Plant Lipid Metabolism Responses to Phosphate Scarcity

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Low phosphate (Pi) availability in soils severely limits crop growth and production. Plants have evolved to have numerous physiological and molecular adaptive mechanisms to cope with Pi starvation. The release of Pi from membrane phospholipids is considered to improve plant phosphorus (P) utilization efficiency in response to Pi starvation and accompanies membrane lipid remodeling. Researchers summarize recent discoveries related to this topic and the molecular basis of membrane phospholipid alteration in response to Pi depletion in plants at different subcellular levels. These findings will help to further elucidate the molecular mechanisms underlying plant adaptation to Pi starvation and thus help to develop crop cultivars with high P utilization efficiency.

lipid metabolism phosphate starvation triacylglycerol

1. Introduction

Phosphorus (P), as an essential macronutrient for plants, is a vital component of nucleic acids, membrane lipids, and adenosine triphosphate (ATP), and is involved in various metabolic processes [1][2]. The phosphate (Pi) directly absorbed by plants is easily fixed in soil, which leads to low P availability, which then severely limits crop growth and production [3]. A traditional method used to manage P deficiency is to increase the application of Pi fertilizers, which leads to the excessive waste of Pi rock resources and environmental eutrophication [4][5]. Over the past few decades, the underlying molecular mechanisms and genetic bases of strategies that plants use to adapt to P deficiency have been extensively investigated; these strategies include changes in root morphology or architecture, the promotion of the expressions of Pi transporter genes, the enhancement of the excretions of organic acids and acid phosphatases, and so on [6][7]. In addition to improving the efficiency of Pi acquisition from soil, an increasing number of studies have also focused on plants' internal P pools for metabolism and remobilization, such as phospholipids [8][9]. Phospholipids store ~30% of cellular organic P, which is an organic P pool; it is used as an internal Pi source that enables plants to cope with Pi depletion [4][10].

Lipid metabolism, especially in terms of membrane lipid remodeling, has been shown to be an indispensable and well-conserved adaptive mechanism for plants' adaption to Pi deprivation [8][9][11]. Most extraplastidic membranes are mainly composed of phospholipids such as phosphatidic acid (PA), phosphatidylcholine (PC), phosphatidylethanolamine (PE), phosphatidylinositol (PI), and phosphatidylserine (PS) [11][12]. Under Pi-starvation stress, membrane phospholipids are hydrolyzed to release Pi groups. This process mainly involves three pathways: the phospholipase C (PLC) pathway, the phospholipase D (PLD) and phosphatidic acid phosphatase (PAP) pathway, and the lipid acyl hydrolase (LAH) and glycerophosphodiester phosphodiesterase (GDPD) pathway

[8]. Meanwhile, to maintain membrane functionality, non-P galactolipids including monogalactosyldiacylglycerol (MGDG) and digalactosyldiacylglycerol (DGDG) or sulfolipids (i.e., sulfoquinovosyldiacylglycerol, SQDG) are synthesized to replace phospholipids and to be incorporated into the membrane [8][11]. It is worth noting that the synthesis of non-P galactolipids and sulfolipids mainly takes place in plastids, in which membranes mainly include MGDG, DGDG, SQDG, and phospholipid phosphatidylglycerol (PG) [8][12][13].

2. Phospholipids' Degradation in Response to P Deficiency

2.1. Phospholipase C Pathway

The plant phospholipase C family includes the phosphoinositide (PI)-specific phospholipase C (PI–PLC) and non-specific phospholipase C (NPC) families according to their substrate specificity [14][15]. Accumulating evidence has shown that PI-PLCs participate in the hydrolyzation of phosphatidylinositol 4,5-bisphosphate to generate inositol 1,4,5-trisphosphate and DAG [16]. The plasma membrane's perception of external stimuli may be changed and triggered to activate lipid signaling to regulate diverse cellular processes [15]. For example, inositol 1,4,5-trisphosphate, one product of phosphatidylinositol 4,5-bisphosphate hydrolyzed by PI-PLCs, is involved in Ca^{2+} release [15]. There are nine PI-PLC members in Arabidopsis named AtPLC1 to AtPLC9; most of them are induced by diverse environment stresses [16][17][18]. Among them, AtPLC2 has been identified as a primary PI-PLC and plays a role in the phospholipid metabolism and endoplasmic reticulum stress responses [19]. However, none of these Arabidopsis *PI-PLC* genes have been reported to be involved in responses to P deficiency.

NPCs, which are different than PI-PLCs and belong to the non-specific phospholipase C family, can function in diverse phospholipids, including phosphatidylcholine (PC), phosphatidylethanolamine (PE), and phosphatidylserine (PS) [8][14]. A total of six members of the Arabidopsis NPC family have been identified, namely AtNPC1–AtNPC6 [20]. Among them, the transcript levels of two members are induced by P deficiency. AtNPC4 has been reported to be the primary contributor to NPC activity under Pi-starvation conditions [20]. Recently, AtNPC4 was confirmed to mainly function in the lipid metabolism in roots during short-term Pi depletion by hydrolyzing PC, the most abundant glycerophospholipid in vitro [20][21][22]. However, the knockout of *AtNPC4* had no effects on the level of PC, suggesting that AtNPC4 is not the predominant enzyme of PC [20]. Recent research also showed that AtNPC4 had high hydrolyzing activity on glycosylinositolphosphorylceramide (GIPC), the most abundant phosphosphingolipid in plants, to generate hydroxyceramide (hCer) in vitro [23]. Additionally, the knockout of *AtNPC4* significantly decreased the loss of GIPC under P-deficiency conditions, indicating that AtNPC4 plays a critical role in the degradation of plasma membrane GIPC, but not PC, in response to Pi starvation [23]. Recently, the C terminus acylation of AtNCP4 was reported to be essential to its plasma membrane association and function in response to P deficiency [24]. On the other hand, AtNPC4 mainly functions in the plasma membrane [20], suggesting that AtNPC4 is also involved in lipid-signaling regulation. DAG, as a product of phospholipids hydrolyzed by NPC, was proposed to mediate lipid signaling in the regulation of root development [22][25]. In Arabidopsis, the *atnpc4* mutant showed a shorter root hair length compared to normal plants under Pi-starvation conditions, suggesting that *AtNPC4* plays a role in the plant lipid-signaling response to early stages of P deficiency, mediating root hair elongation [21]. In addition to AtNPC4, AtNPC5 was also induced by Pi starvation, and the

subcellular localization of AtNPC5 was mainly in the soluble fraction [22][25]. Furthermore, the *atnpc5* mutant significantly reduced the level of DGDG compared to wild types in Arabidopsis [25], suggesting that *AtNPC5* also plays a role in membrane lipid remodeling

2.2. Phospholipase D and Phosphatidic Acid Phosphatase Pathway

Phospholipase D is also found to participate in the hydrolyzation of phospholipids to generate phosphatidic acid and soluble head groups; then, phosphatidic acid could be further hydrolyzed by phosphatidic acid phosphatase to generate DAG and release Pi [8][26][27]. The Arabidopsis phospholipase D gene family member *AtPLDZ2* was reported to be induced by P deficiency in both shoots and roots [28]. AtPLDZ2 localized in the tonoplast and the relative amounts of PC and PE were significantly increased in the *atpldz2* mutant compared to the WT of Arabidopsis roots under Pi-starvation conditions [28][29], suggesting that *AtPLDZ2* plays a role in tonoplast membrane phospholipids' degradation in response to Pi starvation (**Table 1**). Furthermore, the *atpldz2* mutant also decreased the relative amounts of DGDG in Pi-limited Arabidopsis roots, suggesting that *AtPLDZ2* also plays a role in membrane remodeling in roots, especially in DGDG synthesis [28]. AtPLDZ2 was also reported to be involved in root hair development in response to Pi starvation [30]. Under P-deficiency conditions, an increased abundance of AtPLDZ2 proteins derives more PA, which can bind to SORTING NEXIN 1 (SNX1) to decrease vacuole endocytosis and the degradation of PIN-FORMED2 (PIN2), leading to an increase in PIN2 accumulation at the plasma membrane, thus promoting root hair growth [30]. In addition, compared to AtNPC4, AtPLDZ2 also was shown to have greater effects on leaves' lipid remodeling at later stages of Pi depletion [21].

PAPs have been reported to function in P-deficiency-induced membrane lipid remodeling [8]. According to their enzymatic properties, PAPs can be divided into Mg^{2+}-dependent or -independent types [31]. Phosphatidic acid phosphohydrolase (PAH) is an important Mg^{2+}-dependent PAP [8][32]. In Arabidopsis, two *PAH* genes (*AtPAH1* and *AtPAH2*) were identified and suggested to function redundantly in PA degradation in leaves' endoplasmic reticulum (ER) [32]. It is still unknown whether *AtPAH1* and *AtPAH2* are induced by Pi starvation. However, a double mutant using *atpah1* and *atpah2* significantly increased the phospholipid level but decreased the DGDG level, impairing shoot and root growth under P-deficiency conditions [11], suggesting that AtPAH1 and AtPAH2 play roles in the membrane lipid metabolism and remodeling. Lipid phosphate phosphatase (LPP) has been known to belong to the Mg^{2+}-independent PAP family and functions in the hydrolysis of diverse substrates, including PA, lyso-PA, and diacylglycerol pyrophosphate [8][9][33]. Although nine LPP members exist in Arabidopsis, none of them are induced by P deficiency [8][34].

2.3. Lipid Acyl Hydrolase and Glycerophosphodiester Phosphodiesterase Pathway

LAH can hydrolyze phospholipids to generate fatty acids and glycerophosphodiester (GPD), which is further hydrolyzed by glycerophosphodiester phosphodiesterase (GDPD) to generate glycerol-3-phosphate (G3P) and corresponding alcohols (choline, ethanolamine, inositol, glycerol, etc.) (**Figure 1**) [35]. In Arabidopsis, several LAH (or PLA) genes were identified as up-regulated by P deficiency [36]; however, the functions of proteins that were involved in the phospholipid metabolism's response to Pi starvation remain largely unknown. The Arabidopsis

GDPD subfamily has six members, all of which are up-regulated by Pi starvation except for *AtGDPD4* [35]. As a plastid-localized protein, the *atgdpd1* mutant exhibited impaired growth coupled to the reduction in both glycerol-3-phosphate and Pi contents in shoots and roots under Pi-starvation conditions [35], suggesting that *AtGDPD1* plays a role in Pi release from phospholipids in response to P deficiency (**Table 1**). In addition to *AtGDPD1*, Pi-starvation-induced *AtGDPD6* also was functionally characterized to play a role in glycerophosphocholine (GPC) hydrolysis in response to P deficiency [37]. In Arabidopsis, the *atgdpd6* mutant also exhibited decreased root growth under Pi-deficient conditions [37]. However, when G3P was supplemented in the medium, the inhibited root phenotype of the *atgdpd6* mutant was rescued, suggesting that *AtGDPD6* also plays a role in the degradation of glycerophosphodiester and sustains root growth under P-deficiency stress [37]. There are 13 OsGDPD members in rice. Among them, *OsGDPD1/2/3/5* were up-regulated in roots after 7 days of Pi starvation and *OsGDPD1/2/34/5/7/10/11* were up-regulated after 15 days of Pi starvation [38]. Recently, *OsGDPD2* was found to be up-regulated by P deficiency in both shoots and roots, and it was suggested to be downstream of OsPHR2 [39]. Additionally, OsGDPD2 exhibited hydrolysis activities against several glycerophosphodiesters, including glycerophosphocholine (GPC), glycerophosphoinositol (GPI), and glycerophosphoethanolamine (GPE), and played a role in membrane remodeling in response to Pi starvation [39]. In addition, a total of six CaGDPD members were identified in chickpea (*Cicer arietinum*), of which one (*CaGDPD1*) was shown to be up-regulated while three (*CaGDPD2/3/4*) were down-regulated after 15 days of Pi starvation in roots [38]. Moreover, *CaGDPD1* was proved to be localized in the ER and other endomembranes and exhibited high enzyme activity in GPC and glycerophosphoethanolamine (GPE) [38], suggesting that *CaGDPD1* may play a role in chickpea roots' adaption to P deficiency through the hydrolyzation of glycerophosphodiester.

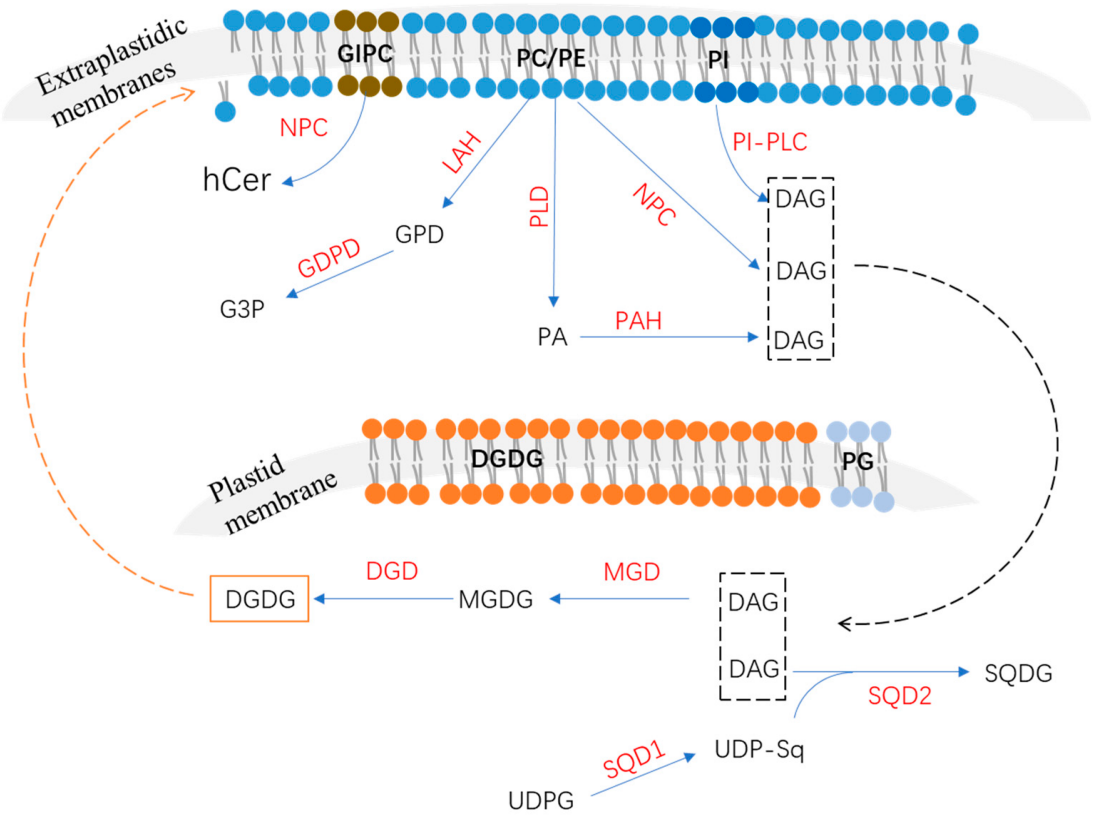

Figure 1. Metabolic pathways in membrane lipid remodeling and related enzymes. The plastid membranes mainly consist of glycolipids, while extraplastidic membranes mainly consist of phospholipids. Under P-deficiency conditions, phospholipids can be degraded to release the phosphate group, then the non-phosphorus galactolipids are compensatively synthesized to replace the phospholipids. GIPC, glycosylinositolphosphorylceramide; hCer, hydroxyceramide; PC, phosphatidylcholine; PE, phosphatidylethanolamine; PG, phosphatidylglycerol; GPD, glycerophosphodiester; G3P, glycerol-3-phosphate; PI, phosphatidylinositol; PA, phosphatidic acid; DAG, diacylglycerol; DGDG, digalactosyldiacylglycerol; MGDG, monogalactosyldiacylglycerol; SQDG, sulfoquinovosyldiacylglycerol; UDPG, uridine diphosphate glucose; UDP-sq, UDP-sulfoquinovose; MGD, MGDG synthase; DGD, DGDG synthase; SQD1, UDP-sulfoquinovose synthase; SQD2, sulfolipid synthase.

3. Non-Phosphorus Lipid Biosynthesis

The compensatory increase in levels of non-phosphorus lipids such as galactolipids and sulfolipids is an important strategy for plants' adaption to P deficiency [40]. It is known that phospholipids, especially with regard to the PC of extraplastidic membranes, are replaced by DGDG in most seed plants, while PG is replaced by SQDG in plastid membranes, which was attributed to the biosynthesis pathway (**Figure 1**) [8][41].

3.1. Biosynthesis of Monogalactosyldiacylglycerol and Digalactosyldiacylglycerol

MGDG is synthesized from DAG by MGDG synthase; subsequently, DGDG can be further synthesized from MGDG by DGDG synthase [8]. Three MGDG synthases (AtMGD1, AtMGD2, and AtMGD3) have been identified in Arabidopsis. According to their N-termina sequence, the three MGDs can be divided into two types [42]. *AtMGD1* belongs to type A and is mainly expressed in green tissues and localized in the envelope of chloroplasts [42]. *AtMGD2* and *AtMGD3*, both of which belong to type B, are highly expressed in nongreen tissue and are localized in plastids [42]. *AtMGD2* and *AtMGD3* are induced by P deficiency but *AtMGD1* is not [42][43]. P deficiency could induce the accumulation of DGDG in roots. Interestingly, the loss of the *atmgd3* mutant or *atmgd2 atmgd3* double mutant was shown to cause lower or even fully abolished DGDG content [44], suggesting that *AtMGD2* and *AtMGD3* may mediate the synthesis of two essential components of membrane lipid remodeling (MGDG and DGDG) in Pi-deficient roots in Arabidopsis. In rice, three MGD members (OsMGD1, 2, and 3) were identified, and all of them were shown to be up-regulated in roots through Pi starvation, especially *OsMGD3* [45][46]. The knockout or overexpression of *OsMGD3* significantly inhibited or enhanced P utilization efficiency and lateral root growth in response to Pi starvation [45]. Furthermore, it was demonstrated that *OsMGD3* was directly regulated by the OsPHR2 transcription factor under P-deficiency conditions [45].

There are two DGDG synthases in Arabidopsis, *AtDGD1* and *AtDGD2*, and both of them are induced by P deficiency [47][48][49]. In Arabidopsis, the *atdgd1* mutant exhibited accumulated DGDG in extraplastidic membranes and the impaired growth of Arabidopsis under P-deficiency conditions [50], suggesting that AtDGD1 plays a general role in DGDG biosynthesis. In addition, the *atdgd2* mutant showed a similar phenotype to that of *atmgd2* and *atmgd3* double mutant in fatty acid species of DGDG, indicating its redundant function [44][47].

3.2. Biosynthesis of Sulfoquinovosyldiacylglycerol

SQGD, as an anionic lipid, is also an important non-phosphorus membrane lipid that is significantly increased by low-P stress. Under P-deficiency conditions, SQDG is synthesized to substitute for PG to maintain Pi homeostasis in Arabidopsis [8]. The P-deficiency-response genes *UDP-glucose pyrophosphorylase 3* (*UGP3*), *UDP-sulfoquinovose synthase* (*SQD1*), and *sulfolipid synthase* (*SQD2*) were reported to participate in the synthesis of SQDG in Arabidopsis [8][51][52][53]. The synthesis of SQGD takes place in two steps: SQD1 catalyzes the assembly of UDP-sulfoquinovose via uridine diphosphate glucose (UDPG) and sulfite, and then AtSQD2 functions in transferring the sulfoquinovose of UDP-sulfoquinovose to DAG to generate SQDG (**Figure 1**) [52]. Mutant *sqd2* could reduce Arabidopsis growth under Pi-starvation conditions [52], suggesting that SQD2 may be involved in the substitution of SQDG for anionic phospholipids in response to P deficiency. In rice, the homolog of AtSQD1—OsSQD1—also was identified to be located in the chloroplast and play a role in lipid composition changes and Pi homeostasis in response to P deficiency [54].

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