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PLANT PHOSPHORUS USE EFFICIENCY IN ACID TROPICAL SOIL

Abstract – Phosphorus is an essential macronutrient for plant growth and development. However, phosphorus availability is low in many soils, and the plant's ability to acquire phosphorus from the rhizosphere is critical in the acid soils of the Brazilian Cerrado. In addition, high levels of fixed phosphate (Pi) in many soils reduce the phosphorus availability to the plants. Thus, Pi deficiency is a significant concern for crop growth and high yields in tropical soils. The intra- and interspecific variations in plant growth under Pi-limiting conditions are complex traits controlled by many induced or suppressed genes, comprising an intricate epistatic regulatory network interacting within cells and the external environment. The microRNA genes (miRNAs), a class of regulators that induce, degrade or repress mRNA transcription and translation, are another critical aspect of this network. As a result, changes in morphology (growth and root architecture) and physiological (enzymes, organic acids, and anthocyanin) can be observed in plants under Pi stress. Furthermore, symbiotic associations with phosphate-solubilizing bacteria and mycorrhizal fungi increase the phosphorus availability to plants. Therefore, understanding the mechanisms involved in plant adaptation to phosphorus deficiency is critical for developing cultivars adapted to low phosphorus levels in the Brazilian Cerrado. This review addresses the molecular mechanisms controlling P-acquisition and P-use by plants and discusses its implications in genetic breeding programs.

Keywords: Pi-use efficiency, microRNAs, Pi transporters, acid soils

EFICIÊNCIA NO USO DE FÓSFORO PELAS PLANTAS EM SOLOS TROPICAIS ÁCIDOS

Resumo – O fósforo é um macronutriente essencial para o crescimento e desenvolvimento das plantas. Contudo, a capacidade das plantas de adquirir fosfato (Pi) da rizosfera é crítica nos solos ácidos do Cerrado brasileiro. Além disso, altos níveis de fosfato fixado no solo reduzem a disponibilidade de fósforo para as plantas. Portanto, a deficiência de Pi é uma das principais preocupações para o crescimento das cultura e altos rendimentos em solos tropicais. As variações intra e interespecíficas na capacidade da planta de crescer sob condições limitantes de Pi é um caráter complexo, controlado por muitos genes induzidos ou suprimidos, formando uma intrincada rede regulatória epistática interagindo com as células e o ambiente externo. Outro aspecto crítico dessa rede, consiste nos genes reguladores microRNA (miRNAs), que induzem, degradam ou reprimem a transcrição e tradução do mRNA envolvidos na absorção e uso de Pi. Como resultado, mudanças na morfologia (crescimento e arquitetura radicular) e fisiológicas (enzimas, ácidos orgânicos e antocianinas) podem ser observadas em plantas sob estresse de Pi. Além disso, associações simbióticas com bactérias solubilizadoras de fosfato e fungos micorrízicos aumentam a disponibilização de fósforo para as plantas. Portanto, o amplo conhecimento dos mecanismos envolvidos na adaptação de plantas à deficiência de fósforo é essencial para o desenvolvimento de cultivares adaptadas aos baixos níveis de fósforo nos solos ácidos brasileiros. Esta revisão aborda diferentes aspectos da aquisição e uso de Pi pelas plantas e discute suas implicações nos programas de melhoramento genético.

Palavras-chave: Eficiência no uso de fósforo, microRNAs, transportadores de fosfato, solos ácidos

Sustainable food production focusing on plant adaptation to stressful environments are a continued priority for developing countries with increasing populations (FAO, 2016). The tropical savannas encompass some of the oldest soils globally and represent 850 million hectares of the earth's terrestrial surface distributed in Africa, South America, and Asia Pacific regions (Pennington et al., 2018). Low fertility, pH, and Pi availability contrasted with high Pi sorption capacity, and toxic aluminum (Al) levels are dominant in these soils. These naturally degraded and infertile acid soils are the principal factors limiting food production in many countries throughout the tropics. This area contains 58 percent of the world's land suitable for agriculture and supports 73 percent of the world's population (ONU, 2017). In addition, a vast tropical area with non-acid soils and low fertility shows low Pi levels due to soil degradation caused by natural factors and human activity. Nevertheless, over the past three decades, more than 20 million hectares of approximately 204 million hectares of the acid savanna in the central region of Brazil have been brought under sustainable crop production (Rausch et al., 2019). In acid soils, soluble phosphorus is readily fixed by clay, iron (Fe), and Al minerals, which reduce the P-availability for plants. Due to the fixation processes, phosphorus mobility is restricted in most soils (10^{-12} – 10^{-15} m^2/sec^{-1}) and stays close to its place of origin or application (Nascimento et al., 2018). Also, crops rarely absorb more than 20 percent of P fertilizer in the first year after application, and the fixed, residual phosphorus remains in the rooting zone and becomes slowly available to succeeding crops.

Tropical soils are phosphorus-deficient

Phosphorus (P) is a vital macronutrient for the metabolism and growth of all organisms (Kamennaya et al., 2020). It plays a central role in virtually all major metabolic processes in plants, including photosynthesis and respiration. Plants preferentially absorb phosphorus from the soil in its fully oxidized anionic form ($H2PO_4^{2-}$; orthophosphate; Pi). At neutral pH, phosphate exists in about equal parts as mono- and divalent anion, contributing to the buffering capacity of the cytoplasm (Weil and Brady, 2017; Fabiańska et al., 2019).

Phosphorus deficiency and aluminum toxicity are the primary concern for crop growth and high yields in acidic soils. Toxic aluminum levels restrict root growth and plant development by reducing the Pi-availability and uptake of nutrients. The fixed forms of phosphorus are relatively stable in the soil and hence unavailable to plants. In addition, plants differ in their ability to use many of the chemical forms of phosphate. As a result, plants experience many morphological, physiological, and biochemical changes to cope with Pi deficiency (Vasconcelos et al., 2020). These changes, plus symbiotic relationship with bacteria and fungi, represent adaptive strategies to increase phosphorus release from the fixed pools in the soil, enhancing the Pi uptake rate and Pi-use by plants (Raghothama, 1999). In the last decades, many studies have demonstrated genetic differences in Pi acquisition efficiency in maize, sorghum, and many other crops cultivated in marginal soils (Parentoni, 1999; Vasconcelos et al., 2020; Vasconcelos et al., 2021).

Phosphorus is a limiting plant nutrient

Phosphate (Pi) is the second most limited essential plant macronutrient, next to nitrogen. Most of the world's Pi occurs in insoluble mineral forms unavailable to plants, and the amount of Pi required for plant growth is greater than the concentration of Pi generally found in most soils (<10 µM) (Plaxton & Shane, 2015).

Many factors, including the parent material, degree of weathering, and climatic conditions, influence the phosphorus content in the soil (Hanyabui et al., 2020). In addition, soil phosphorus levels are significantly affected by erosion, crop removal, and phosphorus fertilization (Alewell et al., 2020). Organic phosphorus, found in plant and animal residues, manures, and microbial debris, is the dominant form of Pi in many soils. Soils with low organic matter content may contain only 3% of their total phosphorus in the organic form, while in organic-rich soil, this value may reach 50% or more (Sukitprapanon et al., 2021). Inorganic forms of phosphorus in soil consist of apatite complexes of iron and aluminum phosphates and phosphorus adsorbed on clay particles. Approximately 80% or more of the applied Pi becomes immobile owing to adsorption, precipitation, or conversion in organic forms (Holford, 1997). Therefore, phosphate present in the organic matter, mainly as phytic acid, must be converted to inorganic forms before available to plants (Balaban et al., 2017). In contrast, elevated uptake of poorly mobile nutrients results in Pi depletion zones around the roots (Giehl & von Wirén, 2014). The contrast between the root peripheral environment with low Pi concentrations (<10 µm) and high Pi concentrations (5-20 mM) generate a steep concentration gradient between soil and plant, making plant Pi uptake strictly an energy-mediated process (Chang et al., 2019).

Plant Pi deficiency symptoms

Plants growing under phosphate deficiency conditions develop several phosphate deficiency symptoms (Meng et al., 2021). The reduction of shoot growth and root proliferation with altered root architecture is the most significant symptoms of Pi deficiency in plants (Niu et al., 2013; Grover et al., 2021). Plant adaptation to Pi stress preserves the Pi content of leaves by lowering the shoot growth but favoring the Pi uptake by enhancing the root growth (Plaxton and Carswell, 2018). Paul and Stitt (1993) correlated a marked increase in root/shoot ratio of Pi-limited tobacco plants with the preferential maintenance of root invertase activity relative to leaves. A high invertase activity effectively draws carbohydrates into the roots by converting the incoming sucrose into free hexoses. This increased sink strength due to the increased sucrose translocation from leaves to roots in P-deficient plants is a significant factor driving the enhanced root growth (Paul & Stitt, 1993).

Plants obtain phosphorus from the soil through the roots. Thus, the primary and lateral root growth inhibition, enhancement of root hair development, and cluster root formation are the main alterations in root morphology necessary to promote Pi acquisition (Niu et al., 2013). Plants produce adventitious roots in the topsoil during Pi limitation while making local changes in lateral root length in Pi-rich patches of subsoil (Liu, 2021). Under Pi deficiency, plants develop

supernumerary root hairs, transfer cell-like walls enriched with mitochondria and rough endoplasmic reticulum, and extensive wall ingrowth depositions in the rhizodermis along their outer periclinal walls. In addition, plants starved for phosphorus show decreased stomatal conductance and CO_2 assimilation. The purpling of leaves with anthocyanin-darkened veins and the remobilization of Pi from shoots (mature and senescence leaves) to sink (young leaves and inflorescences) is another usual symptom of plant Pi-deficiency (Vasconcelos et al., 2018; Chang et al., 2019).

The role of Pi in metabolic regulation

Phosphorus is a pivotal element in many biological processes in all living organisms. It is an essential component of nucleic acids and cellular membranes and plays a central role in photosynthesis, energy conservation, carbon metabolism, cell signaling, and catalyst in many biochemical reactions (Bang et al., 2021). Phosphorus improves crop quality by stimulating plant growth and development, flowering and seed set, and disease resistance. Plants evolved a range of sophisticated metabolic and developmental strategies to enhance the Pi acquisition and remobilization under low Pi availability (Begum et al., 2019). As a plant matures, phosphorus is translocated to the rapidly expanding reproductive organs, where high energy is required to form seeds (Veneklaas et al., 2012). Thus, phosphorus deficiency late in the growing season affects both seed development and crop maturity.

Influence of Pi stress on secondary metabolism

The accumulation of secondary aromatic metabolites, like anthocyanins, flavonoids, and indol alkaloids, is typical of cells experiencing Pi deprivation (Vasconcelos et al., 2018). Anthocyanins play a vital role in ultraviolet light absorption preventing nucleic acid and photoinhibition damages to chloroplasts during Pi-limited photosynthesis. In Arabidopsis plants growing under Pi limitation, typical Pi-deficiency symptoms such as stunted shoots with dark green leaves are easily observed (Bang et al., 2021). Cobbina and Miller (1987) found that reduced Pi concentration results in higher anthocyanin content in shoots, irrespective of Pi concentration, and concluded that the intensification of purple coloration, even though similar anthocyanin contents is possibly due to reduced chlorophyll content in the leaf epidermis.

In addition, a sequence of aromatic pathway reactions recycles a significant amount of Pi from various phosphate ester molecules (Poirier and Bucher, 2002). Also, the differential expression of plastidial and cytosolic isoforms of DAHP synthase (D-ribosylantranilphosphate synthase) in response to Pi availability suggests enhanced carbon flux and Pi release in the cytosol, but not in plastids during Pi limitation (Lynch et al., 2017). However, the function and molecular basis of the phosphate starvation-inducibility of various enzymes involved in aromatic biosynthesis remains poorly understood.

Roots exudates: Secretion of organic acids as a response to phosphate deficiency

Root-induced chemical modifications in the rhizosphere may involve the mobilization and exploitation of sparingly soluble sources of soil P. Depending on the predominant type of Pi fraction in the soil; the Pi solubility can be increased by root-induced acidification (Ca-P) or alkalinization (Al-P, Fe-P) of the rhizosphere (Gérard et al., 2017). In addition, in some plant species, citric acid, frequently detected in root exudates, can mobilize Pi by ligand exchange, dissolution, and occupation of Pi sorption sites (Zhao et al., 2021). However, little is known about the factors that contribute to the differences in the plant's ability to excrete carboxylic acids and protons in response to Pi deficiency.

During Pi deficiency, the roots secret organic acids in acid and calcareous soils (Pantigoso et al., 2020). As a result, Pi is released from Ca-P sources by citric acid-induced rhizosphere acidification leading to intensive chemical extraction of Pi in a limited volume of soil (Dinkelaker et al., 1989). In addition, under Pi-deficiency, white lupin excretes citric acid into the rhizosphere, leading to the dissolution of CaCO3 and promoting the Pi extraction from Ca-P compounds and precipitation of calcium citrate near to the roots (Dinkelaker et al., 1989).

Plants experiencing Pi deficiency release more organic acid from roots than Pi-sufficient plants. The increased synthesis of organic acid in Pi-deficient roots is correlated with the increase in the phosphoenolpyruvate carboxylase (PEPCase) and malate dehydrogenase (MDH) activity (Desai et al., 2014). Indeed, the up-regulation of PEPCase accompanied by increased activity of malate dehydrogenase and citrate synthase has been observed during Pi deficiency in many plant species (Plaxton and Carswell, 2018). Labeling of shoots and roots with $^{14}CO_2$ revealed that PEPCase in proteoid roots provided up to one-third of the carbon required for synthesizing the excreted citrate and malate during Pi deficiency (Johnson et al., 1996). However, the mechanisms regulating PEP (Phosphoenolpyruvate carboxylase) partitioning between primary and secondary metabolism remains poorly understood.

Development of proteoid roots in plant response to phosphate deficiency

In the non-mycorrhizal plants from the Proteaceae family, which are dominant in soils where the Pi availability is deficient, are a range of root specializations (proteoid, clustered, and dauciform roots or capillaroid sand-binding roots) to mine the soil Pi (Lambers et al., 2006). This group also produces highly branched bottle-brush-like clusters of rootlets covered with abundant root hairs. The increased production of proteoid by plants augments the surface area of the roots exposed to soil particles and promotes the acquisition of immobile nutrients.

The proteoid root cells efficiently produce and secrete organic acids and phosphatases, which permit these proteoid-rooted plants to grow in soils with poorly available nutrients (Dinkelaker et al., 1989; Johnson et al., 1996; Gallardo et al., 2020). Proteoid roots have also been shown to be the site of organic-acid biosynthesis, exudation, and phosphatase activity (Johnson et al., 1996). In addition, these modified roots excrete citrate,

which would acidify the rhizosphere and thereby increase the solubilization of mineral Pi from the environment (Dinkelaker et al., 1989). The release of organic acids by active proteoid root cells consists of two separate transport processes: an active H^+ efflux driven by plasma membrane H^+-ATPase and a passive efflux of organic anions mediated by channel-like transporters (Canarini et al., 2019). It has also been demonstrated that proteoid roots of white lupin excrete citric acid into calcareous soils, resulting in intensive chemical extraction of Pi within a limited root zone area. Auxin was shown to be partially responsible for the initiation and development of proteoid roots during the P-deficiency response in white lupin (Gilbert et al., 2000). Auxin inhibitors reduce proteoid root formation under P-deficient conditions but do not affect root development in plants under Pi-sufficient conditions (Liu, 2021). Increased root growth and proteoid root formation allow plants to access Pi in new soil regions, and carbon-rich compounds exuded by the roots may attract beneficial soil organisms or directly mobilize soil P (Pascale et al., 2019).

Phosphatases: A significant component of plant adaptation to Pi deficiency

Plants carry out phosphorus requirements by absorbing phosphorus anions from the soil. In nature, about 3% of the total soil organic P in the arable soils may be found in the microbial biomass and 5 to 24% in the grassland soils (Brookes, 1984). However, the various forms of soil organic phosphorus are unavailable to plants. Thus, the organic form of P in soils must be mineralized to be available for plants (Huang et al., 2018). Plants developed *many* adaptive mechanisms, such as phosphatase-mediated hydrolysis, to cope with persistent Pi deficiency in the soil (Hummel et al., 2021). Acid phosphatases secreted by the roots hydrolyze organic-P compounds in the rhizosphere, increasing the P availability for plants growing under Pi deficient conditions (Adamczyk, 2021).

Both intracellular and extracellular phosphatases production increases during Pi starvation (Zhu et al., 2020). The intracellular phosphatases produced in shoots and leaves are likely to recapture P from organic phosphorus compounds in the intracellular matrix and may also be involved in scavenging Pi from xylem-derived phosphocholine (Zhou et al., 2021). Changes in specific isoforms of plant phosphatases under Pi starvation are commonly observed (Zhu et al., 2020). In plants of tomato, the control of extracellular phosphatase synthesis associated with the cell wall is a repression-derepression process mediated by the Pi concentration in the root cells.

Soil phosphatases from microbial, animal, and plant sources play a significant role in the mineralization processes of organic P substrates (Tian et al., 2021). Microbial oxidation of organic substrates represents an important supplementary source of inorganic phosphate for plants. Due to their large biomass, high metabolic activity, and short lifespans, microorganisms are responsible for most of the phosphatase activity in the soil (Balota and Chaves, 2010). This effect is strongly influenced by changes in organic matter content and the microbial population. The phosphatase activity in the rhizosphere tends to be high because of the

increased microbial numbers and the excretion of enzymes by the plant root.

Mycorrhiza association: the efficient mechanism for plant phosphorus acquisition

The mutually beneficial association between mycorrhizal fungi and plant roots is an essential adaptation for increasing the Pi acquisition by plants (Begum et al., 2019). In this symbiotic relationship, the fungus acquires carbon from the root, and the plant uses the excess of Pi acquired by the fungus. As a result, the plant-fungus interaction dramatically increases the root absorptive surface area and promotes plant growth, while the least amount of photosynthate is transferred to the fungus. Thus, mycorrhizae is universally favorable to plants, and it was estimated that more than 90% of the plants are dependent on this symbiotic association to acquire Pi from the rhizosphere (Campos et al., 2018).

Roots infected by mycorrhizal fungi can account for three to five increments in Pi influx than non-mycorrhizal roots because roots infected by mycorrhiza form an arbuscule, where only small gaps exist between the plasma membrane of the plant and fungal cells (Srivastava et al., 2021). Two energetic transport steps are required for Pi to enter the plant. First, the mycorrhizal fungus must take the Pi up from the soil solution, and later, the cells of a plant must transport it from the space between membranes in the arbuscule. The arbuscular Mycorrhizae (AM) fungi colonize the root of plants and extend their hyphae out of the root into the surrounding environment accessing soil pores that root hairs cannot do due to their smaller diameter (20-50 um) (Campos et al., 2018). Thus, the external hyphae access Pi from the soil from relatively distant locations and make it available to plants. The efflux of Pi acquired by the fungus at the mycorrhizal-plant interface supply the plant demand for phosphorus; in turn, the fungus obtains carbon from the plant root. In AM symbiosis, the fungal hyphae extend between the root cells and form tuft-like branched structures (arbuscules) within the cell lumina that act as the functional interface for Pi exchange (Jain et al., 2007).

The high-affinity fungal phosphate transporters (GvPT and GiPT) have a similar structure and function to the plant phosphate transporters (Versaw and Harrison, 2002). Plant Pi starvation-inducible genes are down-regulated by mycorrhizal colonization (Tian et al., 2017). The downregulation of Pi starvation-inducible genes could be due to P-supply to the plant or carbon demanded by the fungus. However, the phosphate transporter of *Medicago truncatula* (MtPT4), potato (StPT3), and the rice (OsPT11) were shown to be absent in non-mycorrhizal roots but strongly induced during AM symbiosis, indicating their role in symbiotic phosphate uptake (Paszkowski et al., 2002). Various studies have shown that plants could respond differently to diverse AM species at the level of colonization, nutrient uptake growth, and gene expression (Begum et al., 2019). For example, colonization of *Medicago truncatula* by *Glomus mosseae* resulted in a significant reduction of MtPT2 and Mt4 expression and higher P uptake and plant growth. However, the plant colonization by Gigaspora rosea showed the highest levels of MtPT2 and Mt4 gene expression and lowest P

uptake and growth.

Pi acquisition by plants thorough rhyzosphere and endophytic Bacteria and fungi association

Soil communities of P-solubilizing bacteria and fungi (PSM= P solubilizing microorganisms) and phosphate mineralizing bacteria are ubiquitous in the soil environments. PSM solubilizes inorganic phosphorus from organic and inorganic sources by releasing phosphatase enzymes and low molecular weight organic acids into the soil (Balota and Chaves, 2010). Thus, PSM plays a vital role in plant nutrition in acid soils by enhancing P availability to roots by solubilizing and mobilizing scarce minerals containing Fe, P, K, and Mg (Tian et al., 2021). Nowadays, PSM is one of the most important traits associated with plant phosphate nutrition. Thus, the plant-PSM association represents a feasible emerging class of technology to improve phosphorus acquisition by crops in acid soils (Abreu et al., 2017).

High-affinity phosphate transporters for plant Pi acquisition

The ability of plants to respond appropriately to nutrient availability significantly affects their adaptation to the environment. Plants have developed sophisticated mechanisms to survive under Pi-limited conditions (Raghothama, 1999; Srivastava et al., 2018).

The plant roots acquire phosphorus by an energy-mediated cotransport process driven by a proton gradient generated by plasma membrane H+-ATPase. The kinetic characterization of the plant Pi uptake system indicates a high-affinity transport activity operating at a low concentration (micromolar range) and a low-affinity activity operating at a higher concentration of Pi. The low concentration of Pi in soil solution suggested that high-affinity transporters are primarily involved in Pi uptake by plants (Raghothama et al., 1999).

Phosphate transporters enabling proton-coupled Pi transport have been isolated from many plant species. These Pi transporters have been classified into five families: Pht1, Pht2, Pht3, Pht4, and Pht5. Most high-affinity Pi transporters were predicted to localize to the plasma membranes and translocate Pi from the external media containing deficient levels of nutrients into the cytoplasm (Raghothama, 2000a,b; Li Y. et al., 2019). The amino acid identity among the Pi transporters indicates that the high-affinity phosphate transporters are highly conserved in plants (Raghothama, 1999). The high-affinity phosphate transporters family Pht1 comprises seven clades (Li Y. et al., 2019). They have a similar structure with 12 membrane-spanning regions, separated into two groups of six, each containing a sizeable hydrophilic region. The family of Pht1 genes is predominantly expressed in the roots, although some members are expressed in shoots. Pht1 genes are induced in response to Pi deficiency and transcriptionally repressed in the medium supplied with Pi (Raghothama, 2000a). Detailed analysis of the various phosphate transporters using reporter gene constructs revealed their expression in diverse tissues, indicating that they are involved in soil Pi uptake and Pi translocation within the plant. Various studies demonstrated the transcriptional regulation of Pi transporters by Pi stress and

suggested that plants share common regulatory mechanisms in activating genes involved in the Pi starvation response (Raghothama 2000a; Li D. et al., 2019; Yadava et al., 2021).

The Pht2 is another family of low-affinity phosphate transporters involved in the loading of Pi within the shoots and expressed constitutively in plants (Raghothama, 2000b). The gene Pht2:1 is expressed in the leaves, and an experiment with green fluorescent protein fusion showed that the Pht2:1 transporter is localized in the chloroplast membrane (Versaw and Harrison, 2002). In addition, four cDNA clones encoding mitochondrial phosphate transporters (MPT) from soybean, maize, rice, and Arabidopsis were well characterized. The deduced amino acid sequences of MPTs predicted the existence of six highly conserved membrane-spanning domains with a tripartite structure consisting of three repeated segments with two transmembrane α-helices (Kuan and Saier, 1993). These transporters belong to the superfamily, including pyruvate and citrate carriers and uncoupling protein (Kuan and Saier, 1993).

Molecular mechanisms controlling Pi-Uptake by plants

The plant Pi-use efficiency is a complex trait controlled by many induced or suppressed genes, forming a regulatory network. This network interacting with the cellular and external environment is highly influenced by epistatic interactions (Vasconcelos et al., 2021). Thus, the molecular mechanisms underlying genotypic differences in plant Pi uptake from P-deficient soils have been the subject of scientific effort in the last

decades (Vasconcelos et al., 2018; Kumar et al., 2021). Major and minor QTLs associated with P-deficiency were recently identified in cereal crops (Anis et al., 2018). Major QTLs for relative shoot dry weight (RSDW) and relative root dry weight (RRDW) were mapped in chromosome 12 of rice, as well as several minor QTLs on chromosomes 1, 6, and 9 (Ni et al., 1998). Recently, Anis et al. (2018) confirmed the rice data and reported other QTLs associated with low Pi tolerance on chromosomes 2, 3, 4, 5, and 10. A QTL mapping of rice population, developed from a cross between Indica landrace 'Kasakath' (high Pi uptake) with the japonica cultivar Nipponbare (low Pi uptake), demonstrated that about 80% of the variation between both genotypes was due to a single QTL which they referred as Pup1 (Phosphorus uptake 1) (Wissuwa and Ae, 2001). In sorghum, Bernardino et al. (2019) identified QTLs on chromosomes 3 and 7, a homolog of the rice OsPSTOL1 gene coding for a serine/threonine kinase. Those QTLs improve the Pi uptake under low-Pi availability and determine the root morphology and grain yield. For further insight into the role of SbPTs in sorghum Pi-efficiency, near-isogenic lines (NILs) from a cross between the genotypes 101B and 136B have been developed at Embrapa Maize and Sorghum Research Center in Brazil (Vasconcelos et al. 2021).

microRNAs: Another intricate P regulatory network in plants

microRNAs (miRNAs) genes and their transcripts represent another vital aspect of plants'

intricate P regulatory network. These molecules constitute a class of gene expression regulators through post-transcriptional mRNA degradation or translational repression. A large amount of evidence accumulated in the last decades has shown the relationship between miRNAs and the response of organisms during different types of stressful situations. In plants, miRNAs are essential in adaptive responses to different types of biotic and abiotic stresses (Gu et al., 2016). MicroRNAs (miRNAs) function as critical regulators of nutritional stress signaling genes (Kumar et al., 2017). The miR399 and miR827 microRNAs regulate Pi homeostasis (Li D. et al., 2019; Ding et al., 2020). Secco et al. (2013), analyzing the expression pattern of miRNA genes in roots and leaves of rice cultivated under conditions of Pi absence and sufficiency, identified 20 miRNA families that had not yet been associated with phosphorus stress. These authors also determined that the miR399 microRNA marks for degradation its target mRNA encoding the enzyme Ubiquitin (E2PHO2), responsible for the negative regulation of genes involved in the plant response to P (Fujii et al., 2005).

Altered gene expression in response to plant phosphate starvation

Plants have evolved to survive under almost every climate and environmental condition. However, due to the sessile nature of almost all plants, they cannot move to a more favorable environment. Thus, many environmental variables impose significant stresses limiting plant growth and development. The ability of a plant to respond appropriately to nutrient availability is of fundamental importance for its survival in adverse environments. The altered expression of many genes is a remarkable plant response to Pi-stress. Thus, understanding molecular mechanisms of phosphorus uptake is essential for gene manipulation aiming at high-yield crops. The advent of DNA microarray technology has made possible the analysis of global gene expression patterns and revealed unexpected regulatory networks of many cellular processes (Chen et al., 2014). These breakthroughs technologies raised the scientific community's interest in deciphering the intricate interactions among cellular metabolic pathways and the control of metabolic fluxes in microbes, animals, and plants. Evaluations of the expression of thousands of genes in parallel by microarray analysis served as an essential tool in functional genomics, and expression profiles of genes with unknown functions have enabled scientists to assign their putative functions. Concerning phosphorus, studies using microarray technology have reported the transcriptional regulation of phosphate-responsive genes (Yadava et al., 2021).

Genetic variation and development of phosphorus-efficient genotypes

The dwindling supply of rock phosphate reserves and growing demand for increased food production reveal the urgent need to develop new cultivars for phosphorus use efficiency. The traditional and molecular techniques associated with management strategies are feasible approaches to producing Pi-efficient plants. Under
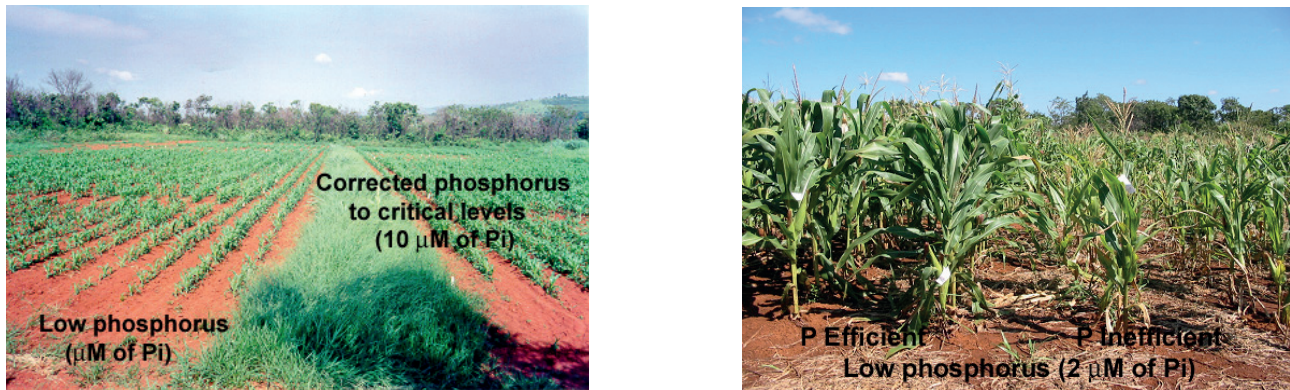
Figure 1. Sorghum and maize genotypes responsiveness to phosphorus stress in dark red oxisols with low and high phosphorus levels (Parentoni, 1999).

Pi stress, morphological and physiological changes can be measured to select Pi-use efficient plants in breeding programs (Figure 1). Using a molecular approach, Mitsukawa et al. (1997) reported that the overexpression of the Arabidopsis high-affinity phosphate transporter gene (*Pht1*) in tobacco increased the Pi uptake and the biomass of transgenic cells under Pi starvation.

Conclusions

Phosphorus availability in soils and P-use efficiency is a bottleneck for plant growth and development. Acid soils with poor Pi content and high levels of fixed Pi represent enormous challenges for crop breeding. Plant Pi-uptake and Pi-use efficiency are complex traits composed of several genes controlled by microRNA genes, and symbiotic associations between plants and phosphate-solubilizing bacteria and mycorrhizal fungi increase. These interactions form an intricate network of positive and negative feedback within cells and the external environment.

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