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Review

Similarities and Differences in the Acquisition of Fe and P by Dicot Plants

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Abstract: This review deals with two essential plant mineral nutrients, iron (Fe) and phosphorus (P); the acquisition of both has important environmental and economic implications. Both elements are abundant in soils but are scarcely available to plants. To prevent deficiency, dicot plants develop physiological and morphological responses in their roots to specifically acquire Fe or P. Hormones and signalling substances, like ethylene, auxin and nitric oxide (NO), are involved in the activation of nutrient-deficiency responses. The existence of common inducers suggests that they must act in conjunction with nutrient-specific signals in order to develop nutrient-specific deficiency responses. There is evidence suggesting that P- or Fe-related phloem signals could interact with ethylene and NO to confer specificity to the responses to Fe- or P-deficiency, avoiding their induction when ethylene and NO increase due to other nutrient deficiency or stress. The mechanisms responsible for such interaction are not clearly determined, and thus, the regulatory networks that allow or prevent cross talk between P and Fe deficiency responses remain obscure. Here, fragmented information is drawn together to provide a clearer overview of the mechanisms and molecular players involved in the regulation of the responses to Fe or P deficiency and their interactions.

Keywords: iron; phosphorus; ethylene; nitric oxide; phloem signals

1. Fe and P Nutrition in Dicot Plants

Iron (Fe) and phosphorus (P) are two essential elements for plant growth [1]. Both elements are abundant in soils but with poor availability for plants. Dicot plants favour their acquisition by developing physiological and morphological responses in their roots [2–6].

The low availability of Fe in soils is mainly due to adverse soil conditions, such as high bicarbonate content, high pH, compaction, heavy metals and flooding. Some of these conditions are particularly frequent in calcareous soils, abundant in arid and semi-arid regions, in which the appearance of Fe chlorosis (internervial yellowing of young leaves due to a lack of chlorophyll) is one of the main problems [7]. Fe has low mobility in the phloem and barely translocates from the old tissues to the growing tissues and/or organs [1,8,9]. Therefore, the first visible symptoms of Fe deficiency occur in young leaves, while the older leaves remain green. If the deficiency conditions persist, necrotic areas may appear on the leaves [10]. With respect to P, it should be noted that the concentration of inorganic phosphate (Pi), the only form of P that can be absorbed by roots, is generally less than the amount needed for the optimal performance of crops [11–13]. This is mainly due to several properties of Pi,

such as reduced mobility, a susceptibility to form insoluble precipitates with cations like magnesium (Mg), calcium (Ca) and other metals, its fixation to organic soil compounds [14], and its adsorption on the surface of Fe oxides [15]. Plants that are P-deficient have a dark green color and often develop red or purple coloration due to the accumulation of pigments from the group of anthocyanins. In addition, they show clear symptoms of dwarfism, with short and thin stems when the deficiency occurs in the advanced stages of growth [16]. P, unlike Fe, is easily redistributed through the plant, moving from one organ to another, from the oldest leaves to the youngest ones, and to flowers and seeds. Consequently, P deficiency symptoms appear first in the mature leaves [16].

The functions performed by Fe in plants are related to its capacity to transfer electrons in a reversible way through changes in its oxidation-reduction state [1]. Fe participates in essential processes for plants such as photosynthesis, chlorophyll synthesis, respiration and nitrogenous nutrition. In addition, it acts as a cofactor in different enzymes involved in the elimination of reactive oxygen species, preventing the cell damage they can cause [1,17,18]. On the other hand, P participates in many important biological processes, including those related to the use of energy by the plant (it is a component of the ATP, among other energy molecules), the synthesis of nucleic acids, photosynthesis, respiration, glycolysis, the activation and deactivation of enzymes, in oxide-reduction reactions, in carbohydrate metabolism, in the fixation of nitrogen (N), and in the composition of biological membranes [1,12].

Plants, throughout evolution, have adopted a multitude of adaptive strategies to solve both Fe and P nutritional stresses. In dicots, some of the morphological and physiological responses induced by Fe or P deficiency in the roots, are similar, such as the formation of subapical root hairs, the formation of cluster roots, the acidification of the rhizosphere and the production and release of organic acids [4,5,19].

Depending on the mechanisms used to acquire Fe from the medium, two types of plants are distinguished: Strategy I (dicots and non-grass monocots) and Strategy II plants (grasses). This review is devoted to dicots (Strategy I plants) and for more details about Strategy II plants, the reader is referred to the review by Kobayashi and Nishizawa [20]. The main characteristic of Strategy I plants is the necessity to reduce Fe^{3+} to Fe^{2+}, by means of a plasma membrane ferric reductase, prior to its absorption through a Fe^{2+} transporter [20,21]. This Fe^{3+} reduction is mediated by a membrane ferric reductase (EC 1.16.1.17) encoded by the *FRO* gene, and Fe^{2+} uptake is mediated by a transporter encoded by the *IRT1* gene [21,22]. When grown under Fe deficiency, Strategy I plants induce several physiological and morphological responses in their roots, with the aim of facilitating Fe mobilization and uptake (Figure 1). The physiological responses include the enhancement of ferric reductase activity and Fe^{2+} uptake capacity, the acidification of the extracellular medium, the increased synthesis and release of organic acids, and the increased synthesis and release of phenolics and flavins to the extracellular medium [20,21,23–26]. These physiological responses are a consequence of the up-regulation of several Fe-related genes, such as *FRO* and *IRT1*, which are activated by specific bHLH transcription factors, like FIT, bHLH38, bHLH39 and others in *Arabidopsis*. Most of them are up-regulated by Fe deficiency in both roots and shoots, except FIT that is only up-regulated in roots [21,27,28]. FIT is also the master regulator of most of the Fe-related genes [21,28]. Besides these bHLH transcription factors, it has been found that MYB transcription factors, like AtMYB72 and AtMYB10, increase their transcription under Fe deficiency and are involved in the regulation of some responses [29,30]. Both are functionally redundant and are required for plant survival in alkaline soils where iron availability is greatly restricted. They play an important role in the release of phenolics to the rhizosphere, making Fe more soluble for plants [30]. AtMYB72 and AtMYB10 are implicated in the Fe deficiency induced up-regulation of *AtNAS4* which encodes NicotianAmine Synthase. The transport of Fe from the cells of the root to the vessels of the xylem is carried out complexed with nicotianamine. Nicotianamine is also implicated in the phloem loading and unloading of Fe [30,31]. Among the morphological responses to Fe deficiency are the development of subapical root hairs (Figure 1), of cluster roots and of root transfer cells [3,23,32].

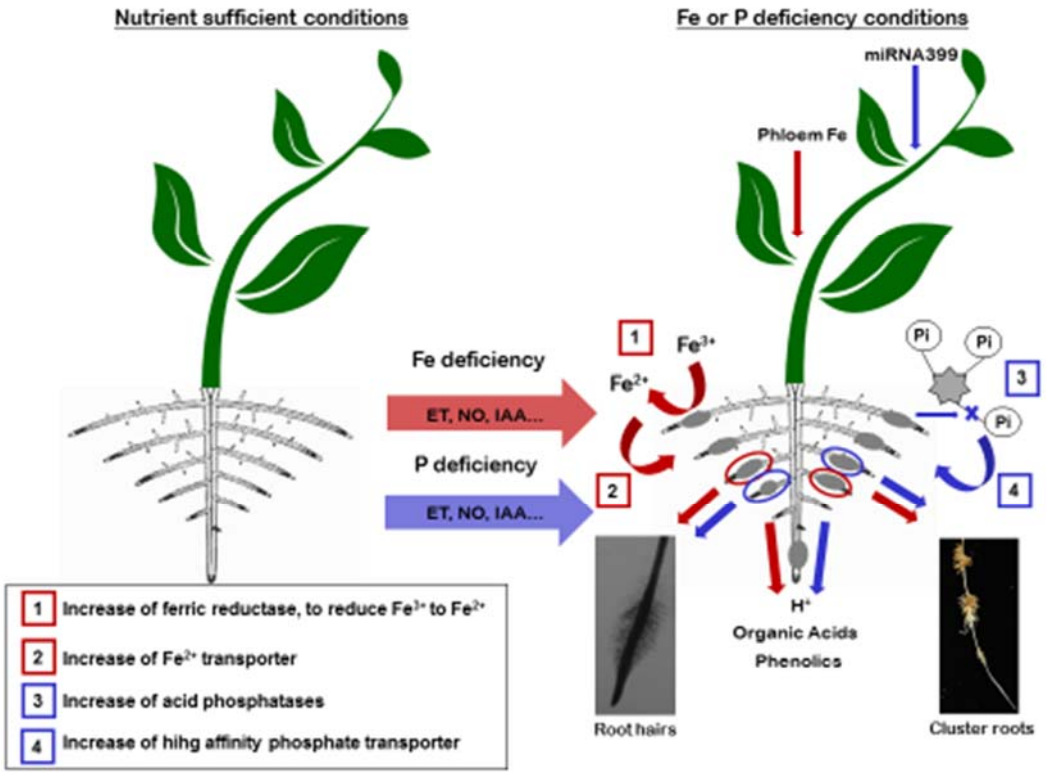

Figure 1. Overview of morphological and physiological responses to Fe (**red arrows**) or P (**blue arrows**) deficiency in dicot plants. The production of ethylene (ET), nitric oxide (NO) and auxin (IAA) is increased by roots of dicot plants under both deficiencies. These hormones up-regulate the expression of genes implicated in physiological and morphological responses to both deficiencies. Under Fe deficiency, dicot plants increase ferric reductase (1) and Fe^{2+} uptake through a Fe^{2+} transporter (2). Under P deficiency, dicot plants enhance the synthesis and release of acid phosphatases (3) and the P uptake through P transporters (4). Both deficiencies induce the acidification of the extracellular medium and the synthesis and release of organic acids and phenolics. In relation to morphological responses, both deficiencies can activate the formation of subapical root hairs and cluster roots. Besides ethylene, NO and IAA, long distance signals become very important in the regulation of the responses to both deficiencies. Phloem Fe could play a role in the inhibition of the expression of Fe acquisition genes in roots. Similarly, miRNA399, overexpressed under P deficiency, could affect P deficiency responses in roots.

P-deficient dicot plants also induce physiological and morphological responses in their roots to promote its acquisition (Figure 1). Some of the physiological responses include the up-regulation of phosphate transporters, like the one encoded by the *AtPT2* gene, also named *Pht1;4*, and enhanced phosphatase activity, like the one encoded by the *AtACP5* gene [2]. Arabidopsis thaliana ACP5 shares the characteristics of type 5 acid phosphatases [33], a class of purple acid phosphatases that is stimulated under low phosphorus availability. Recent studies have demonstrated that secretion of purple acid phosphatases can facilitate utilization of organic P in the rhizosphere [34–36]. Other physiological responses are the increased synthesis and release of organic acids, the up-regulation of ribonucleases, the accumulation of starch and anthocyanins, and the remobilization of internal phosphate [37–39]. The regulation of the physiological responses to P deficiency is not fully understood but in *Arabidopsis thaliana* L. it has been demonstrated that *AtPHR1* and *AtPHR2* ("Phosphate Starvation Response" 1 and 2, respectively), which encode transcription factors of the MYB family are crucial for signaling P deficiency [40–44]. Among the morphological responses to P deficiency are an increase in the root/shoot ratio [45,46] and changes in the root system architecture that is able to absorb

more phosphate, by reducing the growth of the primary root and promoting the appearance of secondary roots with a large amount of root hairs [45,47,48]. Species belonging to the families Proteaceae, Betulaceae, Casuarianaceae, Cucurbitaceae, Cyperaceae, Eleagnaceae, Leguminoseae, Moraceae, Myricaceae and Restionaceae, form proteoid roots when grown with P deficiency. Proteoid roots are clusters of short lateral roots that can excrete up to 20 times more organic acids than normal roots under conditions of P sufficiency [49–52]. Lupin (*Lupinus albus* L.) is one of the model plants for the study of these kind of roots [53].

In previous works, it has been found that Fe deficiency induces the expression of P-related genes, that P deficiency induces the expression of Fe-related genes, and that both deficiencies induce the expression of ethylene-related genes [2,4,54–57]. In addition, increased accumulation of Fe in leaves under P deficiency and of P under Fe deficiency has been found [14,37,56,58–62]. Moreover, P fertilization excess may cause Fe chlorosis in calcareous soils [63,64]. Taken together, all these results suggest the existence of crosstalk between Fe and P nutrition in dicot plants.

2. Hormones and Signaling Substances in the Regulation of Fe and P Deficiency Responses in Dicot Plants

In 1994, Romera and Alcántara [65] published a paper suggesting a role for ethylene in the regulation of Fe deficiency responses in Strategy I plants. At the same time, Borch et al. [66] showed the participation of ethylene in the regulation of P deficiency responses. At present, although the regulation of the genes related to these responses is not totally known, ethylene has been involved in the activation of both Fe acquisition-related genes (*AtFIT*, *AtFRO2* and *AtIRT1*; [3,4,67,68] and P acquisition-related genes [69,70]).

Although ethylene's mode of action is not fully understood, a signalling pathway has been proposed in *Arabidopsis* which includes the transcription factors EIN3 and EIL1 [71]. Both transcription factors are upregulated under Fe deficiency [29] and are involved in FIT stabilization and activity [72,73]. Recently, Son et al. [74], have shown that EIN3 directly binds to the promoters of genes, which are the targets of a key transcription factor that regulates root hair development under P deficiency. These results suggest that transcription factor EIN3 is involved in the responses to both Fe and P deficiencies.

In addition to ethylene, other hormones and signaling substances, such as auxin and nitric oxide (NO), have been involved in the up-regulation of Fe and P acquisition genes [3,4,29,68,75–81]. In both deficiencies, the activating effect of auxin, ethylene and NO depend on the Fe or P status of the plants [68,69,75,76], which suggests the existence of additional Fe- and P-related signals acting in conjunction with ethylene, auxin and NO [82]. In the case of Fe, the expression of Fe acquisition genes in plants grown with low levels of Fe was activated by auxin, ethylene and NO, but they have almost no effect in plants grown with high Fe levels [67,68,75,76]. This suggests that the activation of these genes does not only depend on hormones and signaling substances, like ethylene, auxin and NO, which act as activators, but also on the internal Fe availability, which would act as a repressor [67,68,83]. However, it has been suggested that the repressive signal is not the total Fe in roots, but a Fe signal related to Fe moving through the phloem [82]. There are different experimental results that support this view, some of them obtained with mutants altered in the transport of Fe in either xylem or phloem, which are briefly described in the following paragraph.

The *Arabidopsis frd3* mutant is impaired in the translocation of Fe through the xylem [84,85]. When grown under Fe-sufficient conditions it is chlorotic and with constitutive activation of Fe acquisition genes it accumulates a high Fe concentration in the roots [86]. In this mutant, the foliar application of Fe produces a regreening of the leaves, and at the same time, the down regulation of Fe acquisition genes in the root [67,82]. These results imply that the total Fe concentration in the root is not the repressive signal and suggest a role for a Fe-related signal, moving from the aerial part to the root through the phloem, in the inhibition of the expression of Fe acquisition genes in the root [67,68,82]. In the same way, our group has also published results on the effect of the foliar application of Fe on the *Arabidopsis opt3-2* mutant, which also shows a constitutive activation of Fe acquisition genes when

grown under Fe-sufficient conditions [82,87]. This mutant hosts a T-DNA insertion in the promoter of the AtOPT3 gene, which leads to the reduction of *AtOPT3* gene expression [87]. AtOPT3, whose expression is increased under Fe deficiency, belongs to the family of oligopeptide transporters (OPT), involved in the transport of peptides into the phloem [87,88]. The foliar application of Fe to the *opt3-2* mutant did not inhibit the expression of Fe acquisition genes in roots, as occurred in the *frd3* mutant and in the wild cultivar [82]. This suggests that the phloem Fe compound acting as a repressive signal could be a peptide (probably a Fe-peptide) transported by OPT3 [82,87]. However, recently it has been published that OPT3 could transport Fe ions into the phloem [89]. Even if these results are confirmed, it would not be ruled out that the Fe ions, once inside the phloem, could be bound to organic compounds to be transported. Taken together, the results obtained with the *frd3* and *opt3-2* mutants suggest that Fe availability, represented by a phloem Fe-related signal, could participate in the regulation of Fe acquisition genes in roots along with ethylene and other hormones [82,89,90].

Until recently, the involvement of ethylene in P deficiency has been limited to its role in the regulation of morphological responses, like the inhibition of the growth of the main root and the formation of lateral roots, proteoid roots and root hairs [66,91–96]. Nowadays, however, there is evidence that ethylene also plays an important role in the regulation of physiological responses to P deficiency, as is the case with Fe deficiency [5,69,70,97,98]. Using the P transporter gene, *AtPT2*, as a marker gene to identify mutants with alterations in the regulation of responses to P deficiency, Lei et al. [69] identified a mutant of *Arabidopsis thaliana*, *hps2*, which showed enhanced responses to P deficiency. This mutant exhibits increased *AtPT2* expression under P deficiency, due to the insertion of a T-DNA in the *CTR1* gene (involved in ethylene signaling; [59]). The application of ACC, the precursor of ethylene synthesis, increased *AtPT2* expression while the application of Ag^{+}, an inhibitor of ethylene action completely blocked it. Furthermore, these authors found that *AtPT2* expression was significantly reduced in the *Arabidopsis* ethylene insensitive mutants *in2-5* and *etr1-1* under conditions of P deficiency [69]. In addition to *AtPT2* (*Pht1;4*), the *AtPht1;1* gene, which encodes another transporter responsible for acquiring P from soil, also increased its expression under ACC (1-aminocyclopropane-1-carboxylic acid) treatment and reduced it with Ag^{+}, demonstrating that ethylene is involved in the regulation of the induction of both P transporters [69,97]. Similar results have been obtained with *Medicago falcata* L. plants: the induction caused by P deficiency in the expression of two P transporters (*MfPT1* and *MfPT5*), as well as that of the gene coding for an acid root phosphatase (*MfPAP1*), was clearly inhibited by treatments with AVG (aminoethoxyvinylglycine) and with Cobalt, both inhibitors of ethylene synthesis [99]. On the other hand, the application of ACC produced an increase in the expression of these genes in plants grown in a P sufficient medium [99]. Despite these results, several recently published studies present models of regulation of P deficiency responses where ethylene plays a relevant role but it should act in conjunction with other more specific P-related signals in the regulation of plant responses to this deficiency [69,97]. Again, a parallelism exists in the regulation of Fe and P deficiency responses, suggesting the existence of specific Fe- or P-related signals that interact with ethylene for their activation or suppression.

In supporting the role of specific P-related signals, two mutants of *Arabidopsis thaliana*, *pho1* and *pho2*, which cause failures in P homeostasis in plants, have been identified [100,101]. The P leaf concentration of the mutant *pho1* is very diminished while in the roots it has concentrations very similar to those of the wild cultivar, which suggests that this mutant has a defect in the loading of P into the xylem [100,102–104]. By contrast, the *pho2* mutant accumulates up to three times more P in the aerial part than the wild cultivar, while the root maintains similar levels, or even slightly lower levels than the wild cultivar [43,101,105,106]. The *pho2* mutant could either prevent the transport of P through the phloem, from the aerial part to the root, or have some problem in the regulation of P concentration in the leaves [107]. More recently, it has been shown that the *pho2* mutant lacks a E2 enzyme, which is involved in ubiquitination processes and signaling against P deficiency [104,106]. PHO2 is involved in the degradation of PHO1 via a ubiquitination pathway [106,108]. Micrografting experiments revealed that a *pho2* root genotype is sufficient to yield leaf P accumulation [43]. In the

pho2 mutant, P does not repress a set of P starvation-induced genes, including *AtIPS1*, *AtAT4*, and the Pi transporters *Pht1;8* and *Pht1;9* [43,101]. This suggests that *pho2* alters a P-related repressive signal coming from the aerial part to the root [43]. Other authors have demonstrated, by means of the foliar application of P to lupine plants, that a P-related signal coming from the aerial part represses the formation of proteoid toots and citrate exudation, independently of the concentration of P existing in the root [109].

In the case of P, the nature of the P-related signals, which interacts with ethylene and other hormones in the regulation of P deficiency responses in roots is still unknown. However, there are indications that one of these signals could be a microRNA [110,111]. MicroRNAs are small fragments of RNA that bind to target RNAs, which generally code for transcription factors, in order to degrade them or attenuate their translation to protein [112–116]. In plants, microRNAs are mainly involved in the regulation of growth and development, although their involvement in the regulation of plant adaptive responses to nutritional stresses has also been proven. They have the capacity to act as mobile long-distance signals through the phloem [117–120], and also play an important role in cell-to-cell signaling [121–124]. One of these microRNAs, miRNA399, is overexpressed under P deficiency and directly affects the regulation of P deficiency responses [110,113,114,125,126]. Buthz et al. [119] proposed miRNA399 as the long-distance P-related signal moving through the phloem and involved in the regulation of P deficiency responses in roots. There are models showing the interaction of miRNA399 with the PHO2-E2 enzyme described above, acting together in the signaling against P deficiency and playing an important role in the responses to P deficiency in *Arabidopsis thaliana* [103,106,108,114].

It should also be noted that besides ethylene, other molecules such as auxin, NO and cytokinins have been implicated in the regulation of P and Fe deficiency responses [3]. For example, auxin has been implicated in the production of proteoid roots under P deficiency [127–129]. Neumann et al. [130] found a significant increase in proteoid roots in P sufficient lupine plants on addition of the natural auxin IAA (indole-3-acetic acid), and other authors achieved similar effects after the addition of synthetic NAA (α-naphthaleneacetic acid) [131]. Recently, it has been suggested that IAA has a role as a signal coming from the aerial part and is involved in the regulation of Fe deficiency physiological responses in the roots of cucumber plants (*Cucumis sativus* L.) [77]. These authors, through the application of inhibitors of IAA transport and function, were able to inhibit the expression of Fe acquisition genes in roots, such as *CsFRO1* and *CsIRT1*, as well as the activity of ferric reductase, dependent on the *CsFRO1* gene. Another signaling substance that activates P and Fe deficiency responses is NO. The formation of proteoid roots, as well as the expression of the *LaSCR1* and *LaSCR2* genes, which are crucial for the formation of this type of roots, were induced after the application of GSNO (*S*-nitrosoglutathione), a NO donor, to Fe- and P-sufficient lupine plants [80]. Likewise, both the expression of the aforementioned genes and the formation of proteoid roots were inhibited after the application of cPTIO (2-4-carboxyphenyl-4,4,5,5-tetramethylimidazoline-1-oxyl-3-oxide), a NO scavenger, under P, Fe or P and Fe deficiency conditions [80]. P and Fe deficiencies not only share the same activating signals in their respective responses, but also repressive ones. Cytokinins were first found to be involved in the regulation of nutritional signaling responses in the early 1980s, when different studies showed that the level of cytokinins decreased in conditions of P and N deficiency [132,133]. In the case of P, it has been shown that the exogenous application of cytokinins represses the expression of P acquisition genes [134]. Recently, the same repressor effect of cytokinins was found in the expression of the Fe acquisition genes *FRO2*, *IRT1* and *FIT* [135]. All the above results clearly show that P and Fe deficiency responses share many common components besides ethylene.

3. Crosstalk among Fe and P Deficiencies

Several authors have shown that the induction of some Fe responses due to other nutrient deficiencies is common, although the responses to Fe deficiency are specifically induced under this deficiency. As an example, some Fe deficiency responses are up-regulated by K, S, P or Cu deficiency

in dicot plants [37,56,59,136,137]. On a reciprocal basis, it is also frequent that Fe deficiency conditions induce responses to other nutrient deficiencies. The common participation of similar signals, like ethylene, NO and auxin, in the induction of their responses, could be related to the existence of crosstalk among nutrient deficiencies (reviewed in [3]). According to this view, ethylene, besides P and Fe deficiency responses, is also implicated in the induction of responses to K deficiency [138], to S deficiency [139,140], and to other deficiencies ([3] and references therein). Recently, Rai et al. [141] demonstrated the potential roles of auxin and Zinc (Zn) in mediating local Pi deficiency responses of the root system during growth under different Fe regimes, supporting the existence of crosstalk between Pi, Fe and Zn for maintaining Pi homeostasis.

Plants can increase exudation of phenolics, citrate and protons; they can also induce changes such as proliferation of root hairs, cluster roots and an increased ferric reductase activity under P deficiency conditions, strongly resembling the Fe deficiency response of Strategy I plants [56]. Some Fe acquisition genes, such as *IRT1*-like, *FRO2*-like and *FIT*-like genes, are up-regulated by P deficiency in tomato, lupine and *Arabidopsis* plants ([37,59] and references therein; [56]). The higher Fe accumulation in leaves of P-deficient plants supports the up-regulation of Fe responses by P deficiency [61]. Reciprocally, there is also data showing up-regulation of P deficiency responses under Fe deficiency. For example, the tomato Pi transporter *SlPT1* was up-regulated in roots of Fe-deficient tomato plants [59].

Besides these positive and mutual influences among P and Fe deficiencies, P or Fe excess could negatively affect the responses to the other deficiency. For example, P excess can limit Fe acquisition under certain conditions ([64]; see effect of P on the availability of Fe and vice versa).

4. Effect of P on Fe Nutrition and Vice Versa

First, it should be highlighted that since the mid-twentieth century there has been a large increase in world agricultural production, associated with the use of more productive varieties, monoculture, and the use of pesticides and fertilizers. Sometimes the use of chemical products has been carried out without agronomic justification, leading to the appearance of environmental problems, such as the eutrophication of inland waters [142] and the loss of biodiversity [143,144]. In the more economically developed countries such as U.S., European countries, and more recently in China, where there has been a great intensification of agriculture during the last decades, P content in the soil is mainly an environmental problem [145]. Frequently, very high soil P levels are found, increasing the risk of eutrophication of water resulting from P losses due to erosion and runoff [146]. However, in low-resource agricultural systems, crop yields are limited by a P deficiency that affects 30% of the global arable land area [147]. In addition, the price of phosphate fertilizers has increased considerably in recent decades as phosphate reserves are rapidly declining [148,149].

Some studies have clearly shown the close relationship between Fe and P nutrition [14,60,61]. Misson et al. [60], as well as Hirsch et al. [14], demonstrated that Fe is one of the metals that exhibits higher levels of accumulation in chloroplasts of plants grown under P deficiency. Due to this Fe accumulation, the expression of genes linked to homeostasis and storage of Fe is induced, such as NAS3 (Nicotianamine Synthase 3) or AtFER1 (Ferritin 1), respectively. The induction of these genes suggests the existence of a global and concerted response of plants to P deficiency [14,60]. Ward et al. [61], working with the wild cultivar of *Arabidopsis thaliana* and with the *frd3* mutant, cited above, showed that plants grown under conditions of P deficiency present a significant inhibition of the main root growth as a result of the accumulation of high concentrations of Fe, which becomes toxic. This effect is reversed when the concentration of Fe decreases in the tissues. This supports the development of the plant and even improves the ability of the plant to acquire P. All these results suggest that the control of Fe/P interactions in plants could be a novel and very effective way to improve the P nutrition of crops [61]. At the soil level, the Fe oxides play a very important role in determining P availability in the soil. P is the least mobile and available element for plants [150] due to the great capacity of the P ions to react with the components in the soil, which determines its low solubility. In Mediterranean soils, the mineralogy and the type of reactions that occur further reduce

P bioavailability [15]. The presence of the different phosphate ions in solution is determined by the pH. The oxides of Fe and Al have a prominent role in the adsorption of P ions in soils of wide pH range [15,151], although the greatest absorption occurs when the pH decreases because this causes an increase in the positive charges of Fe and Al oxides [152]. The maximum capacity of adsorption of the different oxides are around 2.5 μmol P m^{-2} for non-crystalline oxides [153], which together with the high specific surface area (100–400 m^2 g^{-1}) and reactivity makes them the main sorbents of P [154,155].

The effect of P on the availability of Fe has been studied for several years. To our knowledge, the first results suggesting P as a factor in aggravating Fe chlorosis were presented by De Kock [58], who found a high P/Fe ratio in chlorotic leaves of different plant species. Brown et al. [156] observed that HCO_3^- increased P availability in soil and its intake by the plant, which negatively affected Fe acquisition. More recently, Sánchez-Rodríguez et al. [64,157], in studies carried out with plant species of different sensitivity to Fe chlorosis grown in calcareous soils, showed that phosphate fertilization alters the availability of Fe in the soil, generally aggravating Fe chlorosis in sensitive plants. This effect is variable, depending on the plant (strategy for acquisition of Fe, species and variety, age) and the content of available P and non-crystalline Fe oxides of the soil.

In contrast to these studies, a considerable number of researchers have not observed any appreciable negative effect of P in the Fe nutrition of plants. Some of these experiments have been done with plants grown in hydroponic culture and others with plants grown in calcareous soils to which different doses of phosphate have been applied. Thus, Mengel et al. [158] found high P concentrations in chlorotic leaves of vine cultivated in calcareous soil (with a considerable amount of P) and interpreted this as a consequence of Fe chlorosis instead of a cause. In this line, no relationship was observed between P excess and Fe deficiency in Mandarin [159] and vine [160,161] cultivated in experimental fields. Similarly, Romera et al. [162] did not observe Fe chlorosis in peach trees cultivated in nutrient solution with low Fe concentration and 10 mM phosphate concentration. These authors found an inhibition of the ferric reductase activity in sunflower and cucumber roots when the phosphate concentration in solution was increased but only in the presence of HCO_3^- [63]. There are also other experiments showing no effect of P on Fe nutrition. Samar et al. [163] studied the problem of Fe chlorosis in apple trees induced by excessive phosphate fertilization, a common problem in Iran. They used 'Delicious' apple trees grown in pots containing fertilized soil with doses of 1.5 and 3 g P kg^{-1}. After 2 years of the experiment, it was observed that this apple variety was not sensitive to high doses of P in the soil, as the leaf chlorophyll content, leaf surface or dry weight of leaves and roots were not affected. The effect of phosphate fertilization was also evaluated in *Prunus* by Balal et al. [164], using calcareous soils in which 0.12, 0.25, 0.74, 2.98 and 14.88 g P (as monoammonium phosphate) were applied per tree. The evaluated genotypes, 'GF677' and 'PP101', were not sensitive to Fe chlorosis induced by phosphate fertilization, and the first even increased trunk diameter, dry weight of leaves and length of shoots.

5. Conclusions and Perspectives

Nowadays, finding new alternatives to the use of P and Fe fertilizers is urgent in order to minimize their environmental impacts, and to lower costs for farmers due to the high prices of both fertilizer [165]. Fe and P are essential elements for plants and are closely interrelated. As examples, the induction of Fe chlorosis, under certain circumstances, could be a consequence of P overfertilization and the immobilization of P in soil could be due to its adsorption to Fe oxides. In addition, there are numerous works that show similarities between Fe and P deficiency responses, both in the type of responses and in their regulation and signaling. As several works have shown, a consequence of this relationship is the existence of induction of P deficiency responses by Fe deficiency and vice versa [2,4,54–56,103]. This is logical if one considers that there are hormones, such as ethylene, involved in the activation of responses to both deficiencies. This common implication of ethylene suggests that it must act in conjunction with other more specific Fe- or P-related signals, more intimately related to each deficiency. In this regard, it should be noted that our group has presented evidence suggesting

that a signal related to phloem Fe interacts with ethylene in the regulation of responses to Fe deficiency. The molecular mechanisms involved in the regulation of Fe and P deficiency responses are complex and not sufficiently understood.

Therefore, it is important to expand the knowledge about these mechanisms, and to identify the common and specific aspects of both deficiencies. The qualitative and quantitative evaluation of the expression along time of already known genes implicated in each of these deficiencies, will allow further investigation of the processes that regulate the responses to both deficiencies and a better understanding of the physiological and morphological responses that plants activate to cope with Fe or P deficiency. Given the close relationship between these two elements, it is necessary to fully understand the physiological and molecular bases of their interaction, to achieve adequate nutrition for both elements and avoid the problems associated with their inappropriate use.

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