levels of *NAC1* mRNA and produced more lateral roots. Evidence suggests that miR164 acts as a negative regulator in auxin-mediated lateral root formation in Arabidopsis. Zhu et al. (2010) found that the lupin *NAC1* gene was up-regulated in tissues under P deficiency while miR164 expression was reduced under P deficiency, suggesting that miR164 and NAC1 may play roles in auxin-mediated cluster root formation in white lupin.

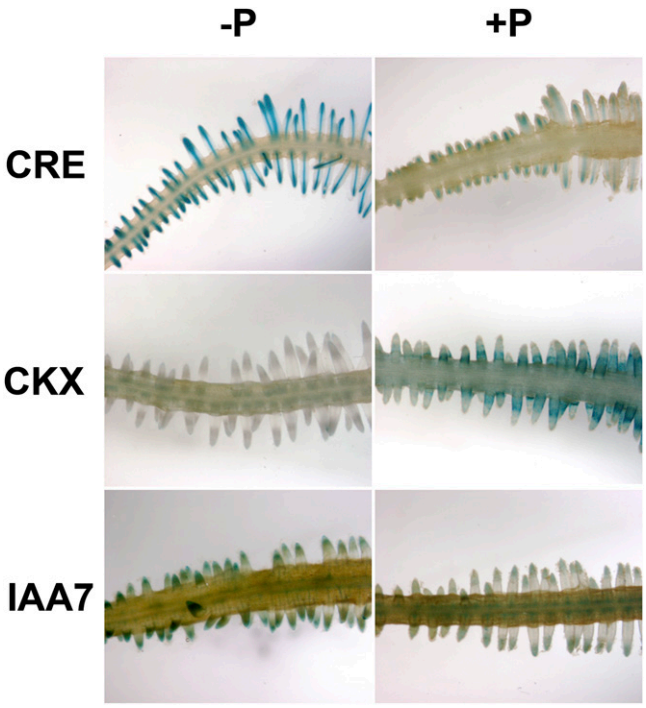

Figure 2. GUS reporter gene activity in P-deficient (−P) and P-sufficient (+P) white lupin cluster roots transformed with *Agrobacterium rhizogenes* containing promoter:GUS reporter constructs for genes involved in hormone signaling. Note the effect of –P and +P on reporter gene activity. CRE, The alfalfa cytokinin receptor gene promoter:GUS construct transformed into white lupin cluster roots; CKX, the white lupin cytokinin oxidase gene promoter:GUS; IAA7, the white lupin *IAA7/axr2* gene promoter:GUS. Photographs are representative of at least five roots representing individual events.

In their classic study of the physiology of cluster roots, Neumann et al. (2000) found that the addition of cytokinins to lupin significantly reduced the number of emerged cluster roots and cluster rootlet elongation. They also found elevated levels of cytokinin in 4-week-old P-deficient white lupin roots as compared with P-sufficient roots. They postulated that auxin stimulates the emergence of cluster rootlets in P-deficient plants, which results in increased production of cytokinin due to the numerous emerged root tips. In mature segments of P-induced cluster roots, we have found ESTs that annotate to cytokinin oxidase (*CKX*; Uhde-Stone et al., 2003b), suggesting that cytokinins are involved in cluster root development and maturation. We have recently transformed white lupin roots with a white lupin *CKX*:GUS reporter and a *Medicago* cytokinin receptor (*CRE*):GUS reporter. Initial results show that *CKX* and *CRE* reporter genes respond to the P status of the plant. *CKX* reporter activity appears to be reduced in P-deficient roots, while *CRE* reporter activity appears to be enhanced (Fig. 2). The *CRE* reporter studies imply that P-stressed roots have heightened sensitivity to P stress while *CKX* expression may be impaired by low P. These results are not congruent with results from Arabidopsis. This may be due to inherent differ-

ences in P stress cytokinin signaling between Arabidopsis and lupin.

Although strong correlative physiological and gene expression data suggest a critical role of auxins and cytokinins in P stress-induced cluster root development, definitive genetic and biochemical experiments have yet to be performed. Salient questions to be addressed include the following. What is/are the internal signal(s) that initiate(s) the cascade of developmental, biochemical, and genetic changes resulting in cluster roots? How is determinancy in cluster roots regulated? Are reactive oxygen and programmed cell death part of the cluster root developmental phenomenon? Can gene knockdown and overexpression studies be harnessed to definitively answer questions regarding the role of growth hormones in cluster root development and function? Can the genetic control mechanisms(s) for cluster root formation be identified and used to enhance P uptake and P use efficiency in other plant species?

SUGARS REGULATE CLUSTER ROOT DEVELOPMENT AND FUNCTION

Suc, derived from photosynthate, and miRNAs have been implicated as critical molecules signaling the P status of plants. Under P-deficient conditions, an increase in Suc biosynthesis has been observed in the leaves of a range of plant species (Foyer and Spencer, 1986; Cakmak et al., 1994; Ciereszko et al., 1996; Morcuende et al., 2007; Müller et al., 2007). Moreover, translocation of mobile carbohydrates, primarily in the form of Suc, via the phloem to the roots increased from either reduced shoot demand or increased root demand (Cakmak et al., 1994; Hermans et al., 2006). Chiou and Bush (1998) showed that Suc could act as a signal molecule in assimilate partitioning. A growing body of evidence now supports Suc derived from photosynthate as part of the systemic signaling leading to P deficiency-induced increase in lateral root formation and increased root hair density (Hermans et al., 2006; Jain et al., 2007; Karthikeyan et al., 2007; Zhou et al., 2008). To test the role of photosynthate and phloem Suc on P stress transcript induction, shoots of white lupin plants were either darkened or had stems girdled to block phloem transport, and the expression of P starvation-induced genes in roots was evaluated (Liu et al., 2005; Tesfaye et al., 2007). Both treatments reduced the expression of a number of genes in P-stressed roots to nondetectable levels within 1 to 4 h. Returning darkened plants to light rapidly restored P starvation-induced gene expression in roots. Zhou et al. (2008) showed that sugars are required for white lupin response to P deficiency, including cluster root formation and the expression of P starvation-induced genes. White lupin plants were grown in vitro on P-sufficient or P-deficient medium supplemented with Suc for 4 weeks. Suc supply stimulated cluster root formation in plants on both P-sufficient and P-deficient agar media. Notably, cluster roots did not form on the P-sufficient medium without Suc added. Transcription of P deficiency-induced *LaPT1* and *LaPEPC3* was magnified by the combination of P limitation and Suc feeding, and *LaSAP* was stimulated by Suc supply independently of P supply. These results suggest that at least two sugar-signaling mechanisms affect P starvation responses in white lupin roots. One mechanism regulates cluster root development and *LaSAP* expression, when P-sufficient roots receive sugar as a signal. The other mechanism controls *LaPT1* and *LaPEPC3* expression, which acts when P is insufficient.

Moreover, Suc has been shown in Arabidopsis to be required for enhanced expression of P starvation-induced genes (Franco-Zorrilla et al., 2005; Karthikeyan et al., 2007; Müller et al., 2007). In P-stressed Arabidopsis roots, P starvation-induced genes showed further enhanced expression when supplemented with 3% Suc (Franco-Zorrilla et al., 2005; Karthikeyan et al., 2007). Müller et al. (2007) evaluated the interaction between P and Suc in Arabidopsis leaves. Using a 2-fold cutoff, they identified 149 transcripts that were regulated by the interaction between P starvation and Suc availability. One group of 47 genes having increased expression in response to P deficiency was further enhanced by Suc. Many of the transcripts in this group encode proteins involved in P remobilization and carbohydrate metabolism. Although Suc appears to be important in signaling P status and the full expression of P starvation-induced genes, the mechanism remains elusive. The Suc-nonfermenting1 kinase: calcineurin B-like protein kinase (SNF1:CIPK) pathway has been implicated as the transduction system for sugar signaling (Hummel et al., 2009; Rosa et al., 2009; Meyer et al., 2010). Whether the SNF1:CIPK pathway regulates sugar signaling during P starvation deserves further investigation.

NITRIC OXIDE PRODUCTION IN CLUSTER ROOTS

In recent years, nitric oxide (NO) has been recognized as a diffusible bioactive molecule that functions in numerous plant processes (Durner and Klessig, 1999; Wojtaszek, 2000; Lamattina et al., 2003). Several reports indicate that NO may play a role in lateral root development (Pagnussat et al., 2002; Correa-Aragunde et al., 2004). Pagnussat et al. (2002) demonstrated that NO is required for auxin-induced adventitious root development in cucumber (*Cucumis sativus*). Application of NO donors induced adventitious root initiation in cucumber explants, and accumulation of endogenous NO was detected in explants after IAA treatment (Pagnussat et al., 2002). Application of the NO donor sodium nitroprusside to tomato (*Solanum lycopersicum*) induced lateral root emergence, whereas depletion of endogenous NO with the NO scavenger 2-(4-carboxyphenyl)-4,4,5,5-tetramethylimidazoline-1-oxyl-3-oxide completely arrested lateral root emer-

gence (Correa-Aragunde et al., 2004), a very similar effect to that of auxin on lateral root development. Correa-Aragunde et al. (2006) further showed that NO mediates the expression of cell cycle-regulatory genes in tomato pericycle cells to induce lateral root primordia formation, suggesting a NO-mediated auxin-dependent cell cycle gene regulation in tomato. Recently, NO was demonstrated to be involved in adaptive responses of white lupin to P starvation (Wang et al., 2010). Accumulation of NO was found in P-deficient white lupin roots, particularly in cluster rootlet primordia prior to and during emergence (Fig. 3). The P deficiency-induced increase in NO production was inhibited by antagonists of NO synthase and xanthine oxidase. Furthermore, the application of the exogenous NO donor sodium nitroprusside enhanced the formation of cluster roots in P-deficient white lupin but not in P-sufficient plants. These studies, together with the findings of Correa-Aragunde et al. (2006) in tomato, support the hypothesis that NO seems to be required in lateral root initiation and root primordia formation. In addition to studies on the role of NO in cluster root formation, Wang et al. (2010) also investigated the enzymes putatively involved in NO generation in cluster roots. Inhibitor studies and gene expression analyses show that a NO-synthase-like enzyme and xanthine oxidoreductase are required for the accumulation of NO in cluster roots. The role of NO in root development acclimation to abiotic stress is not well defined and deserves further attention in white lupin and other species.

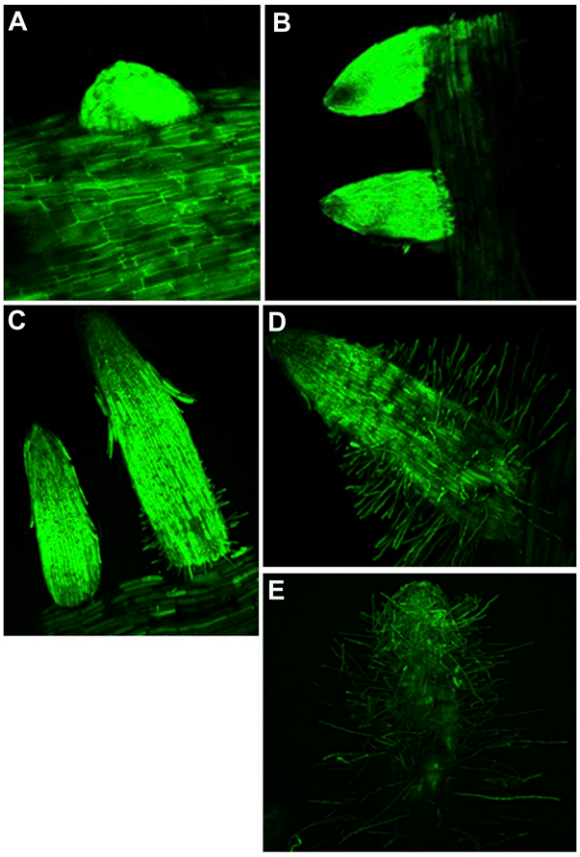

Figure 3. NO fluorescence of cluster roots of white lupin induced by P deficiency at different growth stages. A and B, Juvenile cluster roots. C, Growing cluster roots. D, Mature cluster roots with root hairs. E, Senescent cluster roots. Cluster root segments were incubated in 20 μM 4,5-diaminofluorescein in a solution containing 20 mM HEPES-NaOH, pH 7.5, for 40 min. Fluorescence was detected by confocal laser scanning microscopy.

TRANSCRIPTION FACTORS INVOLVED IN P PERCEPTION

The regulation of gene expression during plant stress is controlled by the transcriptional activation or repression of genes (Chen et al., 2002; Hammond et al., 2004; Valdés-López et al., 2008; Valdés-López and Hernández, 2008). Transcription factors (TFs) are key global regulators of gene expression and are known to play central roles in most biological processes, including the regulation of plant gene expression in response to numerous biotic and abiotic stresses (Sreenivasulu et al., 2007; Century et al., 2008; Hirayama and Shinozaki, 2010). In Arabidopsis alone, approximately 6% (about 1,800) of the total number of genes are composed of TFs, including about 72 WRKYs, more than 600 zinc finger proteins, and 133 MYB TFs (Eulgem et al., 2000; Riechmann et al., 2000; Stracke et al., 2001; Guo et al., 2005). In a microarray analysis, approximately 30% of the 333 TF genes included on the array were up- or down-regulated 2-fold or more during P stress in Arabidopsis (Wu et al., 2003). Misson et al. (2005) and Müller et al. (2007) also reported up to 80 P stress-responsive TF genes in Arabidopsis. Graham et al. (2006) discovered through bioinformatic analysis of P stress-induced genes in Arabidopsis, *Medicago*, *Glycine*, *Phaseolus*, and *Lupinus* that they share in common TF families encoding WRKYs, MYBs, GRAS, zinc finger proteins, and b-HLH proteins, which respond to plant P status. For details on specific TFs implicated in plant acclimation to P deficiency, the reader is referred to several comprehensive reviews that cover the primary literature (Doerner, 2008; Yuan and Liu, 2008; Yang and Finnegan, 2010).

The classic example of transcriptional regulation of P-responsive genes was delineated through studies of the MYB coiled-coil TF phosphate starvation response gene *PHR1* (Rubio et al., 2001; Miura et al., 2005; Nilsson et al., 2007; Valdés-López et al., 2008). Rubio et al. (2001) identified an Arabidopsis mutant, *phr1*, that when grown under P deficiency had reduced accumulation of anthocyanin and defective expression of P deficiency response genes. These results indicated that *PHR1* was a positive regulator of P-responsive gene expression. PHR1 protein binds to an imperfect palindromic consensus cis-element (5′-GNATATNC-3′) found in the promoters of numerous, but not all,

P deficiency response genes (Hammond et al., 2003; Misson et al., 2005; Morcuende et al., 2007). Knockdown of *PHR1* expression mimics the *phr1* mutant, while overexpression of PHR1 results in increased P concentration and enhanced expression of P deficiency response genes (Nilsson et al., 2007). Homologs of *PHR1* have been found in numerous species, including rice (*Oryza sativa*), bean (*Phaseolus vulgaris*), and lupin (Valdés-López et al., 2008; Zhou et al., 2008; Zinn et al., 2009). Analysis of the Arabidopsis genome showed that the P1BS element appears to be specifically overrepresented in approximately 45% of P-responsive genes (Hammond et al., 2004; Misson et al., 2005; Müller et al., 2007). Mutation in either PHR1 or the P1BS element suppresses the expression of genes in Arabidopsis whose promoters contain the P1BS element during P starvation (Rubio et al., 2001; Franco-Zorrilla et al., 2004). Schünmann et al. (2004) observed that the P starvation-induced barley (*Hordeum vulgare*) phosphate transporter gene, *HvPht1;1*, lost the response to P starvation when the P1BS elements were mutated, referring to a conserved role of the P1BS element in the expression of P-regulated genes in monocots. Three white lupin genes (*LaSAP1*, *LaPT1*, and *LaMATE*) have been well characterized as up-regulated in P-deficient cluster roots. The promoters of these genes contain one or more P1BS elements (Liu et al., 2001; Miller et al., 2001; Uhde-Stone et al., 2005). To investigate the functionality of the P1BS element in the P regulation of gene expression in lupin, Zinn et al. (2009) analyzed the promoter region of the *LaSAP1* gene. They found that the induced expression of *LaSAP1* in P-deficient cluster roots requires the presence of a functional P1BS element located within the promoter. Aside from P1BS element analysis, the authors found a defined domain located within the promoter region of *LaSAP1* that specifically interacted with nuclear protein extracts from P-sufficient roots, suggesting the involvement of a TF in negative regulation of gene expression. We have isolated a P starvation-induced *Pho85*-like gene that contains four P1BS elements in the promoter region. Through a series of P1BS mutations fused to a GUS reporter gene, our preliminary study showed that P1BS elements are required to modulate the induced expression of *Pho85*-like in response to P starvation (L. Cheng and C. Vance, unpublished data).

Recently, Yamagishi et al. (2011) reported on a survey of signal perception genes in white lupin. They found four *PHR*-like MYB TFs, none of which showed increased expression under low P. In addition, they found 29 *R2R3*-MYB genes, four of which had increased expression under P deficiency. The transcriptional profiling of another 15 signaling genes showed that transcription of one calmodulin gene, *LaCaM*, was enhanced under P deficiency in cluster roots. This limited study provides a valuable starting point for further research on TF genes and signal transduction.

OVERVIEW

P is a critical element for plant growth and is frequently the limiting nutrient in many soils. Continued production and application of P fertilizer relies on a nonrenewable resource that will peak in about 2050. This will result in significantly increased cost, particularly for developing countries. Significant research efforts in plant acclimation to P stress show that many suites of genes regulated in a coordinated fashion act to modify root growth and development as well as metabolic pathways. Studies of white lupin offer a crop model species as an alternative to Arabidopsis. Development of cluster roots in other species may be a vehicle for the development of crop plants with more efficient P acquisition and use. Highly P-efficient plants could reduce the need for P fertilizer in the developed world, thereby ameliorating the overuse of P, while concurrently enhancing yield in the developing world, where P is frequently unavailable.

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