

The role of nutrient availability in regulating root architecture

José López-Bucio, Alfredo Cruz-Ramírez and Luis Herrera-Estrella

The ability of plants to respond appropriately to nutrient availability is of fundamental importance for their adaptation to the environment. Nutrients such as nitrate, phosphate, sulfate and iron act as signals that can be perceived. These signals trigger molecular mechanisms that modify cell division and cell differentiation processes within the root and have a profound impact on root system architecture. Important developmental processes, such as root-hair formation, primary root growth and lateral root formation, are particularly sensitive to changes in the internal and external concentration of nutrients. The responses of root architecture to nutrients can be modified by plant growth regulators, such as auxins, cytokinins and ethylene, suggesting that the nutritional control of root development may be mediated by changes in hormone synthesis, transport or sensitivity. Recent information points to the existence of nutrient-specific signal transduction pathways that interpret the external and internal concentrations of nutrients to modify root development. Progress in this field has led to the cloning of regulatory genes that play pivotal roles in nutrient-induced changes to root development.

Addresses

Departamento de Ingeniería Genética de Plantas, Centro de Investigación y Estudios Avanzados del Instituto Politécnico Nacional, Unidad Irapuato, Apartado Postal 629, 36500 Irapuato, Guanajuato, México

Correspondence: Luis Herrera-Estrella

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Abbreviations

ABA abscisic acid
abi4-1 *ABA-insensitive4-1*
ANR1 *Arabidopsis NITRATE-REGULATED1*
axr2 *auxin resistant2*
CycB1 *CyclinB1*
HAR1 *HYPERNODULATION ABERRANT ROOT1*
phr1 *phosphate response regulator1*

Introduction

Plant root systems perform many essential adaptive functions including water and nutrient uptake, anchorage to the soil and the establishment of biotic interactions at the rhizosphere. Changes in the architecture of the root system, therefore, can profoundly affect the capacity of plants to take up nutrients and water. Three major

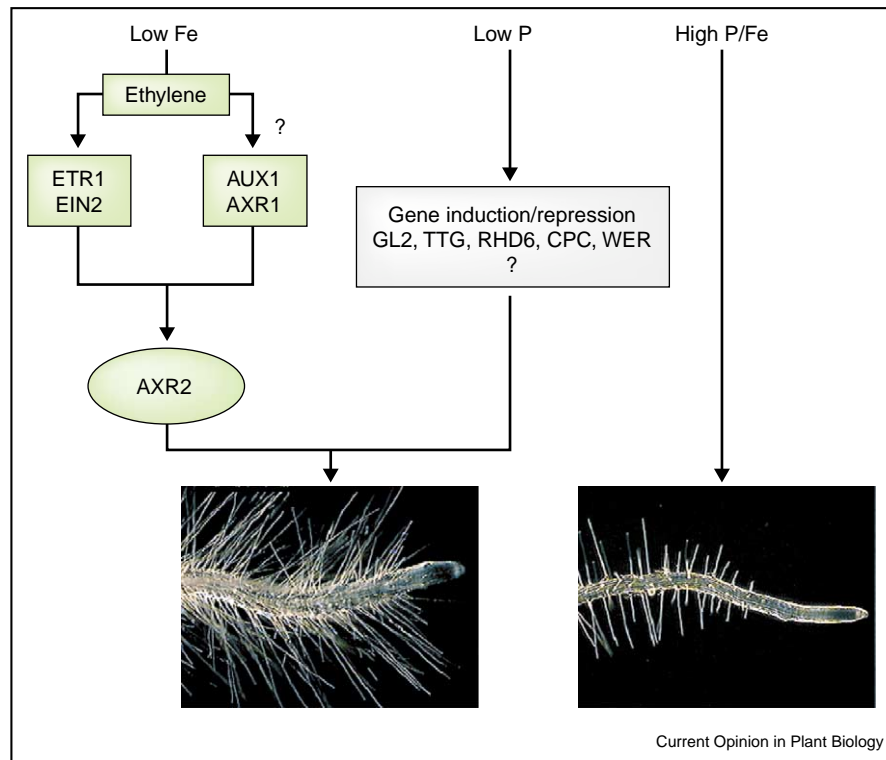
processes affect the overall architecture of the root system. First, cell division at the primary root meristem (i.e. of initial cells) enables indeterminate growth by adding new cells to the root. Second, lateral root formation increases the exploratory capacity of the root system; and third, root-hair formation increases the total surface of primary and lateral roots. Alterations to any of these three processes can have profound effects on root-system architecture and on the capacity of plants to grow in soils in which nutrient resources are limiting.

Soil nutrients are critical elements for plant growth and productivity. The bioavailability of nutrients in the soil solution may determine root growth, root proliferation and specific functional responses that depend on the prevailing nutrient status of the plant. Nitrogen (N), phosphorus (P), iron (Fe) and sulfur (S) are among the nutrients that have been reported to alter post-embryonic root developmental processes.

Nitrogen is one of the most abundant elements on earth. However, it is also the most critical limiting element for plant growth because of its low availability in the soil and because nitrate, the most common form of N fertilizer, is highly soluble in the soil solution and can be easily lost by leaching or by bacterial denitrification [1]. P is the second most critical factor in determining plant productivity because the anionic form of phosphate, in which P is assimilated by plants, is extremely insoluble in the soil solution. This insolubility is due to the affinity of P to cations such as Ca²⁺, Mg²⁺ and Al³⁺, and its ready conversion into organic forms that are not amenable to plant uptake. Micronutrients, such as Fe, that are required in small concentrations for plant growth can become very limiting elements under particular soil conditions [2]. The distribution of nutrients in the soil is not homogenous, with nutrients frequently being found in the upper layers. Hence, plants may enhance their nutrient acquisition by activating developmental programs that alter the architecture of the root system.

Changes in root architecture can mediate the adaptation of plants to soils in which nutrient availability is limited by increasing the total absorptive surface of the root system. The development of root systems is usually highly asymmetric and reflects the ability of roots to adjust their growth and development to environmental factors [3,4]. Here, we review recent evidence supporting the role of nutrients such as N, P, S and Fe as signals for the control of root development. Insights into the mechanisms by which nutrient availability controls the architecture of the root system are beginning to emerge.

Figure 1



Changes in epidermal cell differentiation in response to P and Fe stress in *Arabidopsis*. The deficiency of each of these nutrients induces the formation and elongation of root hairs. Epidermal differentiation that is induced by low Fe concentrations requires ethylene. This response is inhibited in mutants that are defective in ethylene signaling and in the auxin resistant *Arabidopsis* mutants *aux1*, *axr1* and *axr2*, suggesting possible crosstalk between the ethylene and auxin pathways. Epidermal changes that are induced by low P concentrations are not affected in the ethylene and auxin mutants, implying that this response is controlled by an independent pathway [12^{*}]. The P-response pathway may directly alter the expression of regulatory genes that control root-hair formation, such as *GLABRA2* (*GL2*), *ROOT HAIR DEFECTIVE6* (*RHD6*) and *WEREWOLF* (*WER*).

Effects of nutrient availability on epidermal differentiation

One of the most conspicuous changes in root architecture that results from nutrient deficiency is the induction of some epidermal cell files to form root hairs. For instance, under conditions of low P availability, root hairs become longer and denser (Figure 1; [5^{*},6]). The elongation of root hairs is regulated by P availability in a dose-dependent manner through the effects of P on the rate and duration of hair elongation [6]. Recent work in *Arabidopsis* has shown that P deprivation not only affects root-hair elongation but can also produce up to a five-fold increase in root-hair density. This effect is due to an increase in the number of epidermal cells that differentiate into trichoblasts [5^{*}].

Because the surface of root hairs can represent up to 70% of the total root surface area, the relevance of root hairs in nutrient uptake has long been subject to speculation. Comparisons of wildtype *Arabidopsis* and root-hair-less mutants have been used to demonstrate the importance of root hairs for P uptake [7,8]. Under limiting P conditions, the presence of root hairs on wildtype *Arabidopsis*

plants allowed better plant growth, biomass production, P uptake and reproductive output when compared to the root-hair-less mutant *root hair defective2* (*rhd2*). When P availability was high, however, the wildtype plants and root-hair-less mutants had similar growth patterns, P acquisition and fecundity [8]. These results demonstrate that root hairs confer a competitive advantage for plants when growing in soils that have limiting P availability, and may account for the genetic variation in nutrient acquisition reported among different *Arabidopsis* ecotypes [9,10].

Low iron availability induces morphological changes in root epidermal cells that are similar to those induced by P deficiency. When iron is limiting, root-hair formation and elongation increase (Figure 1). The extra root hairs that result from limiting iron availability are often located in positions that are occupied by non-hair cells under normal conditions [11]. Although Fe and P concentrations have similar effects on root-hair density, the analysis of auxin-response mutants suggests that changes in root-hair morphology in response to Fe and P are mediated by different signal transduction pathways [12^{*}]. When grown under

normal nutritional conditions, the roots of the *Arabidopsis* auxin-resistant mutant *auxin resistant2* (*axr2*) are almost completely devoid of root hairs. The formation and/or elongation of root hairs in this mutant does not change after transfer to Fe-free medium. However, this mutant develops normal hairs under P-deficient conditions [12[•]]. These results suggest that different pathways are involved in the induction of P- and Fe-stress-related alterations in root-hair development (Figure 1).

Effects of nutrient availability on root growth and lateral root development

Changes in nitrate and phosphate availability have been found to have contrasting effects on lateral root formation and elongation [13,14[•]]. In *Arabidopsis*, increasing nitrate availability reduces primary root elongation, whereas an increase in P supply has the opposite effect. Lateral root density remains constant across a range of nitrate concentrations, but is dramatically decreased with increasing phosphate supply. Lateral root elongation is suppressed by both high nitrate and high phosphate availability [14[•]].

Nitrate

The lateral roots of *Arabidopsis* show two contrasting responses to high nitrate. Uniformly high nitrate (10 mM) reduces lateral root elongation throughout the root system whereas, in plants grown on a low nitrate concentration (10 μ M), exposure of a section of the primary root to high nitrate induces a local stimulation of lateral root elongation [13]. The global inhibitory effect of nitrate seems to be a response to a nitrate sufficiency status because lateral root elongation under these conditions is inhibited even in regions of the root system that are growing in low nitrate concentrations.

Some of the components of the signaling pathways that regulate root-system architecture in response to nutrient availability have been identified. The *Arabidopsis* *NITRATE-REGULATED1* (*ANRI*) gene encodes a NO_3^- -inducible MADS-box transcription factor, which was isolated in a screen designed to isolate genes whose expression is induced by the presence of patches of high nitrate. The lateral roots of *ANRI*-antisense *Arabidopsis* lines do not respond to localized NO_3^- availability, demonstrating a role for *ANRI* in the root response to nitrate [13]. However, the lateral root growth of these plants is inhibited by globally high nitrate concentrations. The NO_3^- signal therefore appears to have two opposing effects on lateral root development: a localized stimulatory effect, which is mediated by *ANRI*, and a systemic inhibitory effect.

Interestingly, the auxin-response mutant *axr4* is unable to respond to a localized supply of nitrate, providing evidence of an overlap between the auxin and nitrate responses [15]. Signora *et al.* [16[•]] reported that the systemic inhibitory effect of NO_3^- is significantly reduced in three abscisic acid (ABA)-insensitive mutants

(*abi4-1*, *abi4-2* and *abi5*). These mutants have increased lateral root elongation in high nitrate concentrations, indicating that ABA plays a major role in mediating the inhibitory effect of NO_3^- on lateral root elongation.

A crosstalk between nodulation and lateral root development has been found recently in *Lotus japonicus*. *Lotus* plants that are mutated at the *HYPERNODULATION ABERRANTROOT1* (*HAR1*) locus have a hypernodulation phenotype in the presence of *Rhizobium* and increased lateral root formation in absence of this symbiotic bacterium. *HAR1* encodes a putative serine/threonine receptor kinase that has homology to the *Arabidopsis* protein CLAVATA1. *HAR1* is required for shoot-controlled regulation of root growth, nodule formation and the nitrate sensitivity of symbiotic development. It forms part of an as yet unknown signaling mechanism that integrates root development with events in the shoot [17^{••},18^{••}].

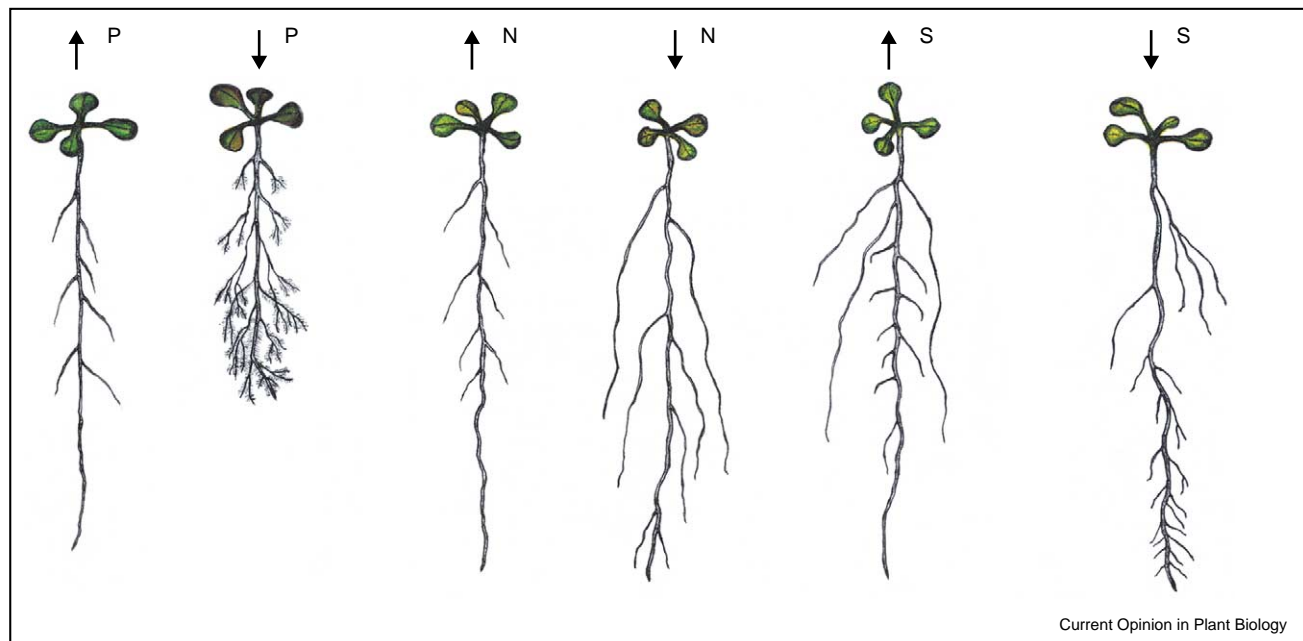
Phosphate

White lupin (*Lupinus albus* L.) is a legume that is well adapted for growth on infertile soils that limit the establishment of other plants, particularly soils with low P availability. For some time, white lupin has served as a model plant for studies of the effects of nutrient stress on root development [19[•]]. When exposed to low P conditions, the root system of white lupin forms proteoid roots, which are clusters of short lateral roots that arise from the pericycle and are specialized in P uptake [20]. These roots have determinate growth, that is, their root meristematic cells divide only for a limited period and then differentiate [20]. After just a few days of growth, proteoid roots become exhausted and form large numbers of root hairs [21]. The increased P-uptake capacity of proteoid roots relative to roots that have indeterminate growth is provided by their increased absorptive surface, increased exudation of organic acids and phosphatase, and possibly greater expression of P transporters [19[•],22].

Studies using *Arabidopsis thaliana* as a model system suggest that some of the root architectural responses to P availability that have been observed in lupines may be ubiquitous in the plant kingdom. Williamson *et al.* [23[•]] presented evidence that moderate concentrations of P favored lateral root growth over primary root growth. They showed that *Arabidopsis* seedlings grown in media containing 100 μ M P had increased lateral root density when compared to seedlings grown under a high P supply (2.5 mM). López-Bucio *et al.* [24[•]] reported that concentrations of P of less than 50 μ M in the medium had a dramatic effect on root architecture (Figure 2). The number of lateral roots was up to five times greater in plants grown in a limiting (1 μ M) P concentration than in plants supplied with optimal (1 mM) P.

The architecture of *Arabidopsis* plants that have been grown in low P concentrations resembles that of the

Figure 2



Responses of *Arabidopsis* root systems to different nutrient supplies. The root systems were grown in nutrient-rich media with or without a high concentration of P, N and S. P and S deficiency can dramatically alter primary and lateral root growth, modifying the overall root architecture [24*,31*]. Contrasting N availability may alter lateral root elongation [13,14*].

proteoid roots of lupins: lateral roots arise in close proximity to each other, have determinate growth and are densely covered by root hairs (Figures 1 and 3). Recently, we have found that low-P-induced determinate root growth in *Arabidopsis* is linked to the inhibition of root meristematic activity (L Sanchez-Calderón, A Cruz-Ramírez, J López-Bucio, L Herrera-Estrella, unpublished results). Kinetic expression studies, using the auxin-inducible reporter *DR5::uidA* [25] and the cell cycle marker *CyclinB1 (CycB1)::uidA* [26], have revealed that exhausted root meristems lose their ability to respond to auxin, a change that correlates with their decreased mitotic activity (Figure 3e,f). Anatomical and biochemical analyses have shown that low-P-grown mature roots lack a normal apex and have increased expression of P transporter genes (Figure 3g,h). By contrast, the roots of high-P-grown plants have high auxin concentrations in their meristems and their cells have high mitotic activity, which correlates with their reduced expression of genes that encode high-affinity P transporters. The low-P-induced pattern of root development seems to be directed towards increasing the P-uptake capacity of the *Arabidopsis* root system by modulating root architecture and by inducing the expression of several genes that are involved in P uptake.

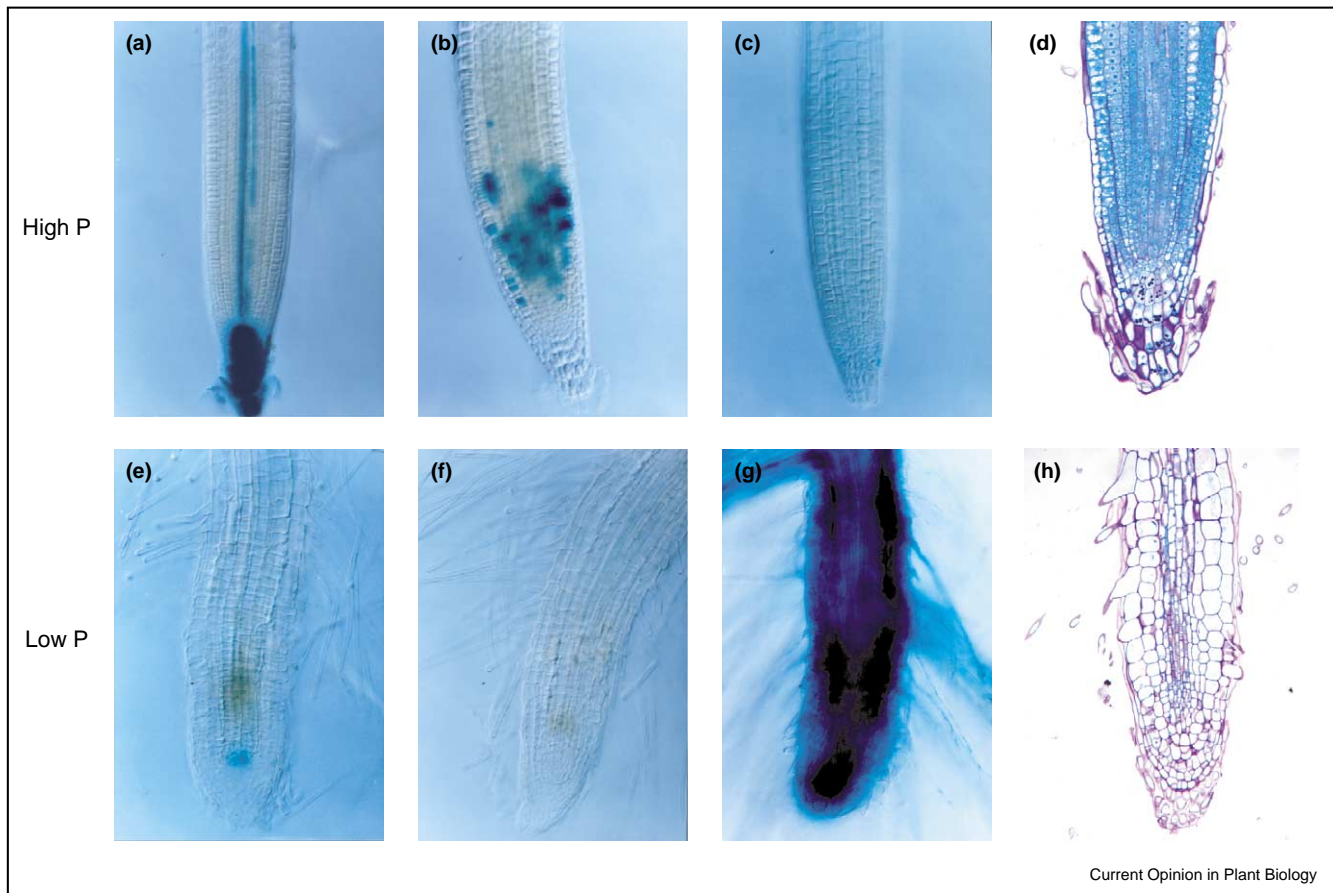
Despite extensive recent information on gene expression during P deficiency, little is known about the components of the signal transduction pathway that activates the P-starvation response [27–29]. Some progress in this field

has been achieved, however, by the isolation of the *phosphate response regulator1 (phr1)* mutant of *Arabidopsis*. This mutant has both an altered root/shoot growth ratio when grown under low P conditions and altered expression of low-P-regulated genes. The *PHR1* gene is related to the *PHOSPHORUS STARVATION RESPONSE1 (PSR1)* gene from *Chlamydomonas reinhardtii*, which encodes a member of the MYB family of transcription factors. Gel-retardation assays showed that PHR1 is able to interact with DNA sequences of low-P-regulated promoters, supporting a role for this protein in the P-starvation signaling pathway [30**].

Sulfate

Arabidopsis plants develop a branched root system when growing under limiting sulfate (SO_4^{2-}) conditions (Figure 2). In *Arabidopsis* seedlings grown on the surface of agar plates supplied with SO_4^{2-} , primary roots elongate and lateral roots develop at some distance from the root tip. By contrast, in plants starved of SO_4^{2-} , lateral roots are formed closer to the root tip and at increased density (Figure 2). The increased growth of the root system under SO_4^{2-} -limiting conditions has been related to the transcriptional activation of the *NITRILASE3 (NIT3)* gene, a member of the nitrilase gene family. Nitrilases are enzymes that are able to convert indole-3-acetonitrile to indole-3-acetic acid. SO_4^{2-} -deprived roots also have increased auxin levels, suggesting a direct role for NIT3 in auxin synthesis and root branching [31*].

Figure 3



Effects of P availability on auxin concentration, mitotic activity, P-transporter expression and root-meristem structure in *Arabidopsis* root tips. Expression patterns for (a,e) *DR5:uidA*, (b,f) *CycB1:uidA*, and (c,g) *pAtPT2:uidA* in the primary root tips of *Arabidopsis* plants grown under low (1 μ M) and high (1 mM) P concentrations. In root tips grown in low P concentrations, the expression of *DR5:uidA* reveals a dramatic decrease in auxin concentration, *CycB1:uidA* expression is inhibited and *pAtPT2:uidA* is highly expressed. (d,h) The meristem structure of primary roots of *Arabidopsis* grown in (d) high and (h) low P concentrations. *pAtPT2*, *Arabidopsis PHOSPHATE TRANSPORTER2 promoter*.

Role of hormones in the control of root architecture by nutrient signals

Plant growth regulators control most of the characteristics of root systems, including primary root growth and the formation of lateral roots and root hairs. Many plant species respond to the exogenous application of auxins by producing large numbers of lateral roots, and to auxins and ethylene by increasing the density and length of root hairs [32,33]. These findings suggest that root responses to nutrients may originate from hormonal signals that are triggered by specific nutrient pathways.

In white lupin and *Arabidopsis*, an important role for auxin transport in the formation of lateral roots has been recently demonstrated. The auxin-transport inhibitors 2,3,5-triiodobenzoic acid (TIBA) and N-(1-naphthyl)phthalamic acid (NPA) were found to inhibit the formation of proteoid or lateral roots in *Lupin* and *Arabidopsis*, respectively [24*,34]. These results show that auxins are

required for the formation of lateral roots under P-limiting conditions. It remains to be determined whether auxin concentration, transport or sensitivity is the key factor that is modified by nutrient availability. *Arabidopsis* plants growing under a limiting (1 μ M) P concentration are, however, more sensitive to auxins in terms of the inhibition of primary root elongation and increase of lateral root density [24*]. This suggests that changes in auxin sensitivity may play an important role in the effect of P deprivation on root-system architecture [24*].

Cytokinins suppress lateral root initiation in low-P-grown plants [24*]. Martin *et al.* [35] showed that the increase in the ratio of shoot/root growth that occurs in response to low P is paralleled by a decrease in cytokinin concentration. Exogenous cytokinins repressed the expression of low-P-regulated genes such as *Arabidopsis thaliana INDUCED BY PHOSPHATE STARVATION1 (AtIPS1)*, suggesting that these hormones not only control root

architecture but also control other aspects of the low-P rescue response.

Nutrient ions as signaling molecules for the regulation of root development

Root growth requires nutrients that are absorbed from the soil and photosynthates that are transported from the shoot. It has been proposed, therefore, that uneven nutrient availability could indirectly affect postembryonic root developmental processes by affecting local metabolic effects. This could explain the response of lateral roots from a nitrate-starved plant, which grow faster upon contact with a nitrate-rich region because of the abundance of nitrate and an increased consumption of photosynthates. Metabolic mechanisms are difficult to reconcile, however, with the stimulatory effect of P deprivation on lateral root growth and root-hair elongation.

It has been shown that metabolic mechanisms are not involved in the control of the *Arabidopsis* root-system response to nitrate. In *Arabidopsis* mutants that are deficient in nitrate reductase, and therefore unable to use nitrate as a nitrogen source, the local responses to high nitrate concentration still occur. This suggests that nitrate can act as a signaling molecule [13,15].

It has been shown in split-root experiments that the roots of P-sufficient plants develop a high density of long root hairs when exposed to media that contains low P concentrations. The effect of P deprivation is therefore local rather than systemic, and the plant can sense the lack of external P. Our research group has found that the effect of low P on lateral root elongation is also localized, supporting the notion that the lack of P is sensed locally in the *Arabidopsis* root system (MF Nieto-Jacobo, L Herrera-Estrella, unpublished results). Alternatively, this local effect could be the result of an inhibitory effect of a high external concentration of P on lateral-root and root-hair formation and/or elongation (Figure 1). In both cases, external P may be perceived in the root meristem and act as a signaling molecule. It will be of great interest to analyze mutants that do not induce root-hair and lateral root formation when growing in low P concentrations or mutants that show a constitutive P-deprivation response when growing in high P concentrations.

Conclusions

The use of model species such as *Arabidopsis thaliana* and *Lupinus albus* has extended our knowledge of the molecular mechanisms through which nutrient signals control root architecture. In general, the responses of root architecture to low nutrient availability seem to be ubiquitous in angiosperms, and may act to increase the efficiency of nutrient capture when nutrients are limiting. Novel information suggests the existence of nutrient-specific signal transduction pathways that interpret the external and internal concentrations of nutrients to modify root devel-

opment. Plant hormones, mainly auxins, cytokinins and ethylene, appear to be key factors in these nutrient-mediated pathways. The nutrient pathways may affect hormone biosynthesis, transport and/or sensitivity [15,24*,31*]. A few genes that control essential steps in the nitrate- and phosphate-signaling pathways have been identified. These include *ANR1* and *PHR1* from *Arabidopsis* and the *HAR1* gene of *Lotus japonicus*. The use of novel growth assays and genetic screens [36,37], in combination with reverse genetic approaches in *Arabidopsis* and other plants, will lead to the identification of more genes that act in these pathways. These techniques will also elucidate the nutrient-hormone signaling networks that control the responses of root architecture to nutrient availability.

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