



Role of soil abiotic processes on phosphorus availability and plant responses with a focus on strigolactones in tomato plants

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Abstract

Background Phosphorus (P) is an essential nutrient for plant growth, taking part in primary cellular metabolic processes as a structural component of key biomolecules. Soil processes as adsorption, precipitation, and coprecipitation can affect P bioavailability, leading to limited plant growth and excessive use of P fertilizers, with adverse impacts on the environment and progressive depletion of P reserves. To cope with P stress, plants undergo several growth, development, and metabolic adjustments, aimed at increasing P-acquisition and -utilization efficiency. Recently, strigolactones (SLs) have emerged as newly defined hormones that mediate multiple levels of morphological, physiological and biochemical changes in plants as part of the P acclimation strategies to optimize growth. Therefore, understanding the soil processes affecting P availability and P acquisition strategies by plants can contribute to improved agronomical practices, resources optimization and environmental protection, and the development of plants with high P use efficiency for enhanced agricultural productivity.

Scope In this review, we discuss the range of abiotic processes that control P retention in soil and how

different concentrations or degrees of P bioavailability can trigger various responses in plants, while critically highlighting the inconsistent conditions under which experiments evaluating aspects of P nutrition in plants have been conducted. We also present recent advances in elucidating the role of SLs in the complex P signalling pathway, with a special focus on what has been discovered so far in the model plant tomato (*Solanum lycopersicum* L.).

Keywords Phosphorus · Strigolactones · Soil abiotic stabilization · Adsorption · Precipitation · Coprecipitation · Tomato · Model crop · Plant responses · Root exudation · Root architecture · P transporters · Enzymatic activity · Phosphatase · Phytase

Abbreviations

AMF	Arbuscular mycorrhizal fungi
InsP6	Inositol hexaphosphate
Pi	Inorganic phosphate
Po	Organic phosphorus
PSR	Phosphorus starvation response
PSI	Phosphorus starvation induced
SL	Strigolactone

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Introduction

Phosphorus (P) is one of the essential macronutrients required by plants for their growth and development

(Vance et al. 2003). It constitutes about 0.2% of the plant's dry matter, participates in primary cellular metabolic processes like photosynthesis and respiration, and is a structural component of key biomolecules such as sugar phosphates, nucleotides and nucleic acids, phospholipids, and energy-rich compounds, in particular adenosine triphosphate (ATP) (Abel et al. 2002; Aziz et al. 2014; Czarnecki et al. 2013; Marschner 1995; Schachtman et al. 1998; Vance et al. 2003). It also contributes to cellular signalling cascades by functioning as a mediator of signal transduction (Ha and Tran 2014).

The extensive use of P-based fertilizers in conventional agronomic practices has significantly fostered plant productivity, enabling agricultural production to support the exponential growth of the human population (Cordell et al. 2009). However, the majority of the P supplied through fertilizers is no longer bioavailable after application due to soil abiotic processes such as adsorption, immobilization, precipitation and coprecipitation, making P one of the most immobile, inaccessible, and unavailable among nutrients (Holford 1997; Niu et al. 2013; Richardson et al. 2009). Phosphorus limitation is estimated to affect crop productivity in over 40% of arable land (Vance 2001). Excessive use of P fertilizers to overcome this problem, coupled with low P utilization efficiency by plants, has resulted in large reserves of residual P in many arable soils (Bouwman et al. 2017). This has led to the progressive exhaustion of phosphate rock reserves and increased costs of P fertilizers, on one hand, and, on the other hand, to detrimental effects on the environment. In fact, a considerable amount of P applied to soil is subjected to erosion and runoff, with transfer from soil to waterbodies, causing algal blooms in lakes, river and coastal waters, as well as the formation of dead zones. All of these issues highlight the unsustainability of the current use of P (Ha and Tran 2014; Rothwell et al. 2020).

Plants have developed a plurality of strategies to cope with P deficiency, including a more efficient use of internal P through P recycling, modifications of the root system architecture traits, physiological adjustments and symbiotic interactions with arbuscular mycorrhizal fungi (AMF) intended to increase P acquisition from the soil (Dixon et al. 2020 and references therein). In recent years, a number of new signalling players and networks have emerged to regulate these responses (Rouached et al. 2010). In particular, several studies have established a major role for strigolactones (SLs),

a group of carotenoid-derived compounds, as signalling molecules that trigger morphological, physiological and biochemical responses associated with plant acclimation to P shortage (Czarnecki et al. 2013 and references therein; Trasoletti et al. 2022). Experimental evidence supports the role of SLs as early modulators of plant response to low P availability. They are able to influence the expression of key regulatory genes and P transporters, and alter the metabolic profile of plants to improve their resilience to P limitation (Gamir et al. 2020). Low or suppressed transcription of SL biosynthetic or signalling genes can affect several plant processes, such as leaf senescence, root growth, and shoot branching (Ito et al. 2015; Koltai et al. 2010b; Yamada et al. 2014). Additionally, SL-deficient or SL-insensitive mutants are hypersensitive to a number of adverse conditions like salinity, nutrient deficiency, drought and osmotic stress, meaning that SLs positively regulate abiotic stress tolerance (Chi et al. 2021; Ito et al. 2015; Santoro et al. 2020, 2021; Yamada et al. 2014; Zheng et al. 2021; Zulfiqar et al. 2021). In this context, it has been shown that exogenous SL act as a biostimulant by increasing plant tolerance to combined water and nutrient stress (Kalozoumis et al. 2021). These effects are associated with the differential activation of other hormone signalling pathways, highlighting the pivotal and interconnected regulatory role of SLs in the adaptive response to plant stresses (Barbier et al. 2021; de Saint Germain et al. 2013; Ito et al. 2017; Jiu et al. 2022; Koltai et al. 2010a, b; Koltai 2011; López-Ráez et al. 2008; Puga et al. 2017; Wang et al. 2022; Yang et al. 2019; Yoneyama et al. 2007a, b, 2012).

To address the challenges of climate change and environmental pollution, a better understanding of the regulatory network behind the activation of plant responses to P limitation can provide novel strategies for developing crops with improved P use efficiency. Among horticultural crops, tomato (*Solanum lycopersicum* L.) is one of the most valuable and widely consumed globally, and represents the cornerstone for biological research on genetic improvement of solanaceous species (Ercolano et al. 2012; López-Ráez and Bouwmeester 2008). In recent years, tomato has emerged as an important model species for research on SLs, leading to the generation of several tomato mutants with altered SL traits. The major SLs produced by this crop have been identified, and it has been established that there is a rapid surge in SL

biosynthesis within its roots as a response to P starvation (Gamir et al. 2020; Kohlen et al. 2012; López-Ráez et al. 2008; Marro et al. 2022; Rial et al. 2019; Vogel et al. 2010). Furthermore, tomato displays a strong P starvation response, characterized by the increase of root/shoot ratio and the secretion of acid phosphatases.

The targets of tomato breeding programs vary widely by location and individual needs, but often focus on enhancing yield, fruit quality, and resistance to pests and pathogens rather than improving nutrient use efficiency (Bai and Lindhout 2007). Nevertheless, using tomato cultivars with high P-use efficiency could allow for the same yield with a lower P input or higher yield with the same amount of P (Bera et al. 2020). Optimizing traits associated with or selecting P-efficient genotypes may promote better P mobilization in soil that would otherwise remain unavailable (Bera et al. 2020).

The purpose of this review is (i) to provide a comprehensive overview of the P processes within the soil–plant system, encompassing a wide range of abiotic processes responsible for the retention of inorganic and organic P in soil, including novel mechanistic insights into the coprecipitation phenomenon, and (ii) to discuss how these processes form soil P fractions that are largely unavailable for plants, thereby eliciting distinct plant responses to cope with P deficiency. Indeed, variation of P concentration in the soil solution during plant growth can lead to remarkably diverse outcomes even within the same plant species. Within the context of this review, we focused our attention on tomato as it serves as an ideal model for investigating the intricate relationship between SLs and the plant's response to P starvation. By examining these responses in tomato, we can gain valuable insights that can be extrapolated to other crop species. Moreover, through the evaluation of the specific mechanisms by which SLs participate in the signaling pathways triggered by P deficiency, we aim to shed light on their fundamental role as early modulators in the adaptive response of plants to P deprivation.

Soil abiotic processes controlling P bioavailability

The distribution, dynamics, and availability of P in soil are controlled by a combination of biological, chemical, and physical processes. It is crucial to

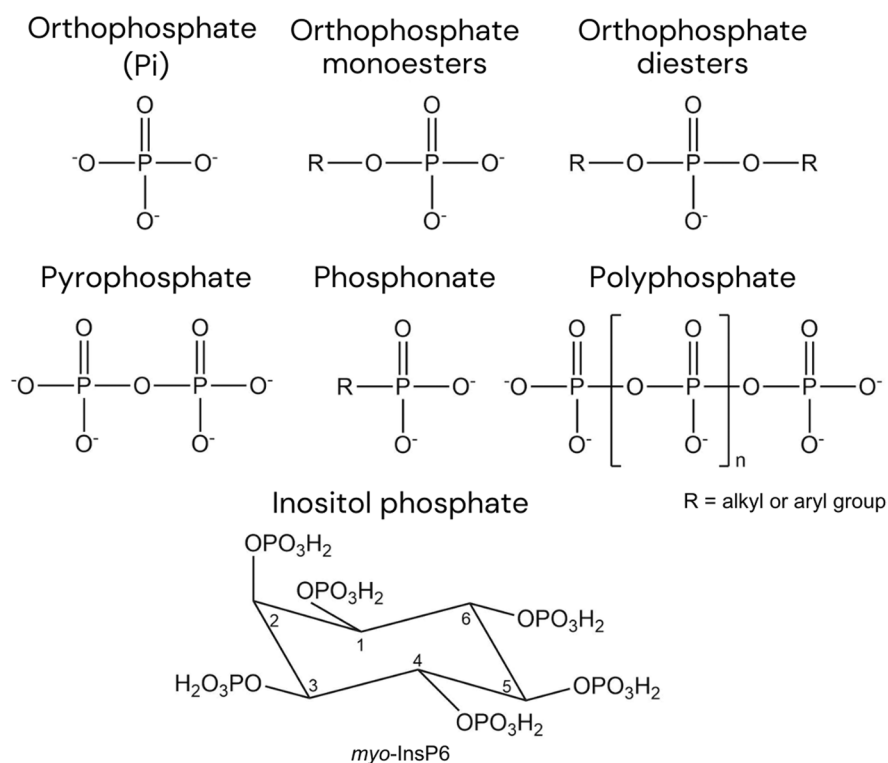
understand these processes since a significant proportion of the P applied to croplands undergoes transformation into forms that are either unavailable or sparingly accessible (Giles et al. 2011). Indeed, soils globally contain a large amount of total P (roughly $90\text{--}200 \times 10^{15}$ g, Liu et al. 2008 and references therein), but only a small proportion of it is immediately available for plant uptake under most soil conditions (Dixon et al. 2020), accounting for around 2500×10^{12} g of P globally (Liu et al. 2008 and references therein). Fertilizers contribute to a minor fraction, approximately 15–20%, of the total P content in plants, while the majority of P is derived from soil P reserves (Johnston and Steen 2000).

The primary source of P for plants is inorganic phosphate (Pi), in the form of orthophosphate ion (Fig. 1). The typical Pi concentration in the soil solution (0.1 to 10 μM) is substantially lower than the P requirement of plants (Frossard et al. 2000; Hinsinger 2001; Raghothama 1999), which varies across different species, ranging from several μM to tens of μM for highly demanding species, such as tomato (Hinsinger 2001 and references therein). Thus, at any given time, the soil solution holds only about 1% of the P required to sustain optimal plant growth, highlighting the need for a continuous replenishment of the element from the inorganic, organic, and microbial P pools in the soil, as P is continuously taken up by plants and microorganisms (Emsley 1980).

Primary P minerals, such as apatites, strengite, and variscite, constitute a very stable pool of P, and therefore the release of P from them is generally insufficient to meet crop demand (Shen et al. 2011). Nevertheless, research has demonstrated that the direct application of phosphate rocks can be relatively efficient in sustaining crop growth, particularly in acidic soils (Liu et al. 2008; Shen et al. 2011). Secondary P minerals including calcium (Ca), iron (Fe), and aluminum (Al) phosphates vary in their dissolution rates depending on mineral particles size and soil pH, and serve as an alternative source of P for plants (Shen et al. 2011).

In addition to P derived from primary and secondary minerals, which make up 35 to 70% of soil total P (Harrison 1987), various organic forms of P (Po) are also present (Fig. 1). The amount of Po depends on factors like vegetation type and climate, and it can account for 20 to 80% of the total P in the soil (Jarosch et al. 2015). Consequently, the Po pool holds

Fig. 1 Orthophosphate (inorganic phosphate, Pi) structure and generic structures of organic P forms (based on Cademenu 2005). For inositol phosphate, the stereoisomer myo-inositol hexakisphosphate (*myo*-InsP6) is represented, in the 5-equatorial-1-axial conformation



the potential to serve as a significant source of P for plants, despite the slow release of phosphate by hydrolysis. However, this process can be accelerated by phosphatase and phytase enzymes present in the soil (Liu et al. 2008 and references therein).

Acidic soils tend to accumulate more total Po than alkaline soils due to the reaction of organic phosphates with Fe and Al, which renders them insoluble (Harrison 1987). The resulting salts or metal complexes of phosphate esters release phosphate slowly through hydrolysis. At later stages of soil development, P is transformed progressively into less-soluble Fe and Al associated forms, causing the Po contents of the soil to decline (Stewart and Tiessen 1987).

Recent advances in analytical chemistry, especially synchrotron-based X-ray absorption near-edge structure (XANES) and solution nuclear magnetic resonance (NMR) spectroscopies have greatly enhanced our understanding of P speciation at the molecular level (Fig. 1, Liu et al. 2017). A considerable portion of Po in many soils exists as stereoisomers of inositol hexakisphosphate (InsP6), with most inputs from plants being in the form of *myo*-inositol hexakisphosphate (*myo*-InsP6, Fig. 1), a storage compound of P in seeds.

It is believed that the *neo*- and *scyllo*-stereoisomers are of microbial origin (Jørgensen et al. 2011; Liu et al. 2018), while the origins, dynamics, and biological function of the *D-chiro*-stereoisomer remain unknown, due in large part to analytical limitations in its measurement in environmental samples (Turner et al. 2012). Orthophosphate diesters, labile orthophosphate monoesters, and organic polyphosphates (Fig. 1), represent less stable forms of Po, that are likely present in the soil solution, where they can be readily degraded by biological processes (Celi and Barberis 2005; Condon et al. 2015; Turner et al. 2002).

All organic forms of P exist in complex equilibria with Pi (Fig. 2), forming a mixture of stable, sparingly available P, and plant-available P pools, such as labile P and soluble P. The relative sizes of the sources and stocks of P in the soil change as a function of soil development and, over time, the Po pool becomes the primary reservoir, especially in tropical soils, due to the insolubility and chemical stability of organic phosphates (Condon and Tiessen 2005). Inositol phosphates, in particular, make up over 60% of the soil orthophosphate monoesters and are the most common organic P species in mineral

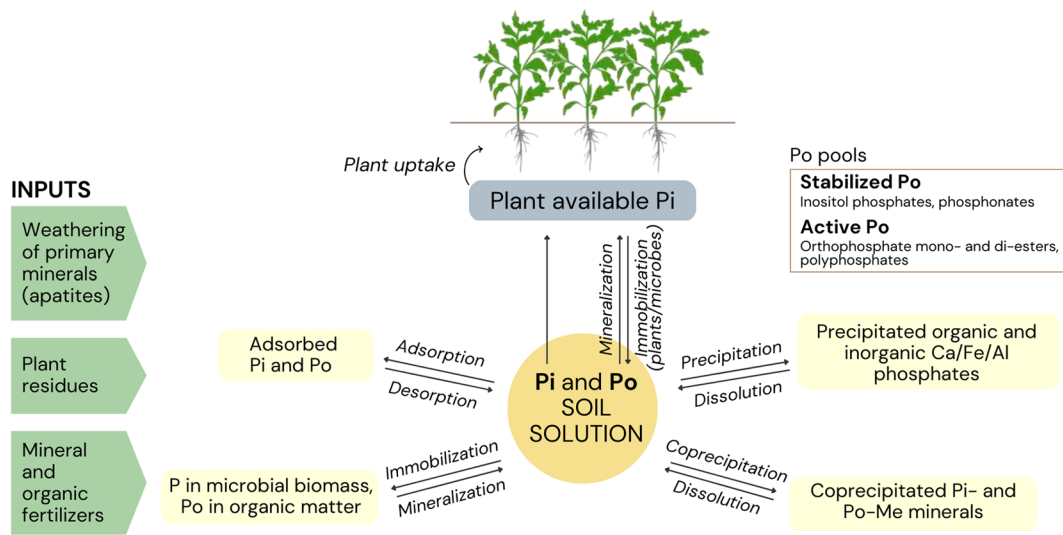


Fig. 2 Phosphorus processes in the soil/rhizosphere-plant continuum (based on Kruse et al. 2015 and Shen et al. 2011). Me, metal; Pi, inorganic phosphate; Po, organic phosphorus

soils (Celi and Barberis 2007; Sims and Pierzynski 2018; Turner et al. 2002). This enrichment can also be attributed to soil microorganisms driving P immobilization in organic P compounds, and their subsequent mineralization to Pi (Dixon et al. 2020; Hinsinger 2001; Turner 2006). As a result, inositol phosphates are selectively enriched in soil relative to more labile P monoesters and diesters, such as glucose-1-phosphate, DNA fragments and phosphoglycerides (Darch et al. 2014; George et al. 2018; Magid et al. 1996).

Adsorption

Phosphorus strongly binds to the surfaces of Fe and Al (hydr)oxides, which are present in soil as positively charged nano- to micro-particles across a wide range of pH (3–8). Adsorption is a major process controlling P speciation and one of the most important rate-limiting factors of P release in soils. With aging, the adsorbed P may be occluded within nanopores of Al and Fe (hydr)oxides, further becoming unavailable to plants (Arai and Sparks 2007; Giaveno et al. 2008; Hauduc et al. 2015; Luengo et al. 2006).

The degree of P adsorption strongly depends on environmental factors (pH, ionic strength, P concentration in solution) and on the chemical and physical

properties of the sorbent phase. These properties include mineral composition, functional groups, stability, particle size, porosity, specific surface area. One crucial parameter that determines the adsorption efficiency is the distance between the singly coordinated –OH groups on the adsorbent surface, which should match the –OH distance in the P molecule (Celi et al. 2020). From the point of view of the adsorbed molecule, it was shown that the adsorption affinity of different P compounds for soil mineral surfaces can be ranked in the following order: inositol phosphates > phosphate > glucose phosphates > DNA > phospholipids (Arai and Sparks 2007; Celi and Barberis 2007; Elzinga and Sparks 2007; Giles et al. 2011; Johnson et al. 2012; Li et al. 2016; Mallet et al. 2013).

In acidic soils, inorganic and organic P are adsorbed on the surface of Al and Fe (hydr)oxides, such as gibbsite, ferrihydrite, hematite, and goethite, by forming various surface complexes (Celi et al. 1999, 2020; Parfitt 1989). Iron and Al (hydr)oxides, in particular, are known to retain more inositol phosphates than other minerals, and poorly crystalline forms are responsible for retaining the majority of P in soils (Celi and Barberis 2007; Jiang et al. 2015; Turner et al. 2007). Ferrihydrite, a poorly crystalline Fe oxide, is one of the most efficient P-retaining Fe (hydr)oxides, due to the small size of its particles,

which provides a large surface area for P adsorption (Celi et al. 1999, 2003; Chen et al. 2020; Giaveno et al. 2008; Johnson et al. 2012). In the case of Pi, the non-protonated and protonated bidentate complexes on the surface of ferrihydrite (Fig. 3) may coexist at pH 4 to 9, while the protonated bidentate inner-sphere complex is predominant under acidic soil conditions (Atkinson et al. 1974; Arai and Sparks 2001; Elzinga and Kretzschmar 2013; Persson et al. 1996). The formation of bidentate mononuclear and monodentate mononuclear complexes has also been proposed, with varying degrees of protonation but weak bond energy (Persson et al. 1996). In the case of Al (hydr)oxides, Pi adsorption is characterized by a maximum at pH 4.0 (Huang et al. 2009 and references therein; Tanada et al. 2003), and the process is highly selective for Pi even in complex solutions and involves ion-exchange

between Pi and the –OH groups on the surface of the mineral (Tanada et al. 2003).

Both inner- and outer-sphere surface complexes can play a role in the stabilization of Po in soil (Celi and Barberis 2005; Chen et al. 2020; Johnson et al. 2012; Ognalaga et al. 1994; Ruyter-Hooley et al. 2015; Yan et al. 2014). For a long time, the association between inositol phosphates and poorly crystalline Fe (hydr)oxides minerals was considered the most important reason for the stabilization of inositol phosphates in soils (Fig. 3, Celi et al. 1999, 2001, 2003; Celi and Barberis 2005). Indeed, the high anionic charge density of these molecules enables their interaction with positively charged surfaces (Fuentes et al. 2014; Giaveno et al. 2008). In this regard, Chen and Arai (2019) observed that the phosphate groups P1, P3 and P2 of *myo*-InsP6 (cfr. Figure 1) contribute

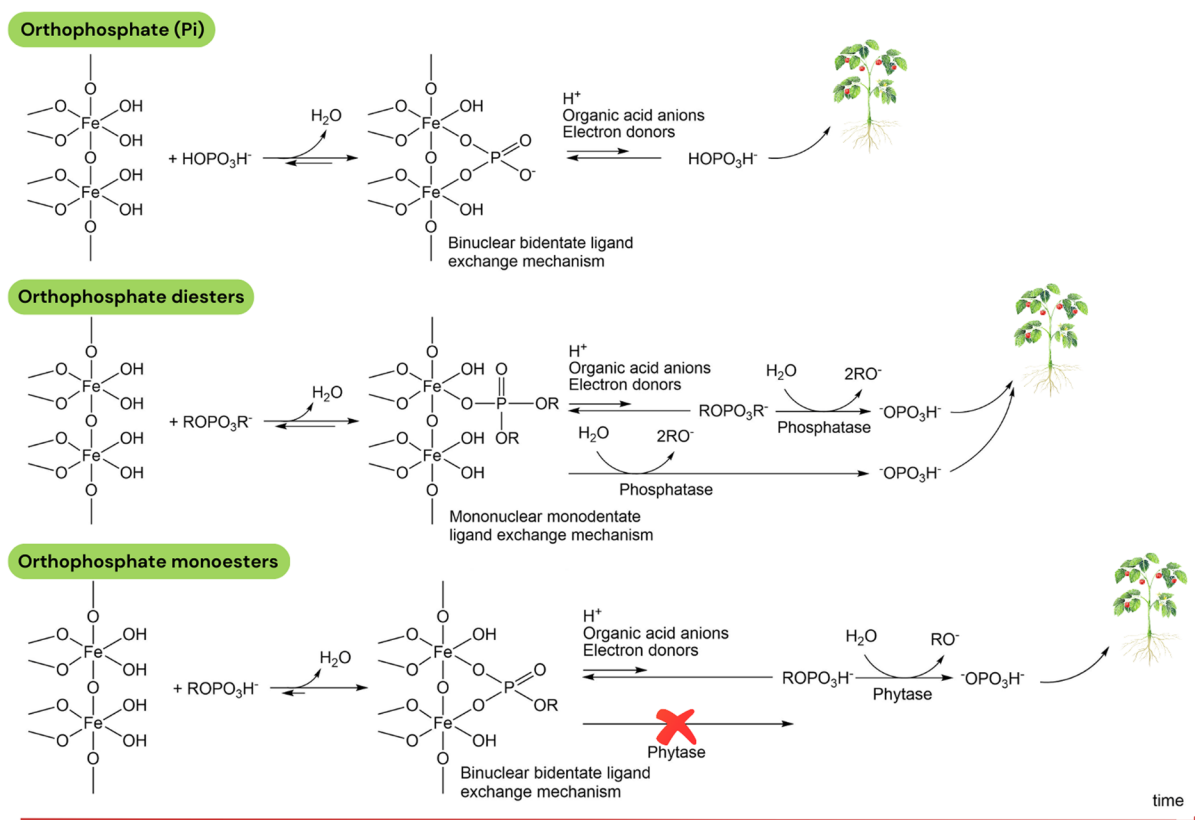


Fig. 3 Adsorption mechanisms of P on Fe (hydr)oxides via i) a bidentate binuclear ligand exchange mechanism (orthophosphate (Pi) and organic P monoesters), and ii) a monodentate mononuclear ligand exchange mechanism (organic P diesters). The retention of organic P compounds on mineral surfaces

reduces phosphatase activity and inhibits phytase activity. Plant and microorganisms can produce protons (H^+), organic acid anions and electron donors to release the organic P compounds from minerals for enzymatic hydrolysis and plant uptake. Adapted from Celi et al. 2022

to the creation of inner-sphere complexes at the ferrihydrite-water interface, whereas adsorption on Al hydroxides involves a combination of both outer- and inner-sphere processes (Guan et al. 2006; Ruyter-Hooley et al. 2015). Since adsorption is believed to take place through only some of the six phosphate groups, the remaining groups can affect the mineral surface characteristics through steric hindrance or altered charge, or can change particle dispersion/flocculation equilibria (Giles et al. 2011 and references therein).

The retention of P can be also affected by the crystallinity and stability of metal oxides. According to Celi et al. (2020), hematite showed lower retention of both Pi and Po compared to goethite and maghemite. Maghemite exhibited greater P retention than goethite, but was found to be less stable and more easily dissolved by organic acid anions like oxalate (Celi et al. 2020). As a result, highly weathered and Fe-rich soils may experience a reduction in inositol phosphate accumulation due to weaker binding of the molecule to the oxide surface, as well as increased efficiency of plant exudates in removing P from the solid phase (Fig. 3) (Celi et al. 2020; Giaveno et al. 2008). Studies on the adsorptive effects of the combined solution of Pi and inositol phosphates showed that the latter inhibited Pi adsorption and caused the desorption of Pi adsorbed on ferrihydrite, an effect which was also observed in soil (Anderson et al. 1974; Berg and Joern 2006; Bowman and Moir 1993; De Groot and Golterman 1993).

The type of interaction of P diesters with soil minerals can vary considerably depending on their molecular properties. Iron (hydr)oxides, for example, adsorb DNA via the backbone phosphate (Fig. 3), but are influenced by the steric hindrance of the nucleotides (Liu and Liu 2014, 2015; Yiu et al. 2013). Extracellular polymeric substances secreted by microorganisms, lipopolysaccharides and membrane-bound proteins located on the outer surface of bacterial cells were found to be involved in bacterial adhesion to Fe (hydr)oxides by forming inner-sphere complexes (Cagnasso et al. 2010; Parikh and Chorover 2006). In a recent study, Santoro et al. (2019) observed that the phospholipid phosphatidylcholine was retained on the surface of ferrihydrite only through a solid/liquid partitioning, possibly forming a bilayer configuration around the Fe core, supporting

results from previous studies (De Cuyper and Joniau 1991; Denizot et al. 1999). Conversely, Cagnasso et al. (2010) reported that the interaction of phosphatidylcholine with the surface of goethite and hematite occurs only through electrostatic attraction, which explains why these compounds are more easily biodegraded and do not accumulate in the environment (Magid et al. 1996).

Organic P adsorption on Al minerals has been recently reviewed by Yan et al. (2023), who reported that the maximum adsorption increases with decreasing crystallinity of Al (hydr)oxides, following the order: α -Al₂O₃ < boehmite < amorphous Al hydroxide. Adsorption density is as well affected by the particle size of the minerals and the Po molecular size, in the order: InsP6 < adenosine triphosphate < glucose-6-phosphate < glycerophosphate, i.e., the maximum adsorption densities increased with decreasing Po molecular size (Yan et al. 2023). Despite having the largest molecular size, InsP6 has been shown to adsorb in greater amounts on amorphous Al hydroxide than other Po compounds because of the transformation of surface complexes to surface precipitates (Yan et al. 2023 and references therein).

In neutral-to-calcareous soils, P can also be adsorbed on the surface of Ca carbonate, clay minerals and organic matter (OM) (Shen et al. 2011). Calcite exhibits a high capacity for P retention, with a stronger effect observed for InsP6 than for Pi. The reaction involves adsorption followed by precipitation of Ca salts (Celi and Barberis 2007). Clay minerals adsorb less organic P than Fe and Al oxides, but with a higher affinity (Celi and Barberis 2005). The adsorption reaction of Pi and Po on clays is not readily reversible, although some P can be released into the solution. The desorption phenomenon depends on factors as pH, percentage of P saturation and presence of competing ligands such as citrate, oxalate or carbonate (Celi and Barberis 2007 and references therein).

Finally, soil OM can participate in the retention of organic P in soil. This can occur through physical or chemical incorporation of organic P in the OM fraction, direct adsorption on the organic surfaces by ionic or hydrophobic interactions or indirect adsorption through polyvalent cations that act as bridges to form ternary complexes (Celi and Barberis 2007 and references therein).

Precipitation and coprecipitation

At low concentrations in the soil solution, P tends to interact with soil components through adsorption or anion exchange, forming weak and reversible electrostatic bonds. High P concentrations, mainly resulting from the application of P fertilizers, can instead cause the precipitation of metal phosphates, following a partial dissolution of soil minerals (Celi et al. 2000, 2020; Celi and Barberis 2005; Sample et al. 2015; Yan et al. 2014). pH values below 6 can in fact promote the dissolution of Al and Fe oxides and hydroxides, and the resulting Fe and Al ions can precipitate directly with P in solution. Phosphorus from precipitated Fe and Al phosphates is apparently more available to plants than most of the P fixed on soil particles, as discussed later in this review.

In calcareous soils, the formation of Ca phosphates is favored by the presence of soluble Ca, which occurs in soil as Ca ions bound to cation exchange sites, different Ca minerals, or residual limestone (Penn and Camberato 2019). Many chemical fertilizers also contain highly soluble Ca phosphates, which can saturate the soil solution with both Ca and P, leading to the precipitation of sparingly soluble minerals such as brushite, monetite and amorphous forms. Over time, these minerals may transform into more stable minerals, such as hydroxyapatite (Essington 2021; Lindsay 1979).

Complexation and precipitation of organic P with polyvalent cations enhance its retention in the colloidal phase. These processes result in a significant portion of organic P being stabilized by mineral components, thereby rendering it unavailable to plants (Celi and Barberis 2007; Giles et al. 2011; Jiang et al. 2015). The ability to form complexes or precipitates mainly depends on the number of phosphate groups present in the organic P molecule (Celi and Barberis 2005). For example, the six phosphate groups of InsP6 make it a strong ligand in soils, with a high ability to bind metal cations producing complexes that are soluble at low pH and insoluble at mid-range pH values (Chen et al. 2020; Martin 1987; Nolan et al. 1987). In soils and sediments, the complexation of P, especially with Fe and Ca and their minerals, can increase Po stabilization, thus turning most of the labile and moderately labile organic P compounds into more resistant forms (Harrison 1987; House and Denison 2002; Zhang et al. 1994).

Apart from adsorption and precipitation, P coprecipitation with Fe resulting from changes in pH, redox potential or ionic strength is a common process in waters and sediments. To date, only a few studies have investigated this process and the interactions between P and Fe dynamics under alternate redox conditions, and even fewer have distinguished between inorganic and organic P coprecipitation. More attention was instead posed to the effect of dissolved OM on the coprecipitation with Fe, which could in any case have indirect effects on P accumulation (Angelico et al. 2014; Colombo et al. 2015; Jones et al. 2015; Kashyap et al. 2014; Mikutta et al. 2008, 2014; Pédrot et al. 2011; Pham and Waite 2008; Shimizu et al. 2013; Sodano et al. 2017; Sundman et al. 2016).

If the soil solution contains Fe(II) as a result of Fe (hydr)oxides reductive dissolution, the occurrence of oxidizing conditions can lead to its oxidation and subsequent precipitation as Fe(III) (hydr)oxides. These minerals have the ability to effectively retain many inorganic and organic anions, including both Pi and Po (Gorra et al. 2012; Huang et al. 2013; Mikutta et al. 2014). When phosphate is incorporated into the nanoparticles of the newly formed precipitate, its retention is significantly enhanced compared to a simple adsorption mechanism (Châtellier et al. 2004, 2013; Luo et al. 2022; Santoro et al. 2019; Senn et al. 2015; Thibault et al. 2009; van der Grift et al. 2016; Voegelin et al. 2013). The presence and concentration of Pi play a significant role in influencing the kinetics and mechanisms of Fe oxidation and precipitation, promoting the formation of Fe(III) phosphates instead of crystalline Fe(III) oxides (Santoro et al. 2019; Thibault et al. 2009; van der Grift et al. 2016; Voegelin et al. 2013). In this regard, Thibault et al. (2009) and Voegelin et al. (2013) observed that even low Pi concentrations inhibit the formation of crystalline Fe (hydr)oxides in favor of less crystalline forms. In support of these studies, Santoro et al. (2019) demonstrated the formation of Fe (hydr)oxides nanoparticles with short-range crystalline order at low Pi concentration, and of amorphous Fe(III) phosphate at increasing Pi loadings. These results suggest that Pi disrupts the overall structural order of the oxide, leading to smaller sizes of the precipitated particles due to Pi surface poisoning (Châtellier et al. 2004; Thibault et al. 2009; van der Grift et al. 2016; Voegelin et al. 2013). The maximum amount of Pi associated with

ferrihydrate particles was observed at a P/Fe ratio of approximately 0.5–0.6, as beyond this point any surplus Pi did not cause additional distortion to the crystal lattice or change to the crystal size (Santoro et al. 2019; Thibault et al. 2009; Voegelín et al. 2013).

Once formed, the stability of the coprecipitated phases could further impact on the bioavailability of the occluded P for plants and microbial communities after the dissolution of Fe oxides (Jiang et al. 2015). The lack of crystallinity of the formed phases suggests their lower stability and higher solubility compared to Fe oxide phases (Châtellier et al. 2013). Mayer and Jarrell (2000) in fact observed the release of over 75% of the retained Pi after coprecipitation, probably due to coagulation and crystalline growth of Fe oxides which expelled P back into solution. Aging of ferrihydrate has been shown to decrease the surface area and the concentration of surface sites per mass unit, releasing P into solution and, as sorption of Pi reduces the positive charge of particles, this can induce aggregation and release of retained ions into solution (Mayer and Jarrell 2000).

Organic P coprecipitation may exhibit different behavior. Inositol phosphate can be retained within the forming system up to a P/Fe ratio of 1, with rapid precipitation kinetics due to its strong affinity for Fe (Santoro et al. 2019). This results in the rapid formation of Fe-InsP6 species that act as crystallization nuclei, accelerating crystal growth on lateral planes while incorporating the organic P compound within the structure. The coprecipitation process involves both adsorption on the newly-formed surfaces of ferrihydrate with subsequent particle aggregation due to electrostatic interactions, and precipitation of the Fe-InsP6 salt at higher P concentrations (Santoro et al. 2019). Chen et al. (2020) reported similar results, showing that coprecipitated Fe-InsP6 material did not cause the transformation of the background ferrihydrate into goethite or hematite during aging. In contrast, the coprecipitation of P diesters, such as phosphatidylcholine with Fe, did not modify the mineral properties of ferrihydrate (Santoro et al. 2019), and resulted in the formation of a phospholipid bilayer on the oxide surface, retained by weak non-specific forces, which may contribute to the fast turnover of this class of molecules in the soil. Similarly, coprecipitation experiments using bacterial cells, whose outer structure consists of a phospholipid bilayer with protein inclusions, did not alter the mineralogy of the

forming secondary Fe-oxides. However, the presence of bacterial cells (and the macromolecules they can release) can affect the size, shape, and spatial organization of the mineral particles (Châtellier et al. 2004).

Plant strategies for unlocking unavailable soil P fractions: a focus on strigolactones and the model plant tomato

The abiotic processes described so far, i.e., adsorption, precipitation and coprecipitation, can lead to soil P fractions that are strongly unavailable for plants. In response to this P-deficiency, plants activate complex regulatory mechanisms known as P starvation responses (PSRs) that include genetic, physiological, and morphological changes aimed at optimizing the so-called P use efficiency (PUE) (de Souza Campos et al. 2019). It encompasses strategies of P acquisition from soil, translocation from root to shoot, allocation, utilization, and remobilization within the plant (He et al. 2019). These strategies typically involve modifications in plants that enhance either P acquisition or P utilization efficiency (PAE and PUE, respectively) (Dixon et al. 2020; Vance et al. 2003). Nutrient acquisition efficiency is an indicator of the plant's ability to absorb poorly available nutrients as P, while nutrient utilization efficiency estimates the capacity of a plant to produce maximum yield per unit of nutrient absorbed (Aziz et al. 2014). Phosphorus starvation responses aimed at increasing PUE include reduced growth rate, remobilization of internal P through scavenging and recycling enzymes, alteration of carbon (C) metabolism, utilization of alternative respiratory pathways, and biosynthesis of low-P membranes (Aziz et al. 2014 and references therein). To enhance P uptake, plants can exude P-solubilizing enzymes and low molecular weight organic acids, acidify the rhizosphere, modify root architecture and root hair development, engage in symbiotic interactions with mycorrhizae or increase the expression and activity of high-affinity P transporters (Aziz et al. 2014; de Souza Campos et al. 2019). Overall, the PSRs and PUE mechanisms play important roles in helping plants to adapt to P-deficient soils and can help improve plant growth and yield in low-P environments.

The various strategies harbored by plants to increase P acquisition and respond to P deficiency

have been extensively reviewed in the past (e.g., Aziz et al. 2014; Bais et al. 2006; Hinsinger 2001; Hodge 2004; Lambers et al. 2006; Niu et al. 2013; Péret et al. 2011, 2014; Shen et al. 2011; Ticconi and Abel 2004; Vance et al. 2003). The following sections will therefore focus on the recent discoveries regarding PSRs in the model plant tomato and the influence of SLs on such responses.

Before going deeper in the following sections, we do have to highlight the important need of appropriate conditions to mimic the real P availability in soil. Indeed, in existing literature, most of the in vitro and field experiments have primarily focused on studying the mechanisms of plant adaptation to a steady low P concentration (Wissuwa et al. 2005). However, it is important to recognize that these conditions may not accurately reflect the natural variation of P availability in soil, which can undergo temporal and spatial changes. Consequently, the strategies employed by plants to adapt to fluctuating P availability have received poor attention. Typically, small-scale studies employ "P deficiency" concentrations that exceed the optimal amount of P required for plant growth, as noted by de Groot et al. (2003). This can lead to plants acclimating to high P concentrations, potentially concealing or delaying the onset of the canonical P starvation responses. Table 1 highlights the broad range of P concentrations used in research papers, along with the specific roles of SL in plant responses to P deficiency. Therefore, when studying plant P starvation responses in soil-less systems, it is crucial to establish appropriate P conditions that support optimal plant growth prior to imposing P shortage. This approach is essential to prevent an excessive accumulation of P that plants may later rely on as a reserve.

Furthermore, plant responses may not solely depend on the initial P concentration, but also on the temporal variation of P availability throughout the experiment. In fact, it must be recognized that in field the amount of P available in the soil solution can fluctuate according to seasonality and fertilization practices, leading the plants to adapt to gradual or sudden decreases in P availability (Fan et al. 2014; Rubæk and Sibbesen 1995). An additional factor to consider is that a significant proportion of P in soil exists as sparingly available sources, which accumulate in the soil, as highlighted in the previous section, forming

the so called legacy-P (Lun et al. 2018; Shen et al. 2011).

From a research perspective, these considerations translate into the need to overcome the use of nutrient solutions (e.g., Hoagland) routinely adopted in most studies investigating plant nutrition responses conducted in soil-less systems, where a soluble source of P such as ammonium, sodium or potassium phosphate is provided (Gerloff 1987). These hydroponic solutions are unbuffered, contain high soluble P concentrations and cannot simulate a real soil solution, which is strongly buffered, chemically heterogeneous, and complex (Bera et al. 2020). As a result, recent research works include a sparingly available P source to represent the conditions affecting P availability in soil more realistically. For example, Bera et al. (2020) formulated a simulated soil solution using insoluble phosphate, which contained high total P but low plant-available P. Other authors added soluble organic P forms (see for instance Zhou et al. 2021), P forms adsorbed on (e.g., Martin et al. 2004) or precipitated with (e.g., Santoro et al. 2022) Fe oxides, Fe/Al/Ca phosphates (e.g., Edayilam et al. 2020), or phosphate rocks (e.g., Rezakhani et al. 2019) in soil-less systems. Table 2 reports a list of papers with related experimental details in which scarcely available P forms were used to study plant responses to P deprivation.

Strigolactones: chemistry, biosynthesis, and production by plants

The collective term "strigolactones" was coined to designate a small group of compounds that are secreted from the roots of various plant species and induce seed germination in root parasitic plants of the genus *Striga*, commonly referred to as witchweeds (Butler 1995). After the discovery of strigol in cotton root exudates as a germination stimulant of *Striga lutea* (Cook et al. 1966), other SLs have been identified in exudates of a number of plant species, and have been shown to stimulate seed germination in root parasitic plants also of the genera *Orobanche*, *Phelipanche* and *Alectra*, resulting in significant losses in agricultural production worldwide (reviewed in Xie et al. 2010). Among the plant secondary metabolites known to induce seed germination of root parasites, SLs are the most active, functioning at concentrations of 10^{-7} – 10^{-15} M (Xie et al. 2010). For

Table 1 Summary of experimental conditions in studies on the interaction of P concentrations and the role of strigolactones (SLs) in plant acclimation strategies

Plant species (and cultivar/variety)	Cultivation	P concentration	P type	SL mutant	Exogenous SL application	Investigated parameter	Reference ^s
<i>Oryza sativa</i> L. cv. Shiohari	Hydroponics	0, 6, 12, 30, 60, 120, 300, 600 μ M	Na_2HPO_4	Tillering dwarf mutants <i>d3-1</i> and <i>d10-1</i>	-	SL role in decreasing the tiller number under low P in rice	Umehara et al. 2010
<i>Arabidopsis thaliana</i> Col-0	Murashige and Skoog medium	High P: 2 mM Low P: 1 μ M	KH_2PO_4	<i>max2-1</i> , <i>max3-1</i> , <i>max4-1</i> , <i>tir1-1</i> (Col-0 background)	15 μ M and 50 μ M GR24	Effects of SLs on root response to low P	Mayzlish-Gati et al. 2012
<i>Pisum sativum</i> L.	Hydroponics (half-strength Tadano and Tanaka medium)	High P: 160 μ M Low P: 0 μ M	$\text{NaH}_2\text{PO}_4 \cdot 2\text{H}_2\text{O}$	<i>ccd8</i> , <i>rms2-1</i> and <i>rms4-1</i> mutant	-	Role of SLs in regulating mycorrhizal development and nodulation in response to nutrient (P, N) deficiency	Foo et al. 2013
<i>Oryza sativa</i> L.	Agar medium and hydroponics	High P: 600 μ M Low P: 0 μ M	NaH_2PO_4	SL-deficient <i>d10</i> , <i>d17</i> , and <i>d27</i> and SL-insensitive <i>d3</i> and <i>d14</i> mutants	1 μ M <i>racGR24</i>	Effects of SLs on leaf senescence	Yamada et al. 2014
<i>Arabidopsis thaliana</i> Col-0	Agar medium	High P: 1 mM Low P: 0 mM	KH_2PO_4	<i>max1-1</i> and <i>max2-1</i> mutants (Col-0 background)	1 μ M GR24	Effect of SLs on PSI anthocyanin accumulation and acid phosphatase production	Ito et al. 2015
<i>Arabidopsis thaliana</i> Col-0	Murashige and Skoog medium	High P: 2 mM Low P: 1 μ M	KH_2PO_4	Col-0 homozygous <i>max2-1</i> line	5×10^{-5} M GR24	Crosstalk between SL and auxin in response to P deficiency	Kumar et al. 2015
<i>Oryza sativa</i> L.	Hydroponics	0, 1, 2, 10, 100 and 300 μ M	KH_2PO_4	SL-deficient <i>d10</i> and <i>d27</i> and SL-signaling <i>d3</i> mutants	-	Response of root development to different level of P and N supply in WT and SL mutants	Sun et al. 2014

Table 1 (continued)

Plant species (and cultivar/variety)	Cultivation	P concentration	P type	SL mutant	Exogenous SL application	Investigated parameter	Reference ^s
<i>Oryza sativa</i> L.	Hydroponics	High P: 300 µM Low P: 2 µM	KH ₂ PO ₄	<i>dl10</i> , <i>d3</i> and <i>d53</i> mutants	-	Role of nitric oxide in regulating root growth and SL signalling under N and P deficiency	Sun et al. 2016
<i>Solanum lycopersicum</i> L. cv. Money Maker	Hydroponics	1) +P: 800 µM -P: 0 µM 2) +P: 800 µM -P: 200 µM	KH ₂ PO ₄	SL-deficient tomato line <i>SICCD8</i> -RNAi line L04 and its wild-type cv. Craigella (LA3247) [2]	0 to 1000 nM 2'- <i>epi</i> -GR24	Role of SLs as regulators of early Pi starvation signalling in plants	Gamir et al. 2020
<i>Solanum lycopersicum</i> L.	Murashige and Skoog medium	1) High P: 625 µM Low P: 6.25 µM 2) High P: 80 µM Low P: 10 µM No P: 0 µM	KH ₂ PO ₄	SL-deficient tomato line <i>SICCD7</i> -silenced line 6936 and its wild-type genotype M82	5 µM <i>rac</i> -GR24 [1]	1) Root system architecture (RSA) changes in response to exogenous SL application 2) RSA phenotyping with varying P concentrations	Santoro et al. 2020
<i>Oryza sativa</i> L. cv. Shiokari and cv. Nipponbare	Hydroponics	High P: 600 µM Low P: 0 µM	Na ₂ HPO ₄	<i>d27-1</i> , <i>d17-1</i> , <i>d10-1</i> , <i>d14-1</i> and <i>d3-1</i> in the "Shiokari" background, <i>d10-2</i> , <i>d17-2</i> in the "Nipponbare" background and <i>d53</i> in the "Norin 8" background	20 µM <i>rac</i> -GR24	Effect of nutrient deficiencies on endogenous SL production and on lamina joint angle	Shindo et al. 2020
<i>Solanum lycopersicum</i> L. cv. Nostymi F1	Hydroponics	High P: 1.5 mM Low P: 600 µM	KH ₂ PO ₄	-	SL-based biostimulant by STRIGOLAB (solanacol 80 pM)	Crop resilience to combined water and nutrient stress following the application of biostimulants	Kalozoumis et al. 2021

Table 1 (continued)

Plant species (and cultivar/variety)	Cultivation	P concentration	P type	SL mutant	Exogenous SL application	Investigated parameter	Reference [§]
<i>Solanum lycopersicum</i> L. cv. Money Maker	Zeolite and sand Hydroponics	1) High P: 1.3 mM Low P: 300 µM 2) + P: 800 µM -P: 0 µM	KH ₂ PO ₄	1) SL-deficient tomato line <i>S/CCD8</i> -RNAi line L09 and its wild-type cv. Craigella (LA3247)	10 nM 2'- <i>epi</i> -GR24	Role of SLs in N starvation and in the N-P signalling interplay	Marro et al. 2022
<i>Solanum lycopersicum</i> L.	Hydroponics	High P: 80 µM Low P: 0 µM	KH ₂ PO ₄	SL-deficient tomato line <i>S/CCD7</i> -silenced line 6936 and its wild-type genotype M82	5 µM <i>rac</i> -GR24	P acquisition strategies as modulated by SLs	Santoro et al. 2021
<i>Solanum lycopersicum</i> L. cv. Craigella	Hydroponics	High P: 0.5 M Low P: 0 M	KH ₂ PO ₄	SL-deficient tomato line <i>S/CCD8</i> RNAi line L09	-	Genes regulated by P starvation and P replenishment	Wang et al. 2021a
<i>Solanum lycopersicum</i> L.	Hydroponics	High P: 80 µM Low P: 0 µM	KH ₂ PO ₄ <i>myo</i> InsP6 COP-Pi COP- <i>myo</i> InsP6	SL-deficient tomato line <i>S/CCD7</i> -silenced line 6936 and its wild-type genotype M82	-	Responses induced by sparingly available inorganic and organic P as modulated by SLs	Santoro et al. 2022

[§]References are listed in chronological order and alphabetically for papers published the same year

Table 2 Summary of experimental conditions in studies on plant acclimation strategies in the presence of sparingly available P forms. Experiments with soluble inorganic phosphate are also reported

Plant species (and cultivar/ variety)	Cultivation	P concentration	P type	Investigated parameter	Reference ^s
<i>Lolium perenne</i> L.	Sand	High P: 132 μM Low P: 0 μM	Phosphated goethite	Plant availability of bridging phosphate	Parfitt 1979
<i>Sorghum bicolor</i> L.	Hydroponics and soil	Hydroponics: 129 μM P Soil: 56 kg P ha ⁻¹	Organic: ethylammonium, glycerol and phenyl phosphates. Inorganic: KH_2PO_4 , $\text{Ca}_3(\text{PO}_4)_2$, $\text{Ca}_2\text{P}_2\text{O}_7$, FePO_4 and AlPO_4	Availability of P from different P compounds and to note genotype differences	Furlani et al. 1987
<i>Trifolium alexandrinum</i> L., <i>Hordeum vulgare</i> L., <i>Avena sativa</i> L., <i>Triticum aestivum</i> L.	Hydroponics and soil	2, 5, 10, 20 mg P/100 ml	Sodium glycerol phosphate, lecithin, phytin	Efficiency of phosphatases to acquire P from organic sources	Tarafdar and Claassen 1988
<i>Lycopersicon esculentum</i> Mill, var Tropic	Hydroponics	High P: 1 mM Low P: 160 μM	KH_2PO_4	Changes in root morphology and acid phosphatase activity during P-deficiency	Garcia and Ascencio 1992
<i>Carex acutiformis</i> , <i>Carex diandra</i> , <i>Carex lasiocarpa</i>	Sand	Control: 600 μM KH_2PO_4 P treatments: 0.013 mg P g ⁻¹ sand Low P: 0 mM P	KH_2PO_4 AlPO_4 FePO_4 InsP6 glycerophosphate	Ability of three <i>Carex</i> species to use organic and inorganic P forms	Pérez Corona et al. 1996
<i>Raghanus sativus</i> L. and <i>Brassica napus</i> L.	Hydroponics and sand	Hydroponics: · High P: 250 μM KH_2PO_4 · Low P: 0 μM KH_2PO_4 Sand: · 0.19 g/pot $\text{Ca}_3(\text{PO}_4)_2$ · 0.15 g/pot AlPO_4	KH_2PO_4 $\text{Ca}_3(\text{PO}_4)_2$ AlPO_4	Role of exuded organic acids in mobilizing sparingly soluble P	Zhang et al. 1997
<i>Lycopersicon esculentum</i> L.	Hydroponics	High P: 250 μM Low P: 0 μM	KH_2PO_4	Characterization and regulation by P of phosphate transporters <i>LePT1</i> and <i>LePT2</i>	Liu et al. 1998

Table 2 (continued)

Plant species (and cultivar/ variety)	Cultivation	P concentration	P type	Investigated parameter	Reference ^s
<i>Triticum aestivum</i> L. cv. Haro, <i>Lycopersicon esculentum</i> L., cv. Mon-cymaker, <i>Cicer arietinum</i> and <i>Lupinus albus</i> L. cv. Amiga	Hydroponics	High P: 250 μM Low P: 0 μM	KH_2PO_4	P deficiency-induced metabolic changes related to exudation of carboxylic acids and protons in selected species	Neumann and Römheld 1999
Pasture grasses and legumes	Agar medium	1x, 2x, 4x, 10x, 20x, $40 \times P_{\text{crit}}^*$ * P_{crit} = critical P concentration obtained for each pasture species in a preliminary hydroponic experiment	NaH_2PO_4 , InsP6, glucose-1-phosphate (GIP)	Abilities of a range of temperate grass and legume species to use Pi, InsP6 and GIP for growth	Hayes et al. 2000b
<i>Lycopersicon esculentum</i> L. Mill cv. Capita	Aeroponics	High P: 250 μM Low P: 0 μM	KH_2PO_4	Isolation and characterization of a tomato P-starvation-induced gene (<i>LePS2</i>) representing an acid phosphatase	Baldwin et al. 2001
<i>Lycopersicon esculentum</i> Mill cv. Capita	Hydroponics	Free access treatments: 1 mM or Daily addition to a P-free medium: 70, 120, 170, 220, 270, 320 $\text{mg g}^{-1} \text{d}^{-1}$ High P: 750 μM Low P: 0 μM	KH_2PO_4	Effects of P and light on growth and dry biomass partitioning	de Groot et al. 2001
<i>Zea mays</i> L.	Culture vessels with nutrient solution	High P: 750 μM Low P: 0 μM	KH_2PO_4	Mechanisms allowing maize genotypes to adapt to low available P soils	Gaume et al. 2001
<i>Lupinus albus</i> L.	Hydroponics	1, 5, 25 mmol P m^{-3}	NaH_2PO_4	Effect of P deficiency on H^+ and organic acid anions exudation	Sas et al. 2001
<i>Arabidopsis thaliana</i>	Agar medium	High P: 2.5 mM Medium P: 500 μM Low P: 100 μM	KH_2PO_4	Effects of P availability on root system architecture	Williamson et al. 2001
<i>Lycopersicon esculentum</i> Mill cv. Capita	Hydroponics	High P: 55 μM Low P: 0 mM	KH_2PO_4	Growth response to N and P limitation, and their interaction	de Groot et al. 2003

Table 2 (continued)

Plant species (and cultivar/ variety)	Cultivation	P concentration	P type	Investigated parameter	Reference ^s
<i>Triticum aestivum</i> L., <i>Cicer arietinum</i> L.	Soil	60 mg P kg ⁻¹	InsP6 FePO ₄	Interspecific complementation in P utilization by wheat/chickpea intercropping	Li et al. 2003
<i>Arabidopsis thaliana</i>	Phytigel medium	High P: 1 mM Low P: 1 μM	KH ₂ PO ₄	Role of ethylene in regulating root elongation under P deficiency	Ma et al. 2003
<i>Glycine max</i> L. cv. Merr.	Sand	High P: 200 μM Low P: 0 μM	KH ₂ PO ₄	Exudation of organic acids induced by P deficiency and/or Al toxicity	Dong et al. 2004
<i>Zea Mays</i> L.	Hydroponics	High P: 250 μM Low P: 0 μM	KH ₂ PO ₄	Physiological and morphological responses of roots to low P stress in genotypes with different P efficiency	Liu et al. 2004
<i>Lolium perenne</i> L.	Sand	4 mg P (KH ₂ PO ₄ and InsP6) 4 mg P + 1.4 g Gt (Goethite (Gt) + Pi, Gt + InsP6) 1.4 g Gt + 5.94 mg P (Gt-Pi) 1.4 g Gt + 3.96 mg P (Gt-InsP6)	KH ₂ PO ₄ InsP6 Gt + Pi Gt + InsP6 Gt-Pi Gt-InsP6	Assessment of P availability to ryegrass in the presence of Pi or InsP6 added in solution or sorbed on Gt	Martin et al. 2004
<i>Arabidopsis thaliana</i>	Agar medium	High P: 1 mM Low P: 1 μM	NaH ₂ PO ₄	Cellular processes responsible for the inhibition of root growth caused by P deprivation	Sánchez-Calderón et al. 2005
<i>Oryza sativa</i> L. cv. NIL-Pup1 and Nipponbare	Hydroponics	3.2, 6.4, 9.6, 100 μM	KH ₂ PO ₄	Influence of source or sink limitation in reduced plant growth under P deficiency	Wissuwa et al. 2005
<i>Lycopersicon esculentum</i> cv. Money-maker	Murashige and Skoog medium	High P: 2.5 mM Low P: 0 μM	KH ₂ PO ₄	Influence of P deprivation on coordinate synthesis of the principle P-starvation-inducible acid phosphatase isozymes	Bozzo et al. 2006

Table 2 (continued)

Plant species (and cultivar/ variety)	Cultivation	P concentration	P type	Investigated parameter	Reference ^s
<i>Triticum aestivum</i> , <i>Brassica napus</i> , <i>Cicer arietinum</i> , <i>Pisum sativum</i> , <i>Lupinus albus</i> , <i>Lupinus angustifolius</i> , <i>Lupinus cosentinii</i> <i>Arabidopsis thaliana</i>	Sand Agar medium	40 mg P kg ⁻¹ High P: 500 µM Low P: 5 µM	KH ₂ PO ₄ AlPO ₄ , FePO ₄ , Hydroxylapatite NaH ₂ PO ₄	Relationship between carboxylate release from roots and ability to utilize P from sparingly soluble forms Molecular basis of <i>LPR1</i> QTL	Pearse et al. 2007 Svistoonoff et al. 2007
<i>Brassica</i> (14 diverse cultivars)	Hydroponics	NH ₄ H ₂ PO ₄ : 200 µM TCP: 0.2 g L ⁻¹ RP: 2 g L ⁻¹	NH ₄ H ₂ PO ₄ TCP (tricalcium phosphate) RP (rock phosphate)	Elucidate P-stress-induced P-solubilization and acquisition of sparingly soluble P-sources	Akhtar et al. 2008, 2009a, b
<i>Solanum lycopersicum</i> L. cv. Money Maker	Hydroponics	High P: 200 µM Low P: 0 µM	KH ₂ PO ₄	Regulation of SL biosynthesis	López-Ráez et al. 2008
<i>Vigna unguiculata</i> L. Walp	Sand	High P: 840 µM Low P: 70 µM Rock P: 135 mg P kg ⁻¹	KH ₂ PO ₄ Zin-Rock (133 mg P g ⁻¹)	Contribution of AMF symbiosis to P uptake from sparingly available or soluble resources	Ngwene et al. 2010
<i>Arabidopsis thaliana</i>	Sand	High P: 500 µM Low P: 0 µM	KH ₂ PO ₄	Local and systemic gene regulation by P starvation	Thibaud et al. 2010
<i>Gossypium hirsutum</i> L., <i>Triticum aestivum</i> L. and <i>Lupinus albus</i> L.	Sand	High P: 40 (2010), 150 (2011) mg P kg ⁻¹ sand Low P: 0 mg P kg ⁻¹ sand	KH ₂ PO ₄ Ca(H ₂ PO ₄) ₂ AlPO ₄ FePO ₄ Hydroxyapatite (RP)	Ability of cotton to access P from sparingly soluble P sources compared with wheat and white lupin	Wang et al. 2010, 2011
<i>Brassica napus</i> L.	Soil	High P: 31 mg P kg ⁻¹ sand Low P: 0 mg P kg ⁻¹ soil	KH ₂ PO ₄ AlPO ₄ FePO ₄	P-acquisition ability of two rapeseed genotypes supplied with sparingly soluble sources of P	Zhang et al. 2011
<i>Brassica napus</i> L.	Hydroponics	High P: 1 mM Low P: 5 µM	NaH ₂ PO ₄ and Na ₂ HPO ₄	Role of cytokinins on P efficiency	Shi et al. 2012
<i>Solanum lycopersicum</i> L. cv. Sekaiichi, Momotaro and M82, <i>Astragalus sinicus</i> L., <i>Medicago sativa</i> L., <i>Lactuca sativa</i> L., <i>Tagetes patula</i> L., <i>Triticum aestivum</i> L.	Hydroponics	8, 20, 80, 160 µM	NaH ₂ PO ₄ · 2H ₂ O	Effects of N and P deficiencies on SL exudation	Yoneyama et al. 2012

Table 2 (continued)

Plant species (and cultivar/ variety)	Cultivation	P concentration	P type	Investigated parameter	Reference ^s
<i>Sorghum bicolor</i> L. Moench cv. Hybrid	Hydroponics	High P: 160 μM Low P: 8 μM	$\text{NaH}_2\text{PO}_4 \cdot 2\text{H}_2\text{O}$	Effect of N and P fertilization on SL production and exudation	Yoneyama et al. 2013
<i>Solanum lycopersicum</i> L. cv. Micro-Tom	Sand	High P: 1 mM Low P: 50 μM	NaH_2PO_4	Study of Pht1 gene family	Chen et al. 2014
<i>B. papyrifera</i> , <i>O. violaceus</i> , <i>M. alba</i> , <i>B. napus</i>	Hydroponics	High P: 50 μM Low P: 0 μM	KH_2PO_4	Characteristics of root-exuded organic acids and P extraction in calcareous soils	Zhao and Wu 2014
<i>Cucumis sativum</i> L.	Sand	6.4 mg P kg^{-1} of growth medium (2.56 mg P pot^{-1})	KH_2PO_4 and InsP ₆ adsorbed on Fe oxides	Contribution of <i>Trichoderma asperellum</i> T34 to plant uptake of sparingly available P forms	Garcia-Lopez et al. 2015
<i>Oryza sativa</i> cv. Nipponbare	Hydroponics	High P: 300 μM Low P: 0 μM	NaH_2PO_4	Role of OsPT8 in P redistribution of rice	Li et al. 2015
<i>Arabidopsis thaliana</i>	Agar medium	High P: 2.5 mM Low P: 0 μM	KH_2PO_4	Link between callose-regulated cell to cell signalling in root meristems and perception of P availability	Müller et al. 2015
<i>Arabidopsis thaliana</i>	Agar medium	High P: 630 μM Low P: 0 μM	KH_2PO_4	Characterization of an <i>Arabidopsis</i> mutant hypersensitive to P deficiency-induced inhibition of primary root growth and enhanced lateral root formation	Dong et al. 2017
<i>Solanum lycopersicum</i> L.	Hydroponics	High P: 200 μM Low P: 10 μM	KH_2PO_4	Regulation of root architecture and proton exudation under differential P availability	Zhang et al. 2018b
<i>Triticum aestivum</i> L. cv. Crac and Tukan	Hydroponics	High P: 200 μM Low P: 10 μM	KH_2PO_4	Physiological and molecular mechanisms underlying the differences between two cultivars with different PAE	de Souza Campos et al. 2019

Table 2 (continued)

Plant species (and cultivar/ variety)	Cultivation	P concentration	P type	Investigated parameter	Reference ^s
<i>Triticum aestivum</i> L.	Perlite	Soluble P: 60 mg P L ⁻¹ Insoluble P: 60 mg P kg ⁻¹ of RP	KH ₂ PO ₄ Hydroxyapatite (RP)	Alleviative role of silicon and P-solubilizing bacteria in mitigating P-deficiency stress	Rezakhani et al. 2019
<i>Solanum lycopersicum</i> L. cv. Money Maker	Hydroponics	High P: 200 µM Low P: 0 µM	KH ₂ PO ₄	Development and validation of an efficient UHPLC-MS/MS method for SL analysis in root exudates and extracts	Rial et al. 2019
<i>Solanum lycopersicum</i> L.	Hydroponics	High P: 500 µM NaH ₂ PO ₄ Low P: 400 µM TCP	Hoagland solution with Ca ₃ (PO ₄) ₂ or NaH ₂ PO ₄	Developing a successful scheme to identify P-efficient tomato varieties	Bera et al. 2020
<i>Andropogon virginicus</i>	Sand	36 mg P 600 g ⁻¹ sand	KH ₂ PO ₄ , FePO ₄ , Ca ₃ (PO ₄) ₂	<i>A. virginicus</i> potential to mobilize uranium when exposed to different P forms	Edayilam et al. 2020
<i>Solanum lycopersicum</i> L. cv. Money Maker, <i>Sorghum bicolor</i> L. cvs Shanqui red and SRN39, <i>Oryza sativa</i> L. cv. Shiokari, IR64, Apo, <i>Pisum sativum</i> L. cv. Sprinter, RoR12	Hydroponics/sand	Tomato: 200 µM vs 0 µM Sorghum and rice: 400 µM vs 0 µM Pea: 200 µM vs 0 µM	KH ₂ PO ₄	Design and validation of an efficient UHPLC-MS/MS method for SL analysis in root exudates and extracts	Floková et al. 2020
<i>Solanum lycopersicum</i> L. cv. Pusa Ruby	Hydroponics	High P: 1.25 mM Low P: 0.3 µM TCP	KH ₂ PO ₄ TCP	Identification and analysis of purple acid phosphatases under P deficiency	Srivastava et al. 2020
<i>Solanum lycopersicum</i> L. cv. Marmande	Hydroponics	High P: 100 µM P Low P: 0 µM P	KH ₂ PO ₄	Evaluate the effect of P deficiency on the ability of tomato to re-acquire specific exuded compound	Tiziani et al. 2020

Table 2 (continued)

Plant species (and cultivar/ variety)	Cultivation	P concentration	P type	Investigated parameter	Reference [§]
<i>Solanum lycopersicum</i> L. var. Moneymaker	Sand	0 vs 60 mg P in 60 g quartz sand	Pi Gt-Pi InsP6 Gt-InsP6	Determine whether AMF release significant amounts of low molecular weight organic acids to liberate P bound to Fe oxides	Andrino et al. 2021
<i>Solanum lycopersicum</i> L. cv. Micro-Tom	Hydroponics	High P: 500 μ M Low P: 50 μ M	KH_2PO_4	Content of major metabolites associated with tomato fruit quality	Li et al. 2021
<i>Saccharum officinarum</i> L.	Sand	Sparingly available forms: 100 mg P kg^{-1} sand Low P: 5 mg P kg^{-1} sand (KH_2PO_4)	KH_2PO_4 AlPO_4 $\text{FePO}_4 \cdot 4 \text{H}_2\text{O}$ $\text{Ca}_3(\text{PO}_4)_2$ InsP6	Variation among sugarcane genotypes supplied with soluble and sparingly soluble P sources	Zhou et al. 2021
<i>Solanum lycopersicum</i> L.	Hydroponics	High P: 80 μ M Low P: 0 μ M	KH_2PO_4 InsP6 COP-Pi COP-InsP6	Responses induced by sparingly available inorganic and organic P as modulated by SLs	Santoro et al. 2022

[§]References are listed in chronological order and alphabetically for papers published the same year

over 40 years SLs were known only as germination stimulants and were therefore considered to be waste or harmful metabolites until their function as a host-recognition signal for AMF was discovered by Akiyama et al. (2005). About 80% of land plants engage in symbiosis with these soil-borne microorganisms, in which organic C from the plant is exchanged for minerals absorbed by the fungus through an extensive network of hyphae (Gutjahr and Parniske 2013; Schmitz and Harrison 2014). This symbiotic relationship enables plants to access and acquire P more efficiently. Interestingly, the production of SLs in non-mycotrophic plant such as *Arabidopsis*, white lupin and spinach suggests that these molecules may have other roles in plant biology beyond their involvement in the AMF symbiotic pathway (Yoneyama et al. 2008). In 2008, Gomez-Roldan et al. (2008) and Umehara et al. (2008) independently classified SLs, or their downstream metabolites, as a novel class of phytohormones that function as long-distance branching factors regulating shoot branching by suppressing the growth of preformed axillary shoot buds. In their respective studies, both research groups demonstrated the effect of SLs on shoot branching through the application of synthetic SL analogue GR24 (Fig. 4d). In the study by Gomez-Roldan et al. (2008), the application of GR24 to shoot branching mutants of pea resulted in the restoration of the wild-type branching phenotype. Similarly, Umehara et al. (2008) observed the same phenomenon in rice mutants upon treatment with GR24.

In addition to their role in controlling shoot branching, SLs are relevant molecules that modulate the coordinated development of roots (e.g., primary and lateral root development, root hair elongation) and shoots (Akiyama et al. 2005; Gomez-Roldan et al. 2008; Kapulnik et al. 2011; Koltai 2011). Moreover, SLs have been implicated in the regulation of leaf senescence, secondary growth, reproduction (including flower and seed setting), and protection against pathogens and root-knot nematodes (Decker et al. 2017; Xu et al. 2019). Numerous studies have also proved that SLs mediate part of the molecular, biochemical and morphological responses needed for plants to acclimate to nutritionally poor environments (i.e., P deficiency) (Andreo-Jimenez et al. 2015; Brewer et al. 2013; de Souza Campos et al. 2019; Decker et al. 2017; Ito et al. 2017; Koltai 2013; Marzec et al. 2013; Sun et al. 2016; Yamada

et al. 2014), water deprivation (Cardinale et al. 2018; Visentin et al. 2016), low light stress (Mayzlish-Gati et al. 2012), and heat and/or cold stress (Chi et al. 2021).

To date, 30 canonical SLs have been characterized from plant root exudates (Yoneyama and Brewer 2021), with a tricyclic lactone (ABC ring) and 2'R configured butenolide ring (D ring), being these two structural features required for biological activity (Fig. 4) (Flematti et al. 2016; Scaffidi et al. 2014). Strigol- and orobanchol-like SLs differ for the stereochemistry of the B-C-ring junction: the C ring of the strigol-like SLs is in the β orientation, whereas that of orobanchol-like SLs is in the α orientation (Fig. 4a,b) (Al-Babili and Bouwmeester 2015). The AB part in both families can be modified through methylation, hydroxylation, epoxidation or ketolation, giving rise to the diversity of SLs.

Strigolactones are mainly biosynthesized in the roots, where they are produced at very low concentrations (in the pico- and nanomolar range), typically as a blend of molecules specific to the species. The biosynthesis occurs via the carotenoid pathway (Matusova et al. 2005), with the core biosynthetic module comprising the DWARF27 (D27) isomerase and carotenoid cleavage dioxygenase 7 (CCD7) and 8 (CCD8) that work sequentially to convert β -carotene to SLs universal precursor carlactone (Alder et al. 2012; Jia et al. 2018; Machin et al. 2020). Supporting the role of CCD7 and CCD8 in SL biosynthesis, tomato plants with antisense *SICCD7* construct exhibit increased branching and their root extracts induced 90% less germination of *Orobanche ramosa* seed compared to their wild-type (Koltai et al. 2010b; Vogel et al. 2010). On the other hand, tomato plants with RNAi-silenced *SICCD8* showed increased shoot branching, reduced plant height and reduced SL exudation (Kohlen et al. 2012). These SL mutants represent a powerful tool to unravel the capacity of SLs to influence and control plants physiological processes, and in particular the responses to nutritional stresses. By catalyzing repeated oxygenation reactions that can be coupled to ring closure, the CYP711A subfamily of cytochrome P450 oxygenases then convert carlactone into tricyclic-ring-containing canonical (Fig. 4a,b) and non-canonical (Fig. 4c) SLs (Kyojuka et al. 2022). Modifying enzymes further increase the diversity of SLs (as reviewed in Mashiguchi et al. 2021). In tomato, *SICYP722C* was demonstrated

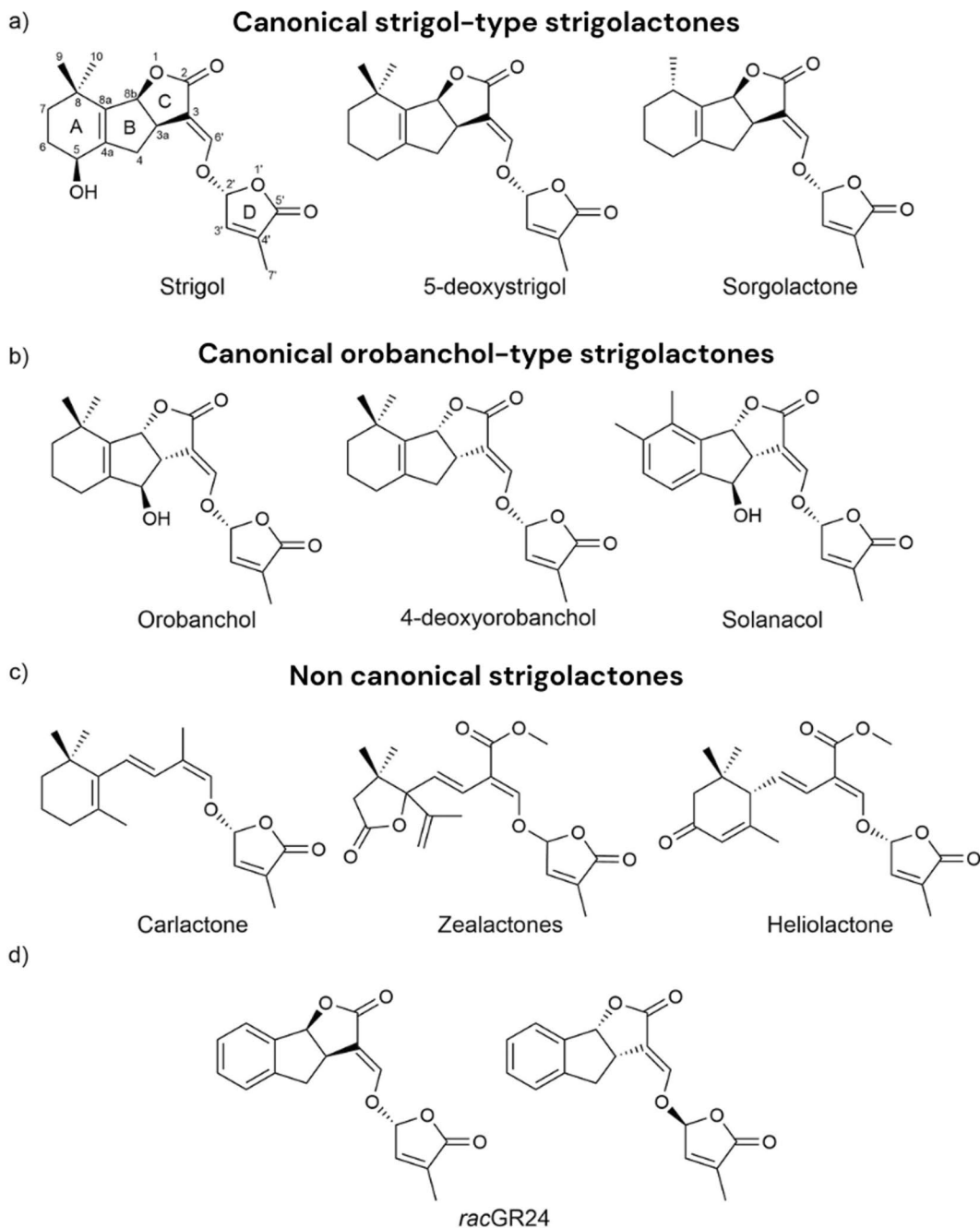


Fig. 4 Chemical structure of strigolactones (SLs). Naturally occurring SLs can be divided into two families: a) the strigol family and b) the orobanchol family, based on stereochemistry around the BC rings. Chemical differences within a family are related to substitutions on the A or B rings. All naturally

occurring SLs found to date display C2'-(R) stereochemistry via the enol-ether bridge that connects the C and D rings; c) 'Non-canonical' SLs (lacking the tricyclic lactone); d) GR24, shown as its two stereoisomers, is the most used synthetic SL. Based on Bürger and Chory 2020

to convert carlactone to orobanchol, probably via 18-hydroxy-carlactone (Wakabayashi et al. 2019).

Strigolactones function in plants through a signal transduction pathway mediated by receptor proteins (Xu et al. 2021). In SL-insensitive *dwarf 14* (*d14*) rice mutants, an α/β -fold hydrolase family protein was found to be implicated in SL signalling for the regulation of shoot branching (Arite et al. 2009; Ruyter-Spira et al. 2013), together with the F-box protein D3/MORE AXILLARY GROWTH2 (MAX2), which is part of the complex with the Skp1-Cullin-F-box (SCF) E3 ubiquitin ligase complex (Barbier et al. 2019 and references therein; Smith and Waters 2012; Xu et al. 2021).

F-box genes, including MAX2, also play a pivotal role in P starvation responses in tomato and are plausible targets of the transcription factor PHR1, which regulates most typical P starvation responses (Akash et al. 2021; Srivastava et al. 2021). In parallel, karrikins (KARs), smoke-derived butanolide signalling compounds, are perceived by a D14 homolog, KARRIKIN INSENSITIVE2 (KAI2) (Ahmad et al. 2020; Yang et al. 2019). Although only three mutations seem to be required to turn the non-SL receptor KAI2 into a receptor able to recognize SL (Arellano-Saab et al. 2021), the biological functions of KARs and SLs in plant growth regulation are different. Karrikins, for instance, are not active in hyphal branching of AMF or in inhibition of shoot branching (Xie et al. 2010; Yang et al. 2019), and in the model plant *Arabidopsis thaliana*, KAI2-mediated signalling alone regulates root hair density and length as well as root skewing, straightness and diameter, seed germination and stress response, while both KAI2 and the SL receptor D14 pathways regulate shoot branching, lateral root density and epidermal cell length (Kramna et al. 2019; Kyozuka et al. 2022; Villaecija-Aguilar et al. 2019).

Many studies suggest that the production of SLs is species-specific and, within individual species, different varieties can generate different SLs and/or mixtures of them (as reviewed in Čavar et al. 2015). In tomato, orobanchol, solanacol and the two isomers of didehydro-orobanchol are the main SLs produced, but several additional SLs have been detected in root exudates and extracts, including strigol-type SLs (Kohlen et al. 2013; López-Ráez et al. 2008; Zhang et al. 2018a). Since SLs have a dual role in plant development adjustments in response to nutritional stresses and in the establishment

of symbiosis with AMF, their levels in roots and root exudates are strongly influenced by the availability of nutrients, particularly P. When P becomes scarce, SL biosynthesis and exudation increase (López-Ráez et al. 2008; Yoneyama et al. 2007b, 2012; Umehara et al. 2010). In tomato, SL exudation is enhanced by the lack of external P, not nitrogen (N) (Yoneyama et al. 2012). Rial et al. (2019) and Marro et al. (2022) reported the presence of orobanchol ($2 \mu\text{g L}^{-1}$) and solanacol ($60 \mu\text{g L}^{-1}$) in the exudates of P-starved tomato plants. Notably, these compounds were not found in the exudates or root extracts of P-sufficient plants. Similarly, Gamir et al. (2020) observed a significant increase in the quantities of orobanchol and solanacol in tomato roots after one week of P starvation.

It is not surprising that SLs are produced in low concentrations in plants, given their potent activity at concentrations as low as 10^{-13} M for the establishment of the symbiosis with AMF (Akiyama and Hayashi 2006), 10^{-7} to 10^{-15} M for the germination of seeds of parasitic weeds (Xie et al. 2010), and 10^{-8} M for GR24 effect on lateral buds (Gomez-Roldan et al. 2008). An intriguing aspect of SL production is that the relative amount of SLs varies between root exudates and tissues, and different results can be obtained even under similar plant growing conditions (Zhang et al. 2018a). For example, Floková et al. (2020) detected similar amounts of orobanchol and solanacol (around $1 \mu\text{g L}^{-1}$) in root exudates of P-deficient tomato plants. However, the concentrations differed considerably in root tissue extracts, with solanacol being more than twice orobanchol. In a previous similar experiment, Rial et al. (2019) reported very different amounts of orobanchol and solanacol in tomato root exudates and extracts. Specifically, solanacol was found to be 35 times more abundant than orobanchol in root exudates, whereas similar concentrations for each SL were determined in root exudates and extracts of the same sample. Overall, the divergences observed in these studies underscore the need for an improved and standardized strategy for extracting, concentrating and quantifying these rapidly degradable molecules, despite significant advances in the development and optimization of highly sensitive UHPLC-MS/MS methods (Floková et al. 2020; Rial et al. 2019). In particular, the use of appropriate solvents and extraction conditions seems crucial to achieve maximum recovery and stability of SLs for accurate quantification.

Plant responses to P deficiency: a matter of concentrations

Root architecture modifications

Modifications of root growth and architecture are the best-documented responses of plants to P starvation (Czarnecki et al. 2013; Lynch 2007). To implement a prompt reaction to P shortage, plants must first sense the P status both locally and systemically in order to orchestrate the appropriate responses, with a large set of genes (> 1000) being regulated (de Souza Campos et al. 2019). In fact, P-deficiency-induced remodeling of root development is an active cellular process, mainly determined by an internal genetic program rather than being a consequence of reduced metabolic activity due to nutrient shortage (Péret et al. 2014). Svistoonoff et al. (2007) provided evidence for an important role of the primary root tip in sensing P deficiency and/or responding to it in *Arabidopsis*, highlighting how external P supply rather than internal P status triggers the local root growth response to P availability (Abel 2011). The spatial configuration of plant roots, also referred to as root system architecture, is highly plastic in response to low P conditions, and is characterized by a modular structure which enables exceptional flexibility and allows root deployment in nutrient-rich zones (Hodge 2004). Common root system architecture responses to P deficiency are high root/shoot ratio, topsoil foraging, highly branched root system with species-dependent modification of primary root, increased number and length of lateral roots and root hairs, and formation of cluster roots (Hodge 2004; López-Bucio et al. 2003; Lynch 2007; Niu et al. 2013; Ramaekers et al. 2010; Péret et al. 2014; Williamson et al. 2001). Many species such as maize and *Arabidopsis* adopt the strategy of lateral root modification under P deficiency (Dixon et al. 2020 and references therein). In contrast, in tomato plants, high P levels have been shown to increase lateral root number (Jiang et al. 2015). However, like many other species, tomato plants can respond to P deficiency by increasing root surface area and decreasing total root weight and average root diameter (Garcia and Ascencio 1992).

It has been widely demonstrated that SLs play a critical role in regulating the coordinate development of roots and shoots in response to P shortage (De Cuyper et al. 2015; Kapulnik et al. 2011; Koltai

2011; Ruyter-Spira et al. 2011; Shindo et al. 2020; Sun et al. 2014). Recently, Santoro et al. (2020) suggested that SLs contribute to adjusting the root traits of tomato plants which may aid soil exploration under low P availability. Specifically, SLs were found to increase the primary root length, the number of lateral roots, and biomass allocation to the roots. Results from the same set of experiments but with different P concentrations and timing of P deficiency establishment indicate that plant responses can be highly dependent on the level of P stress applied and on the occurrence of an acclimation period before total P deprivation. Constant P provision or sudden P depletion are not common conditions for plants in open field environments. Phosphorus availability in soils can gradually decrease due to plant uptake or fixation processes, leading to P deficiency. Therefore, a low synthesis of SLs can impact the ability of tomato roots to respond to a gradual P decrease when plants are allowed to acclimate before becoming completely P-deprived. According to Santoro et al. (2020), under conditions of P starvation, SL-depleted plants presented a decrease in total root length compared to plants that have sufficient P levels. This reduction was not due to inhibition of primary root elongation, but to a decline in the number and length of lateral roots, and was attributed to the extensive cell and tissue alterations observed in the root tips of P-starved SL-depleted plants, possibly caused by the depleted synthesis of SLs. These findings reinforce the prominent role of SLs in regulating lateral root formation and development in tomato plants, as previously observed in *Arabidopsis* and rice mutants (Kapulnik et al. 2011; Ruyter-Spira et al. 2011; Ito et al. 2015; Mayzlish-Gati et al. 2012; Sun et al. 2019), but also the inability of other hormones controlling cell division and differentiation processes at the root apex to completely overcome alterations in root morphology when SLs are depleted (Niu et al. 2013).

A common response of plants to low P levels is also the stimulation of root hair formation (Niu et al. 2013). Root hairs can occupy up to 90% of the root surface, facilitating water and nutrient uptake and allowing for soil exploration at reduced metabolic costs (Aziz et al. 2014; Czarnecki et al. 2013; Hodge 2004; Lynch 2007; Ramaekers et al. 2010). The hair length of tomato roots was shown to increase from 0.1 to 0.2–0.7 mm as the external P concentration decreased from 100 to 2 μM (Foehse and

Jungk 1983). By enhancing root hair length and density, roots can significantly increase the soil volume explored for P absorption, resulting in increased P availability as root hairs may assist in the exudation of P-mobilizing compounds such as organic acid anions, protons, and phosphatases (Ramaekers et al. 2010). Root hair development, like other root traits, is under hormonal control (Omoarelojie et al. 2019). The SL-auxin crosstalk, in particular, was initially proposed to regulate root hair formation and elongation, with SLs triggering increased auxin accumulation in root epidermal cells by modulating auxin flux from the root (Czarnecki et al. 2013; López-Bucio et al. 2003; Koltai et al. 2010a; Kapulnik et al. 2011). However, these reports have been recently revised, leading to the conclusion that the KAI2-initiated sibling pathway and not SLs is responsible for root hair changes in *Arabidopsis* (Villacija-Aguilar et al. 2019). The KAI2 receptor and its unidentified SL-like ligand appear to ultimately regulate root hair length and density under normal P growth conditions in this species, while SLs regulate lateral root density (Villacija-Aguilar et al. 2019). Whether the same holds true for tomato plants has yet to be thoroughly investigated. Thus, further research is needed to elucidate and differentiate the respective contributions of SLs and KAI2 in driving root adaptations in tomato plants. Nonetheless, decreased SL levels were observed to impede root hair elongation in P-deficient tomato roots, possibly by altering auxin levels in epidermal cells (Santoro et al. 2020).

Morphological changes in roots upon P starvation are not only the result of hormonal control but also of complex interactions between P and other nutrients, especially Fe (Rouached et al. 2010). In *Arabidopsis*, Fe accumulates more in P-starved plants than in plants with sufficient P and inhibits primary root elongation in a concentration-dependent manner (Svistoonoff et al. 2007; Ward et al. 2008). Similarly, inhibition of root growth in tomato plants treated with P-Fe coprecipitates has been attributed to Fe toxicity at the root tip (Santoro et al. 2022). Root tip inhibition is a key determinant of root system architecture remodeling triggered by low P, and this Fe-requiring response involves the LPR1 and LPR2 ferroxidases, leading to apoplastic accumulation of Fe(III) and a concomitant increase in reactive oxygen species and callose deposition in the root meristem (Müller et al. 2015; Puga et al. 2017; Svistoonoff et al. 2007). As a

result, the intracellular symplastic movement of Fe is reduced, which might interfere with the intercellular movement of the SHORT ROOT protein, a key regulator of radial root patterning, impairing root growth (Puga et al. 2017).

Root exudation

Under normal growing conditions, plant roots exude a variety of substances into the rhizosphere, significantly influencing its chemistry, soil microorganisms, and plant growth (reviewed in Aziz et al. 2014; Baetz and Martinoia 2014; Bais et al. 2006; Bertin et al. 2003; Hinsinger 2001; Vance et al. 2003; Wang and Lambers 2020). The nature of plant root exudates varies significantly in response to P deficiency. It might involve proton release to acidify the rhizosphere, organic acid anion exudation to mine sparingly available P and the release of phosphatases or phytases to mobilize organic P through hydrolysis (Aziz et al. 2014; Neumann and Römheld 1999; Wang and Lambers 2020 and references therein).

Proton (H^+)-ATPase activity is the driving force behind rhizosphere acidification, coupling ATP hydrolysis with proton transport and establishing electrochemical gradients across the plasma membrane (Fig. 5a) (Duby and Boutry 2009). Root-induced acidification can decrease the rhizosphere pH by 2 to 3 units compared to the bulk soil, which may result in significant dissolution of sparingly available soil P, particularly in alkaline to mildly acidic soils where Ca phosphates are present (Hinsinger 2001; Marschner 1995). Furthermore, the release of H^+ in the rhizosphere could also increase the availability of P adsorbed on metal oxides (Bertrand et al. 1999), and promote the hydrolysis of organic P forms by P-hydrolyzing enzymes, as phytases have an optimal working pH close to 5 (Giaveno et al. 2010). These hydrolytic reactions can produce additional protons, therefore contributing to the acidification of the soil solution.

Proton exudation as a mechanism for coping with P deficiency has been observed in various plant species including bean, tea, white lupin, and tomato (Dixon et al. 2020 and references therein). When exposed to low P concentration, tomato plant release approximately $80 \text{ nM } H^+ \text{ h}^{-1} \text{ g}^{-1}$ fresh weight whereas at high P level the release is around $30 \text{ nM } H^+ \text{ h}^{-1} \text{ g}^{-1}$ fresh weight (Zhang et al. 2018b). In

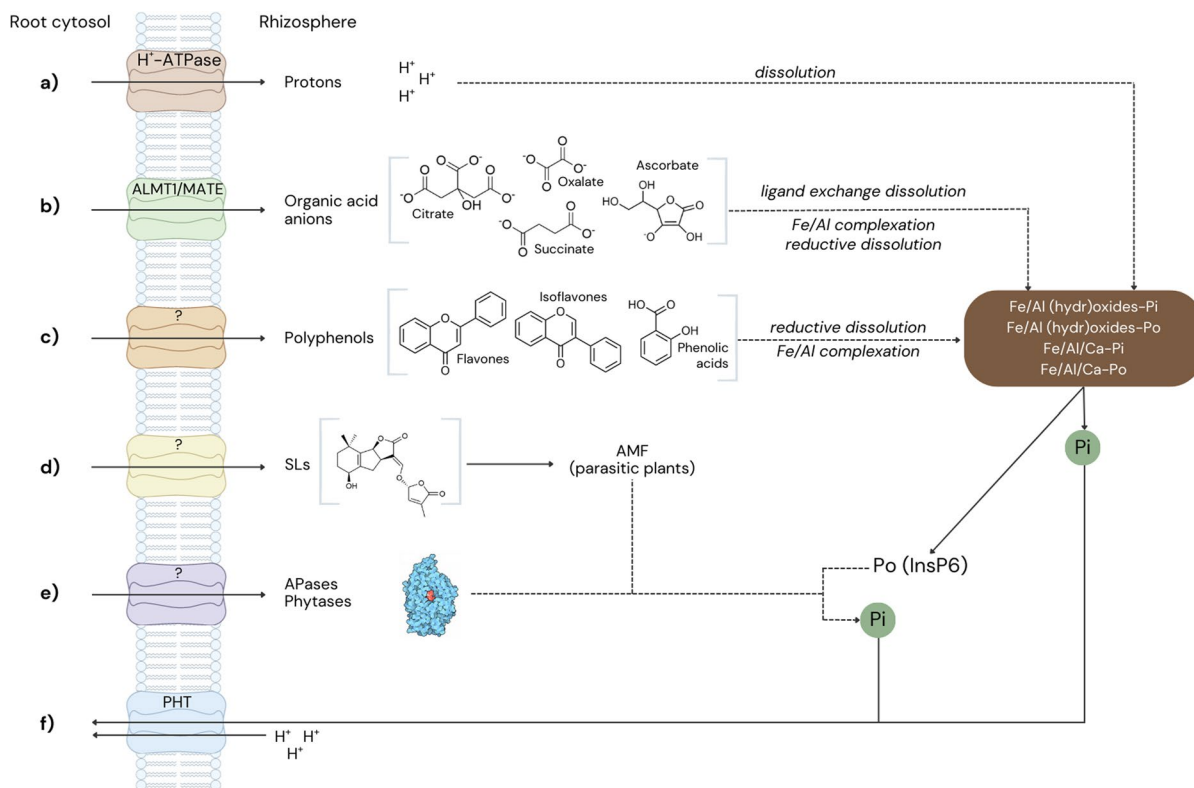


Fig. 5 Root exudates and their influence on plant phosphorous (P) uptake. a) Protons (H^+), b) organic acid anions and c) polyphenols cooperate to solubilize the inorganic (P_i) and organic (P_o) P pools by dissolving, reducing and chelating P-(hydr) oxides and Fe/Al/Ca-phosphates. d) Strigolactones (SLs) in the exudates indirectly influence P acquisition by favoring the symbiosis with arbuscular mycorrhizal fungi (AMF), while e) acid phosphatases (APases) and phytases liberate P from

P-containing organic compounds. The transporters responsible for phenolics and acid phosphatase efflux are not known. f) High-affinity phosphate transporters (PHT) are responsible for P uptake at the root level, cotransporting protons. ALMT, aluminum-activated malate transporter; MATE, multidrug and toxic compound extrusion; InsP6, inositol hexaphosphate. Based on Chai and Schachtman 2022

tomato plants, the release of protons in root exudates is influenced by SLs, as reported by Santoro et al. (2021, 2022), who noted that exogenous application of GR24 triggers rhizosphere acidification in P sufficient tomato plants, resembling the response observed under P deprivation. In a hydroponic experiment, the same authors found that wild-type tomato plants showed a prompt increase in H^+ release in response to P starvation, whereas SL-depleted mutants exhibited a delayed response (Santoro et al. 2021). Similar findings were obtained in a long-lasting experiment, where P was provided to wild-type and SL-depleted tomato plants in the form of coprecipitated P_i or no P (Santoro et al. in review, personal communication). Under both conditions, the acidifying activity of roots started to be evident

in both genotypes after 5 days since the beginning of the experiment, and remained equivalent until day 12, after which proton exudation increased severely in wild-type plants and only slightly in SL-depleted ones. These results underscore the importance of timing and process kinetics in influencing and differentiating the adaptive responses of the two genotypes, which depend on SL production. Factors operating alongside SLs in the signalling pathway induced by P deficiency could balance the dysregulated response of SL-depleted plants to compensate for and restore the exudation to wild-type plants' levels, as observed in rice and *Arabidopsis* mutants in terms of root architecture modifications (Mayzlish-Gati et al. 2012; Sun et al. 2014). In a recent study however, P was provided in hydroponics as, among

others, sparingly available organic forms (soluble and Fe-coprecipitated InsP₆), and in that case proton exudation appeared to be more related to the type of P source than to SL production (Santoro et al. 2022).

Besides proton release, increasing C exudation is a common strategy to enhance P acquisition. Among the pool of C compounds, organic acid anions are important for plant mineral nutrition and microbial growth in the rhizosphere environment (Fig. 5b) (Jones 1998), and can reach the concentration of 70 to 200 μ M in the soil solution near the root surface under P deficiency (Jones et al. 1996). Organic acid anions include acetate, aconitate, citrate, malate, fumarate, lactate, oxalate, and succinate (Aziz et al. 2014; Lambers et al. 2006), with citrate and oxalate being by far the most effective in solubilizing unavailable P forms (Hinsinger 2001). Organic anions increase the availability of Pi and Po for plants by complexing and chelating cations bound to P, such as Fe, Al, and Ca (Gerke 2015; Hinsinger 2001; Römheld and Marschner 1990), competing with Pi for sorption sites (Fink et al. 2016) and mobilizing P bound in humic-metal complexes (Adeleke et al. 2017; Gerke 1994). Organic acid anions can also have a synergistic effect on secreted P-solubilizing enzymes by changing the chemical structure or molecular size of the extracted organic P to make it more accessible to enzymatic action (Hayes et al. 2000a,b; Wang and Lambers 2020).

Johnson and Loeppert (2006) observed that the order of effectiveness of P release from ferrihydrite by organic acid anions at pH 4 was citrate > malate > tartrate >> oxalate = malonate = succinate. Ferrihydrite released more P (and Fe) than goethite, a result that indicates that under low P conditions the exudation of these anions could be more effective at increasing P availability in soils dominated by poorly than high crystalline Fe oxides.

Although it is commonly accepted that the exudation of organic acid anions leads to rhizosphere acidification (Hinsinger 2001), emerging studies have shown that, in the context of tomato plants, these two processes are biochemically separate and exhibit a weak correlation, despite their spatial coordination (Wang and Lambers 2020). Moreover, in order to maintain charge equilibrium, cations as K⁺, Na⁺ and Mg²⁺ are concurrently excreted alongside the organic acid anions (Lambers et al. 2006; Wang and Lambers 2020).

The dominant organic acid anions released by exudation can vary between genotypes and are species-specific. In the case of tomato, citrate and oxalate are the main anions exuded, followed by succinate and fumarate (Dixon et al. 2020; Santoro et al. 2021). Enhanced organic acid anion exudation following P starvation has been reported in many plant species, such as white lupin (Johnson et al. 1996; Kihara et al. 2003; Neumann 2000), alfalfa (Lipton et al. 1987), rice (Tawarayama et al. 2013) and oilseed rape (Hoffland 1992), but it appears that P deficiency does not trigger any substantial increase in organic anions exudation in tomato plants (Dixon et al. 2020; Neumann and Römheld 1999; Santoro et al. 2021). Nevertheless, exogenous SL application was found to have an impact on the metabolic profile of tomato roots, including the production of organic acids (Gamir et al. 2020). Notably, when tomato plants were grown under optimal P supply, low doses of 2'-*epi*-GR24 resulted in an alteration of malate and citrate production, partly resembling the effect observed under P limitation (Gamir et al. 2020). Responses to P deficiency involving organic acid anion release from roots however seem to depend on the specific anion. Santoro et al. (2021) observed a slight increase in succinate exudation by both SL-producing and SL-silenced tomato plants under low P conditions, while oxalate exudation increased only in the latter. In contrast, under P-repleted conditions, enhanced exudation of organic acid anions by SL-depleted tomato plants was observed and ascribed to unnecessary activation of molecular, physiological and biochemical responses to sustain an elevated P uptake with a high C cost (Santoro et al. 2021).

Genetic improvement of organic acid anion exudation could be useful in selecting more P-efficient tomato genotypes, which would reduce the application of costly P-containing fertilizers while protecting against Al toxicity and low P availability that typically constrains plant growth in acidic soils (as exemplified by Wang et al. 2013). Oxalic acid, in particular, is the simplest dicarboxylic acid, with high acidity ($pK_{a1} = 1.23$) and strong chelating capacity for Ca, Al and Fe (Ryan et al. 2001). Due to its chemical properties, it could be an optimal target molecule for plants breeding as it may be more easily released by tomato roots than other metabolic intermediates (Zhao and Wu 2014). Organic acid anions released by plants may also inhibit the crystallization of Al

and Fe hydrous oxides, reducing the rate of P occlusion (Schlesinger 1991). At the same time, they can be rapidly adsorbed onto soil particles or metabolized by soil microorganisms (Wang and Lambers 2020). Despite the potential of organic acid anion exudation genetic improvement, some authors do not expect a close correlation between their quantities in the rhizosphere and plant P acquisition, as the plant may release only small amounts of them due to the C cost associated with their exudation (Dixon et al. 2020; Wang and Lambers 2020).

Plants may also enhance the exudation of isoflavonoids, phenolics and mucilage under P deficiency (Fig. 5c) (Lambers et al. 2006). For instance, roots of pigeon pea exude piscidic acid, alfalfa exudes alfafuran, and P-deficient cluster roots of white lupin exude isoflavonoids (Vance et al. 2003 and references therein). These compounds can act as chelators or electron donors, reducing Fe(III) to Fe(II) and leading to oxide dissolution with the possible release of bound P. However, they are reportedly less effective than organic acid anions (Neumann and Römheld 2002). On the other hand, phospholipids may increase P concentration in the soil solution by directly competing with phosphate ions for adsorption sites or by altering the energetics of the interaction between the phosphate ion and the adsorption site (Read et al. 2003).

Finally, to overcome P deficiency in soil, plants enhance the release and activity of intracellular and extracellular acid phosphatase and phytase (Fig. 5e) (Dixon et al. 2020; Vance et al. 2003). This mechanism is particularly important when plants grow in soils containing high amounts of organic P pools. Soil organic P compounds sorbed onto soil particles are first mobilized by organic acid anions and then hydrolyzed to release plant available Pi (Lambers et al. 2006). Acid phosphatases can hydrolyze a wide range of organic P compounds, such as ATP, phosphoenolpyruvate, and phosphoproteins (Tarafdar et al. 2001), while phytases specifically hydrolyze phytates (*myo*-inositol penta- and hexa-phosphate), which are fairly resistant to other phosphatases (Hayes et al. 2000b). The increase of phytase activity serves as a crucial mechanism for efficiently recycling the internal P pools within the plant, as phytate is a major storage form of P in many plant tissues, especially the seeds (Konietzny and Greiner 2002; Srivastava et al. 2020). In tomato, two monomeric secreted acid

phosphatase isoenzymes have been identified (SAP1 and SAP2), which mobilize external organophosphates (Bozzo et al. 2006). In addition, a P-starvation induced (PSI) gene, *LePS2*, coding for an internal acid phosphatase has been characterized, whose transcripts are rapidly induced in tomato plants and cell cultures in the absence of P, while being repressed by P supply (Baldwin et al. 2001).

The manipulation of acid phosphatases has been proposed as an efficient strategy to improve P acquisition efficiency. For instance, in soybean and rice the overexpression of purple acid phosphatases AtPAP15 and OsPAP21b, respectively, increased P acquisition, utilization, and remobilization (Srivastava et al. 2020 and references therein). To date, this approach has not been extended to tomato, but research has shown that most of the 25 purple acid phosphatases members coded by the tomato genome are activated under P deficiency, which could fast-track the biotechnological efforts for improving P use efficiency by tomato in the future (Srivastava et al. 2020).

Exogenous application of *racGR24* has been reported to promote anthocyanin accumulation and activate acid phosphatases, suggesting a role for SLs in modulating early PSRs in plants (Ito et al. 2015). Recent studies by Gamir et al. (2020), Marro et al. (2022) and Santoro et al. (2020, 2021, 2022) have demonstrated that the deficiency in SL synthesis can impact the susceptibility to P shortage and related regulatory mechanisms in tomato. Notably, SL-deficient plants harbor higher root phytase and phosphatase activity than SL-producing plants under normal P conditions (Santoro et al. 2021, 2022). The increased phosphatase activity may indicate a more intense release of P from P-containing cellular constituents, such as membrane phospholipids, to facilitate P recycling in the plant and metabolism reprogramming to avoid P-requiring C metabolic pathways (Bozzo et al. 2006; Vance et al. 2003). The elevated activity of phytases suggests instead that plants may be attempting to mine P from phytate or using the internal phytate-derived P (Baldwin et al. 2001; Brinch-Pedersen et al. 2002; Hayes et al. 2000b). This difference in the activity of P-mobilizing enzymes was observed only under P sufficient conditions, as it remained consistent between the SL-depleted and the wild-type genotypes during P depletion (Santoro et al. 2021, 2022). Based on these findings, the authors inferred that while the typical PSRs were

activated in P-sufficient SL-depleted tomato plants perhaps because of altered P signalling and perception, the onset of these responses in the same genotype when P-starved was not as intense as conceivable given their elevated P requirement for supporting optimal growth, concluding that the negative effects of the lack of SL control on plant responses appear to occur under all P conditions. Similarly, Ito et al. (2015) observed that the application of SL induced various P starvation events in *Arabidopsis* plants under both high and low P conditions, such as anthocyanin accumulation, acid phosphatase production, and root hair elongation. These results suggest that SL signalling is involved in multiple responses to P availability, not only under low P, possibly by mediating and/or compensating for signalling defects caused by P deficiency.

Soluble InsP6 was found to stimulate the production of phytases by tomato plants, especially when SL-depleted (Santoro et al. 2022). High phytase activity was also determined in tomato plants supplied with InsP6 coprecipitated with Fe, albeit with little effect on P acquisition (Santoro et al. 2022). This is likely because the efficacy of phytases and in general of P-solubilizing enzymes can be reduced when InsP6 is retained on a surface (Fig. 3, George et al. 2007). In support of this, Giaveno et al. (2010) stated that phytases are unable to hydrolyze inositol phosphates when these are adsorbed on soil particles, highlighting that the efficacy of these phosphohydrolases can be greatly altered by the substrate availability, microbial activity, and soil physical and chemical properties (George et al. 2007; Giaveno et al. 2010; Violante and Caporale 2015), and that the effect of root exudation on P bioavailability and acquisition should be systematically evaluated, also as a function of the P source.

Mycorrhizal associations

The association between AMF and plant roots is considered one of the most important symbiotic relationships between plants and microorganisms (Redecker and Raab 2006). This symbiosis occurs in the roots of more than 80% of plants with fungi from the phylum *Glomeromycota* (Smith and Read 2008). In exchange for photosynthetically fixed C, root colonizing AMF translocate water and nutrients, primarily P and N, to the host plants, effectively increasing the surface area

of plant roots and enabling greater soil exploration and P uptake (Smith and Read 2008). Specifically, the hyphae of AMF can exploit either soil Pi by mining for distant pools of available P, or the soil organic P pool by producing phosphatase enzymes (Ezawa et al. 2005; Nasto et al. 2014; Sato et al. 2015). They can also increase the local soil P availability, improving the utilization of sparingly soluble P forms and reducing the risks of soil erosion and P losses (Cavagnaro et al. 2006; Gianinazzi et al. 2010; Parihar et al. 2019). The ability of AMF to mobilize P from less-accessible sources can lead to higher shoot P content, photosynthetic capacity, and P use efficiency. This is again related to the release of organic acid anions, which can dissolve or exchange ligands with components retaining P in the soil (Andrino et al. 2021). For all these reasons, this type of symbiosis is maximized under P deficiency, while high soil P levels generally reduce AMF colonization of the roots (Nagahashi and Douds 2004).

Mycorrhizal P uptake is generally regulated by the plant P status. In tomato, for instance, when P concentration in the plant is high the mycorrhizal uptake pathway is repressed almost completely (10% P taken up via mycorrhiza, Nagy et al. 2005). Conversely, when plant P concentrations are low the mycorrhizal uptake pathway becomes dominant (75% P taken up via mycorrhiza). In addition, recent field experiments have revealed that AMF symbiosis increases tomato fruit biomass and nutrient content to the same degree of fertilizers (Tran et al. 2022).

The establishment of AMF symbiosis relies on molecular communication between the host plant and AMF, which is conveyed by root-exuded metabolites (Fig. 5d) (Guillotin et al. 2017). Plant root exudates produced under P-limited conditions are more stimulating towards the hyphal elongation and branching of AMF than exudates produced under adequate P supply (Mashiguchi et al. 2021). Strigolactones are the key symbiotic signals that can induce hyphal branching, stimulate cell proliferation, and spore germination in AMF (Akiyama et al. 2005). Analyses of root exudates have shown that the content of SLs increases significantly under P deficiency in many plant species, including tomato, to promote AMF symbiosis, and that AMF symbiosis in turn induces changes in the transcriptional and hormonal profiles of tomato roots, reducing SL production (Andreo-Jimenez et al. 2015; López-Ráez et al. 2011). Among the various

natural and synthetic SLs, (+)-orobanchol was found to have the highest activity, followed by 5-deoxystrigol, while the synthetic analogue GR24 had a high activity comparable to that of (+)-strigol. A tight regulated hormonal interplay is however responsible for the successful interaction between AMF and plant roots. Specifically, auxin has been identified as playing a key role in regulating the early stages of AMF formation by controlling the amount of SLs in the roots (Guillotin et al. 2017). This molecular dialogue offers a promising starting point for the development of new strategies to enhance P uptake by plants, as AMF have shown to be effective biostimulants for the sustainable management of agricultural ecosystems (Andreo-Jimenez et al. 2015 and references therein; Arcidiacono et al. 2023; Chandrasekaran et al. 2021; Yoneyama et al. 2019): understanding the hormonal mechanisms underlying their interactions with plants can lead to the development of more efficient and sustainable agricultural practices.

Internal P remobilization, gene expression, and metabolic changes

Phosphorus deficiency triggers a process of within-plant remobilization of P, where the element is moved from structures and processes where it is least required, such as from senescent to developing tissues (Dixon et al. 2020; Maillard et al. 2015; Vance et al. 2003). Phosphorus is mainly stored in vacuoles, where 85 to 95% of P reserves are normally located. Unlike cytoplasmic P concentration, which remains relatively constant (5–10 mM) and independent of external P supply, vacuolar P concentration varies widely (Schachtman et al. 1998 and references therein). Vacuolar P could be almost undetectable under P starvation, but when plants have an adequate P supply, Pi is converted into organic storage compounds, primarily InsP6 (Haran et al. 2000; Schachtman et al. 1998). Internal P is fairly mobile, which allows for the temporary mobilization and maximum utilization of P reserves in response to P deficiency. This strategy may result in reduced growth rates, decreased vacuolar P content, reuse of P from membrane lipids and reduced nucleic acid P pools (Rausch and Bucher 2002). Besford (1979) observed that P deficiency induced a rapid export of P from tomato plant leaves after the transfer of plants from a P-rich to a P-free medium. More recently, the identification

of phosphate transporters such as *Pht1;5* in *Arabidopsis* and *OsPht1;8* in rice, involved in P redistribution from source to sink organs according to the P status of the plant, has shed light on the molecular mechanisms underlying P remobilization in plants (Li et al. 2015; Nagarajan et al. 2011).

Intracellular acid phosphatases play a crucial role in the recycling of P from expendable intracellular organophosphate pools. A study with tomato suspension cells revealed that low P induced the expression of a phosphatase involved in internal P remobilization. This explains the ability of tomato seedlings, as observed in a parallel experiment, to use stores of phytate and prevent the onset of the typical morphological and biochemical symptoms of P deficiency during the first 10 days of growth (Bozzo et al. 2006).

Adaptation to P deficiency also implies important changes in gene expression. Wang et al. (2021a) observed that two days of P starvation resulted in 57 up-regulated genes and the downregulation of only one gene compared to control P conditions in tomato. The number of differentially expressed genes increased to 331 and 406 at 3 and 4 days of P starvation, respectively. The maximum number of differentially expressed genes observed after 4 days was likely due to the plant acclimation to P depletion. One day of P resupply reduced the expression of 139 P starvation upregulated genes, while increasing the expression of 28 downregulated genes, indicating that these genes were highly responsive to variation in P availability (Wang et al. 2021a).

Sugars play a critical role in regulating the transcription of PSI genes in plants (Khurana et al. 2021 and references therein). Sucrose non-fermenting 1-related protein kinases (SnRK) genes mediate plant signalling pathways in response to various abiotic and biotic stresses by phosphorylating target proteins (Khurana et al. 2021). Khurana et al. (2021) identified 40 SnRK members in the tomato genome, grouped into three subfamilies (SnRK1, SnRK2, and SnRK3) and found that SISnRK3.10a, SISnRK3.15a and SISnRK3.26 were activated at varying levels under P starvation. Although the functional role of PSI SnRK genes are still unknown in tomato, SnRK1 members in *Arabidopsis* interact with PHT1;4 and PHO1 (Carianopol et al. 2020).

De Groot et al. (2001) observed significant metabolic changes in P-depleted tomato plants, which

revealed important effects on plant growth and physiology. Severe P limitation resulted in a decreased rate of photosynthesis and reduced production of assimilates, whereas the application of increasing P concentrations led to improved growth rather than increased plant P concentration. The authors also found that the importance of morphological changes versus physiological responses varied with the severity of P limitation, with mild P limitation mainly affecting plant morphology and severe P limitation influencing physiological responses (de Groot et al. 2001). These findings highlight the significant impact that even slight differences in P provision can have on plant responses at different levels. Therefore, careful consideration of the level of P-deficiency is crucial when setting up P stress experiments.

Phosphorus deficiency can have far-reaching consequences on the metabolic processes that control crucial fruit quality traits. Li et al. (2021) observed that low P treatment during tomato fruit ripening caused an overaccumulation of main pigments and key organic acids linked to tomato fruit sourness, while the content of soluble organic sugars responsible for fruit sweetness was reduced. These changes were attributed to alterations in enzyme activities in relevant metabolic pathways, such as the γ -aminobutyric acid shunt (Li et al. 2021).

The massive transcriptional reprogramming that plants undergo under P deficiency can lead to increased production of SLs (López-Ráez et al. 2008; Gamir et al. 2020; Marro et al. 2022). Phosphorus starvation upregulates the SL biosynthetic genes such as *D27*, *CCD8*, *MAX1* and *CYP722C* in tomato, while their expression is repressed upon P replenishment (Wang et al. 2021a). A recent research by Wang et al. (2021a) sheds light on the functional link between increased SL biosynthesis and transcriptional modifications. This study shows that SLs play a crucial role in regulating the PSR as plant hormones, beyond being just the end products of the response. In the tomato *CCD8* RNAi line (SL-depleted), about 96% of the PSR genes were less affected by P deficiency than in the wild-type. The presence of SLs was found to be essential for two thirds of the transcriptional changes referred to genes involved in the suppression of phospholipid biosynthesis, degradation of phospholipids and biosynthesis of sulfolipids and galactolipids under P starvation (Wang et al. 2021a). Other biosynthetic pathways that are reprogrammed under P

starvation and as a function of SL production include those involved in the production of phenylpropanoids and carotenoids, pantothenate and CoA, and alkaloids (Wang et al. 2021a). Gamir et al. (2020) also reported that some metabolites (e.g., azelaic, linoleic and alpha-linolenic acids) related to plant immunity were accumulated in tomato under P limitation and exogenous SL application, while SL-deficient mutants were more susceptible to pathogens due to the low accumulation of these metabolites. Such results clearly indicate that SLs are not just the end-product of the PSR in plants, but play a major role in the regulation of the PSR itself.

High-affinity phosphate transporters and P uptake regulation

Phosphorus is absorbed by plants as the orthophosphate anion in the form of H_2PO_4^- and HPO_4^{2-} (Fig. 3). This process is driven by a proton gradient generated by plasma membrane H^+ -ATPases (Liu et al. 1998; Victor Roch et al. 2019) and, after uptake, P can remain as Pi or can be incorporated into organic molecules forming an ester with a hydroxyl group of a carbon chain such as sugar phosphates, or by attaching to another Pi via an energy-rich pyrophosphate bond (Fig. 3, Marschner 1995). The root is the primary organ for nutrient uptake from soil, and P acquisition depends on rapid root growth and large root area to increase soil exploration. While the root cap contributes to about 20% of total P uptake, P acquisition at the elongation zone is marginal (Kanno et al. 2016a, b). The concentration of P in root cells can be up to 1000-fold higher than in the soil solution, making P uptake an energy-mediated process that involves multiple epidermally located transport systems (Czarnecki et al. 2013; Duby and Boutry 2009; Hinsinger 2001; Schachtman et al. 1998). Plants have both low- and high-affinity P uptake systems to facilitate this process (Furihata et al. 1992). The low-affinity system is constitutive in plants and operates at the mM range (Raghothama 1999), whereas the high-affinity system is induced under low P conditions in the μM range, thus increasing the potential for enhanced P uptake from low P soils (Fig. 5f) (Chen et al. 2014). It is important to note that only the high-affinity system operates in the rhizosphere, where P concentrations are typically low (Hinsinger 2001 and references therein).

Most of the genes encoding for membrane-bound phosphate transporters are expressed in the roots and are categorized into five families (He et al. 2019; Victor Roch et al. 2019). Among these, the PHOSPHATE TRANSPORTER 1 (PHT1) gene family's high-affinity Pi/H^+ symporters are primarily responsible for P uptake from soil and subsequent redistribution in plants. A total of eight putative PHT1 genes (*LePT1* to 8) have been identified in the tomato genome (Chen et al. 2014), with *LePT1* and *LePT2* consisting of 12 membrane-spanning regions and sharing a high sequence similarity with other high-affinity P transporters (Dixon et al. 2020). The expression of these genes varies depending on the plant P status and developmental stage. *LePT1* and *LePT7* are ubiquitously expressed in roots, stems, young leaves, flowers, and fruits, and their transcripts are abundantly accumulated during P starvation (Chen et al. 2014; Zhang et al. 2018b). *LePT2* and *LePT6* are predominantly expressed in the roots of P-deficient plants, while *LePT3*, *LePT4* and *LePT5* are strongly upregulated in roots colonized by AMF under low P conditions (Chen et al. 2014; Gómez-Ariza et al. 2009; Zhang et al. 2018b). Conversely, *LePT1*, *LePT2*, *LePT6*, and *LePT7* are downregulated in mycorrhizal tomato roots under low P supply (Chen et al. 2014).

Liu et al. (1998) demonstrated that the transcript levels of *LePT1* and *LePT2* in tomato roots significantly increased within 1 day of transferring plants to a P-deficient medium, likely due to the depletion of internal P reserves and/or lack of P supply to the roots. This effect was most prominent after 5 days of P starvation, and resupplying P to P-starved tomato plants repressed *LePT1* and *LePT2* transcripts to their uninduced levels within 2 days. In addition, based on the findings of a split-root experiment, the authors hypothesized that the signals responsible for the P starvation response may arise internally due to changes in the cellular P concentration (Liu et al. 1998). Earlier reports have shown that providing P to a portion of the root system can partly or completely compensate for P deficiency in other parts of the root system by increasing nutrient uptake rates and derepressing the expression of P transporters genes (Drew and Saker 1984).

The expression of high-affinity P transporters can be affected by exogenous SL application, as shown in some studies (Gamir et al. 2020; Marro et al. 2022; Santoro et al. 2021, 2022). For example, Gamir et al. (2020) found that short-term application of 2'-*epi*-GR24

enhanced the expression of *LePT2*. Interestingly, the SL-deficient tomato line *SICCD8-RNAi* displayed altered transcript levels of key regulatory elements of phosphate transporters, such as *PHO2*, which were also less sensitive to P starvation (Gamir et al. 2020). Marro et al. (2022) confirmed these findings, supporting the role of SLs in regulating the PSR response. However, SL deficient lines can apparently modulate their responses based on the level of P deficiency. Santoro et al. (2021, 2022) found that *LePT1*, *LePT2* and *LePT4* were upregulated by P starvation in wild-type tomato plants, but not in the *SICCD7*-silenced line, for which in turn these genes were up-regulated when P was sufficient. Discrepancies in these outcomes have been ascribed to difference in P concentrations used for treating tomato plants. The concentration of P used by Santoro et al. (2022) for the P-sufficient treatment (80 μM) should simulate the typical range of P concentration in the field (Hinsinger 2001), and was sufficient for wild-type tomato plants, but revealed a defect in SL-depleted plants, likely due to altered perception and/or production of internal P stocks. Furthermore, Santoro et al. (2022) investigated the PSR activation when different P forms (soluble and sparingly available), both inorganic and organic, were supplied. In this case, SL-depleted plants tended to be more effective in accessing sparingly available P forms than wild-type plants, thanks to higher PHT transcription and phytase activity. Therefore, the differences in external P concentration and P source may have triggered diverse regulatory signals of PHT transporters in the two genotypes, highlighting the fine-tuned regulation of SLs in response to differential external P availability and the need to consider the specific applied conditions, which makes generalizations difficult at this stage of SL research.

Complex signalling network underlying plant responses to P deficiency: which role for strigolactones?

The activation of PSRs requires a fine-tuned coordination and integration of local and systemic (or long distance) signalling pathways, involving a number of genes and signalling molecules (Ham et al. 2018; Puga et al. 2017). Phosphorus homeostasis is regulated systemically, with most of the genes related to P transport, recycling, and signalling being controlled at the systemic level, including those involved in phospholipid remobilization and galactolipid and sulfolipid synthesis (Thibaud et al.

2010). It is also mediated by the perception of Pi at the cellular level in different organs, followed by inter-organ communication of P concentration via long-distance systemic signalling (Ham et al. 2018; Marro et al. 2022; Puga et al. 2017). Even though Pi is known to act as a signal in regulating diverse responses to P limitation, it does not appear to be a long-distance signal from root to shoot (Ticconi and Abel 2004). Instead, the allocation or recycling of P between shoots and roots is believed to provide the systemic signal (Lin et al. 2008 and references therein). Changes in root development are instead locally regulated by P availability in the external medium (Péret et al. 2011), with sensing of external P concentrations likely occurring at the root tip and inducing modifications in root architecture (Müller et al. 2015; Ticconi and Abel 2004; Svistoonoff et al. 2007). This process is dependent on the auxin receptor TRANSPORT INHIBITOR RESPONSE1 (TIR1) and MORE AXILLARY GROWTH 2 (MAX2), a F-box protein that also functions as a key signalling component in the SL pathway (Al-Babili and Bouwmeester 2015; Mayzlish-Gati et al. 2012; Wang and Smith 2016; Wang et al. 2021b).

Much of the P starvation signalling pathway centers on the transcriptional activator PHOSPHATE STARVATION RESPONSE 1 (PHR1) and related transcription factors that regulate the main PSRs. These include induction of P scavenging and transport activities, membrane lipid remodelling, increase in root/shoot ratio, and repression of photosynthesis and photorespiration (Fig. 6b) (Puga et al. 2017 and references therein). PHR1 is expressed constitutively in *Arabidopsis*, and its activity is regulated by the plant P status. Recent studies have highlighted the critical roles of SPX domain-containing proteins SPX1 and SPX2 in sensing external and internal Pi levels (Puga et al. 2017; Zhou et al. 2015). These proteins can detect inositol phosphates as a P signal and negatively regulate PHR1 activity. Inositol octaphosphate (InsP8) has been recently identified as the intracellular P signalling molecule serving as the ligand of SPX1 for controlling P homeostasis in plants (Dong et al. 2019). A high level of intracellular P promotes the synthesis of InsP8, which binds to the SPX domain in SPX1 and promotes the binding of SPX1 to PHR1, blocking PHR1 transcriptional activity (Fig. 6a) (Dong et al. 2019). Under P deficiency conditions, the interaction between SPX1 and PHR1 is abolished due to a decrease in InsP8. This enables the PHR1-mediated activation of

P starvation-induced gene expression, which promotes P uptake and relieves P-mediated negative post-translational control of PHT1 transporters by inducing the expression of microRNA399 (miR399). miR399 is transported through the phloem from the shoots to the roots, where it triggers post transcriptional inhibition of PHO2, a protein that controls PHT1 turnover via ubiquitination. This leads to decreased proteolytic degradation of PHT proteins and enhanced P uptake (Ham et al. 2018; Lin et al. 2008; Liu et al. 2012; Puga et al. 2017). As a consequence of this mechanism, *Arabidopsis* plants overexpressing miR399 or the *pho2* mutant over accumulate P in the shoots (Lin et al. 2008). PHR1 also controls the induction of the genes that encode *IPS1* (TPS11 in tomato) and related non-coding RNAs that sequester and negatively modulate miR399 to prevent the interaction miR399-*PHO2* and the degradation of *PHO2* transcripts. Therefore, the triad *IPS1*-miR399-*PHO2* has a central role in the regulation of P acquisition by plants and P homeostasis, particularly in long-term P deprivation (de Souza Campos et al. 2019; Puga et al. 2017). A P starvation response partially independent from the PHR1 pathway described above is root tip inhibition. The signalling pathway of this response involves extracellular P sensing and depends on local P levels (Puga et al. 2017). It is distinct from that centered around PHR1, which is controlled by the overall plant P status. For this reason, the two signalling pathways are qualified as operationally different, although they are integrated because they share crosstalk (Puga et al. 2017).

Recent discoveries suggest that SLs are involved in regulating P signalling in plants, as the expression of the triad *IPS1*-miR399-*PHO2* was modified following exogenous SL application or in SL-biosynthesis mutants (Gamir et al. 2020; Marro et al. 2022; Santoro et al. 2021, 2022). Short-term application of 2'-*epi*-GR24 to tomato plants increased the expression of *PHO2*, *IPS1*, and miR399 genes, which were already promoted by P starvation (Gamir et al. 2020). Exogenous SL application induced the expression of *IPS1* and miR399 genes under optimal P conditions, partly mimicking the effect observed under P starvation, and increased SL concentration under both P deficiency and optimal P conditions, when SLs levels in plants are usually very low. This supports the evidence that SLs act as signals that trigger plant responses to P deficiency (Gamir et al. 2020). Interestingly, the authors found that the SL-deficient line *SICCD8-RNAi* displayed altered

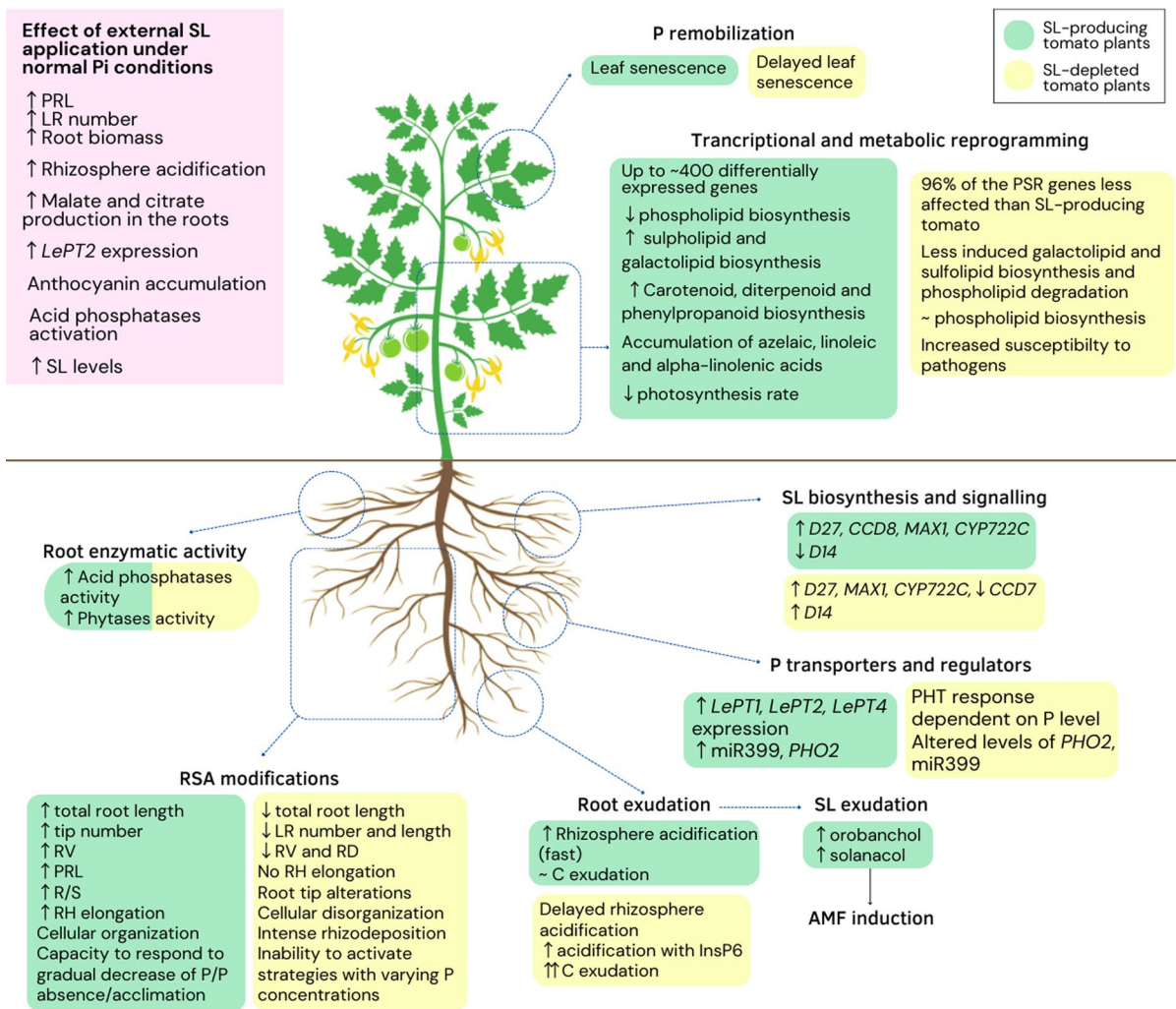


Fig. 7 Conclusive conceptual summary of how strigolactones (SLs) are involved P-deficiency responses in tomato plants. Belowground, they influence root architecture, root exudation, enzymatic activity and the expression of P transporters and their regulators. Their exudation can indirectly increase P uptake through the instauration of symbiosis with arbuscular

mycorrhizal fungi (AMF). In the shoots, they have an effect on P remobilization and on transcriptional and metabolic reprogramming. InsP6, inositol hexaphosphate; LR, lateral root; PRL, primary root length; RD, root diameter; RH, root hair; RSA, root system architecture; RV, root volume

multifaceted result highlight that there is still much to be discovered regarding the effect of SLs on the signalling pathway activated by scarcely available P forms.

Concluding remarks

In recent years, the significant roles of SLs in the adaptation of plants to environmental constraints,

particularly low P availability in agricultural soils, have gained great attention. This review tried to combine the extending knowledge on abiotic P processes occurring in soil that limit P availability to plants with the emerging roles of SLs in tomato plant P nutrition and responses to P scarcity, as summarized in Fig. 7. While acting as germination stimulants for parasitic weeds, SLs also control plant development and enhance symbioses, making them

an important but to date potential tool to improve crop productivity and resilience. Field trials have validated the potential use of SLs (as well as SL analogs or inhibitors) as agrochemicals or genetic targets in breeding programmes, with applications in improving nutrient uptake, drought tolerance, increasing yield and controlling parasitic weed germination. However, many of the activities of SLs remain unexplored, and their commercial deployment is currently hindered by difficulties related to the absence of an affordable source of SLs or SL analogues and their low stability. The development and use of specific and stable SL analogues may allow cost-effective and efficient agricultural use, as well as the identification or generation of under-producing SL mutants/transgenic plants, including tomato, with an increased ability to scavenge P from scarcely available forms in the soil. In addition to this, a comprehensive understanding of the P processes at the soil–plant interface can open new opportunities to optimize P recycling and circularity and increase plant P acquisition efficiency while minimizing crop requirements. This would help to reduce P losses to the environment and mitigate the ecologically damaging impact of P on water resources, ultimately leading to more sustainable agriculture. For this to happen, it is necessary to consider the specific factors under which experiments are carried out that may influence P acquisition: diverse plant species and age, growth medium composition, especially type and concentration of provided P, duration of exposure, and SL concentration (in the case of SL treatments). The detailed control of these factors and the adoption of conditions that best mimic the soil abiotic processes may provide a deeper understanding of the fine-tuned action of SLs in regulating plant responses to different crop scenarios and find new solutions to improve agriculture sustainability.

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Declarations

Competing interests The authors have no conflicts of interest to declare.

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