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DOI

[10.1093/plphys/kiac534](https://doi.org/10.1093/plphys/kiac534)

Publication date

2025

Document Version

Final published version

Published in

Plant Physiology

License

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[Link to publication](#)

Citation for published version (APA):

Laxalt, A. M., van Hooren, M., & Munnik, T. (2025). Plant PI-PLC signaling in stress and development. *Plant Physiology*, 197(2), Article kiac534.
<https://doi.org/10.1093/plphys/kiac534>

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Plant PI-PLC signaling in stress and development

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Abstract

Phosphoinositide-specific phospholipase C (PI-PLC) signaling is involved in various plant stress and developmental responses. Though several aspects of this lipid signaling pathway are conserved within animals and plants, clear differences have also emerged. While animal PLC signaling is characterized by the hydrolysis of PIP₂ and production of IP₃ and DAG as second messengers to activate Ca²⁺ and PKC signaling, plant PI-PLCs seem to predominantly use PIP as substrate and convert IP₂ and DAG into inositolpolyphosphates and phosphatidic acid (PA) as plant second messengers. Sequencing of multiple plant genomes confirmed that plant PLC signaling evolved differently from animals, lacking homologs of the IP₃ gated-Ca²⁺ channel, PKC and TRP channels, and with PLC enzymes resembling the PLCζ subfamily, which lacks the conserved PH domain that binds PIP₂. With emerging tools in plant molecular biology, data analyses, and advanced imaging, plant PLC signaling is ready to gain momentum.

Introduction

Phosphoinositide-phospholipase C (PI-PLC or PLC) (EC 3.1.4.11) signaling was first discovered in animal systems, where activation of G-protein coupled receptors or receptor tyrosine kinases was shown to trigger the hydrolysis of the minor phospholipid phosphatidylinositol 4,5-bisphosphate (PIP₂) to produce 2 second messengers: inositol 1,4,5-trisphosphate (IP₃) and diacylglycerol (DAG). The water-soluble IP₃ triggers an increase in cytosolic Ca²⁺ by activating ligand-activated Ca²⁺ channel at the ER, while DAG remains at the plasma membrane (PM) to recruit and activate members of the protein kinase C (PKC) family. Both messengers regulate numerous molecular events and many cellular and physiological processes (Katan and Cockcroft 2020).

Initially, evidence for the existence of a PLC-signaling system in plants rapidly followed the mammalian paradigm, that is, sowing the presence of PIP₂ and its precursor PI4P, the enzymes that produce them (i.e. PI 4-kinase [PI4K] and PIP 5-kinase [PIP5K]), and a PLC activity hydrolyzing them in vitro (reviewed in Munnik et al. 1998a, 1998b; Drøbak et al. 1999; Stevenson et al. 2000; Meijer and Munnik 2003). Furthermore, by showing that microinjected IP₃ was able to release Ca²⁺ from an intracellular store and to cause stomatal closure (Blatt et al. 1990; Gilroy et al. 1990), it seemed that the plant PLC story was similar to that of animals (Munnik et al. 1998a, 1998b; Ng et al. 2001; Krinke et al. 2007). However, over the years, several fundamental differences between plant and animal PLC signaling emerged, showing these pathways evolved independently and work differently (see Box 1). Most crucially, flowering plants lack homologs for PKC or ligand-gated-IP₃ receptors and contain very low levels of PIP₂ in their PM at basal conditions (Zonia and Munnik 2006; Munnik and Testerink 2009; Munnik and Vermeer 2010; Munnik and Nielsen 2011; Munnik 2014). So why would plants evolve a PLC system based on IP₃ and DAG while both effectors and substrate are

missing? The answer seems to lie in the use of PI4P as plant-PLC substrate and that the hydrolytic products IP₂ and DAG are instantly converted into signaling molecules, that is, various water-soluble inositolpolyphosphates (IPPs) and the lipid second messenger, phosphatidic acid (PA) (Munnik and Vermeer 2010; Testerink and Munnik 2011; Arisz et al. 2013; Vermeer and Munnik 2013; Munnik 2014). Nevertheless, under certain conditions (stress, developmental, polar growth), PIP₂ synthesis can be spatiotemporally activated for its own signaling purposes, which may also end as PLC substrate with a subsequent production of IP₃ (Fig. 1; Munnik and Vermeer 2010; Munnik 2014). A summary of the crucial differences between plant and animal PLC signaling is highlighted in Box 1.

Plant PLC messengers

Inositolpolyphosphates (IPPs)

PLC-generated IP₂ or IP₃ is rapidly phosphorylated by different IPP kinases (IPKs, IMPKs) into a range of higher IPPs, of which IP₆ is most famous (Flores and Smart 2000; Lemtiri-Chlieh et al. 2000; Lemtiri-Chlieh et al. 2003; Munnik 2014; Lorenzo-Orts et al. 2020; Riemer et al. 2022). IPK2 has 3-, 5- and 6-kinase activity while IPK1 phosphorylates IP₅ on the final 2- position of the inositol ring (Fig. 1). Historically, IP₆ (also known as phytate) is known as P₁-storage molecule in seeds (and likely other cells, tissues), but over the years, it has emerged as an important signaling molecule and signaling precursor, as IP₆ can be further phosphorylated to IP₇ by ITPK1, and from IP₇ to IP₈ by VIH1/VIH2 kinases, both of which are implicated in signaling too (Munnik 2014; Laha et al. 2015, 2016; Wild et al. 2016; Jung et al. 2018; Zhu et al. 2019; Lorenzo-Orts et al. 2020; Riemer et al. 2022; Guan et al. 2022, Guan et al. 2023).

Received June 25, 2024. Accepted September 26, 2024

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Advances box

- Multiple plant PLC families have been sequenced; all members belong to the same PLC ζ subfamily as described in animals. It is still unknown how this isoform is regulated and activated.
- PLC-KO and -OE mutants have revealed specific roles in plant stress signaling and development.
- Not PI(4,5)P₂ but PI4P appears to be the predominant PLC substrate.
- Plant PLC signaling does not work via the canonical IP₃/Ca²⁺ and DAG/PKC routes as described in animals. Both IP₃ receptor and PKC (or TRP channels, another important set of targets) are missing from flowering plant genomes. Instead, IPPs and PA are emerging as plant second messengers downstream of PLC.
- The first receptor-activated PLC/DGK pathway has been unravelled, revealing a crucial role in basal disease resistance in *Arabidopsis* (flg22, FLS2, BIK1, PLC2, DGK5, RbohD).

In guard cells, PLC-produced IP₆ induces the release of intracellular Ca²⁺ during ABA-mediated stomatal closure (Flores and Smart 2000; Lemtiri-Chlieh et al. 2000; Lemtiri-Chlieh et al. 2003; Mills et al. 2004). IPPs are also crucial in signaling other hormones, with IP₆ being essential as cofactor for auxin receptor, TIR1, and IP₅ and IP₈ as cofactor for the jasmonate receptor, CO11 (Tan et al. 2007; Hao and Yang 2010; Sheard et al. 2010; Mosblech et al. 2011; Calderón-Villalobos et al. 2012; Munnik 2014; Laħa et al. 2015, 2016). Without IPPs, these receptors, and thus the cells and tissues expressing them, would be blind for the particular hormone, allowing yet another interesting layer of regulation that has so far been ignored. IP₆, IP₇, and IP₈ have all been emerging to play key roles in phosphate signaling (Stevenson-Paulik et al. 2005; Williams et al. 2015; Dong et al. 2019; Zhu et al. 2019; Jia et al. 2021; Ried et al. 2021; Riemer et al. 2022), with IP₆ acting as cofactor for GLE1, a nuclear pore protein that transports mRNA (Lee et al. 2015), and others being sensed by SPX domains present in multiple target proteins, including nutrient transporters (Lorenzo-Orts et al. 2020). In pollen tubes, IP₄ prevents cell expansion by inhibiting a chloride-efflux channel, similar as in mammalian systems (Zonia et al. 2002). Thus, various IPPs are involved in a wide variety of plant signaling events, and potentially this may be initiated by activation of a PLC (Munnik 2014; Riemer et al. 2022). Most evidence, however, is still indirect and circumstantial (e.g. Zhang et al. 2018b, 2018c; Verslues et al. 2023).

Phosphatidic acid (PA)

PLC-generated DAG is rapidly converted into PA by DGK, which is measurable within minutes if the right method is used (Arisz et al. 2009). This PA has emerged as an important second messenger in various signaling pathways, including salt, osmotic, and cold stress but also in disease resistance and symbiosis (Munnik et al. 2000; Van der Luit et al. 2000; den Hartog et al. 2001; Meijer et al. 2001a, 2001b; 2003; Laxalt and Munnik 2002; De Jong et al. 2004; Konig et al. 2007; Laxalt et al. 2007; Distéfano et al. 2008; Mishkind et al. 2009; Sueldo et al. 2010; Raho et al. 2011; Arisz et al. 2013; Meijer et al. 2017; D'Ambrosio et al. 2018; Li et al. 2019; Kong et al. 2024). The problem of measuring PA is that

Box 1.

Differences between animal and plant PLC systems. Based on amino acid sequence and domain organization, animal PLCs have been classified into 6 subfamilies. All plant PLCs belong to the PLC ζ class (see Fig. 1). PLC ζ represents the most simple isoform, containing only the core domains found in every PLC: the catalytic X and Y domains, 2 Ca²⁺-binding EF hands to stabilize the catalytic site, and a C2 domain that allows Ca²⁺-dependent binding to the membrane. Interestingly, PLC ζ is the only isoform that lacks a PH domain that binds PI(4,5)P₂ in the plasma membrane. Other domains known to regulate animal PLCs—small or trimeric G-proteins, or receptor tyrosine kinases—are all missing in plants (Munnik 2014). How plant PLC is regulated and activated is unknown. In vitro, eukaryotic PLCs use both PI4P and PI(4,5)P₂ as substrate, but in vivo, flowering plants contain hardly any PI(4,5)P₂, whose levels are typically ~30- to 100-fold lower than in animals (Munnik and Vermeer 2010). This may also explain the lack of the PIP₂-binding PH domains in plant PLCs. They also lack homologs of the IP₃ receptor PKC or TRP channel, the most important animal targets of canonical PLC signaling. Plants do have relatively high amounts of PI4P in their plasma membrane, so in vivo, plant PLCs are likely to use PI4P as standard substrate (Munnik 2014; De Jong and Munnik 2021). Subsequent hydrolysis generates IP₂ and DAG, for which no direct targets are known in plants. Instead, evidence is emerging that both components are rapidly converted into molecules with second messenger properties, that is, various IPPs (e.g. IP₆, IP₈), and PA and DGPP, respectively (Munnik and Vermeer 2010; De Jong and Munnik 2021). In animals, IPPs and PA are important signaling molecules too, but plants have exploited this much further, perhaps due to the importance of P_i for plant growth and that IPPs serve also as excellent P_i-storage molecules, adding another dimension to signaling and sensing. Plants also lean much more heavily on PLD signaling, which generates PA from structural phospholipids (Yao et al. 2024). Under certain conditions, PIP₂ synthesis is activated in plants, where it seems to function as lipid second messenger—that is, by polyamines; salt, heat, and osmotic stress; and during polar tip growth of root hairs and pollen tubes or expansion of the cell plate during cell division (Heilmann and Heilmann, 2024). Subsequent hydrolysis by PLC would then not only attenuate PIP₂ signaling but could also initiate IPP and PA signaling pathways.

multiple pools exist within cells, of which most is not related to signaling but rather functions as precursor for lipid biosynthesis of bulk phospholipids and glycolipids at the luminal sites of ER and plastids, respectively (Testerink and Munnik 2011; Li-Beisson et al. 2013). Lastly, PA can also be generated through PLD hydrolysis of structural phospholipids, which may have a signaling role too or may simply reflect membrane remodeling or breakdown during phosphate shortage or wounding (Bargmann et al. 2009; Li et al. 2009; Nakamura et al. 2009; Hong et al. 2016). With so many PA pools, and the small amounts of DAG being phosphorylated from PLC hydrolysis of the low abundant PPIs, a simple PA measurement from a cell or plant tissue lipid extract by LC- or GC-MS analysis is unlikely to measure PLC/DGK responses (Arisz et al. 2000, 2003, 2009; Munnik 2014). With differential ³²P_i-labeling and transphosphatidylation assays, it is possible

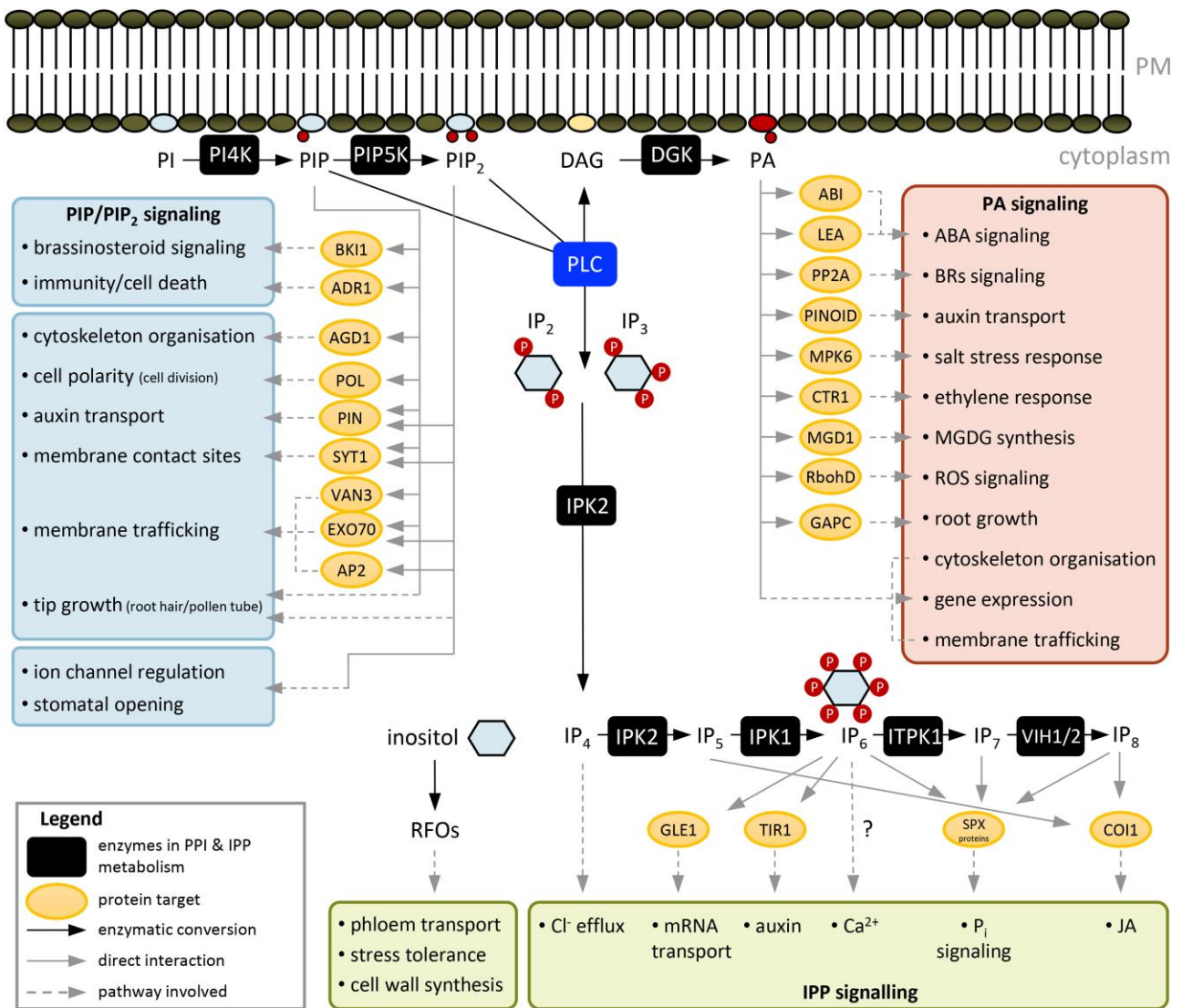


Figure 1. PLC signaling in plants stress and development. PIP and PIP₂ are synthesized by PI4-kinase (PI4K) and PIP 5-kinase (PIP5K), respectively. Both lipids have their own signaling functions and are substrate to PLC, generating DAG and IP₂ or IP₃, depending on the substrate. DAG is rapidly phosphorylated by DGK to generate the lipid second messenger PA, while IP₂ and IP₃ are phosphorylated by inositol polyphosphate (IPP) kinases IPK2 and IPK1 to form IP₅ and IP₆ that function as signaling molecules or can even be further phosphorylated by ITPK1, VIH1, and VIH2 to form the pyrophosphorylated species IP₇ and IP₈ that are involved in signaling too. Alternatively, IPPs can be broken down to inositol for subsequent production of RFOs. Targets and cellular processes are indicated. Part of PA signaling can also be generated through PLD (not indicated). The gene coding for the IP₆-mediated Ca²⁺ release (Lemtiri-Chlieh et al. 2003) is still unknown and indicated by (?).

to distinguish between them (Munnik et al. 1998a; Arisz et al. 2009). Yet another layer of complexity is that there are other enzymes that could generate DAG in response to stress, such as NPC (non-specific phospholipase C, which hydrolyzes structural phospholipids) and triacylglycerol lipase, whose substrates are present in mass amounts and of which generated DAG could be phosphorylated by DGK too. Using a DAG biosensor, a fluorescent protein fused to the C1 domain of PKC that binds DAG, revealed hardly any free DAG at the cytosolic leaflets of membranes, with no increases upon stresses known to trigger rapid PA responses, implying that the rapid conversion of PLC-generated DAG into PA by DGK likely occurs within the same complex (Vermeer et al. 2017).

Over the years, PA signaling has been associated with many processes, such as, but not limited to, endocytosis, membrane trafficking, actin cytoskeleton dynamics, osmoregulation, PIN

localization, regulation of transcription factors, and ROS production (Fig. 1) (Munnik 2001; Wang et al. 2006; Li et al. 2009; Testerink and Munnik 2011; Pleskot et al. 2013; Thomas and Staiger 2014; Wu et al. 2014; Hou et al. 2016; Ufer et al. 2017; Pokotylo et al. 2018; Yao and Xue 2018; Li et al. 2019; Li and Wang 2019; Wang et al. 2019; Kolesnikov et al. 2022). Various potential PA targets have been identified (Testerink et al. 2004; McLoughlin et al. 2012, 2013; Gao et al. 2013; Wu et al. 2014; Julkowska et al. 2015; Putta et al. 2016; Pandit et al. 2018; Yao and Xue 2018; Kim et al. 2019; Kolesnikov et al. 2022; Kong et al. 2024), and an increase of PA at the PM, or anywhere else at the cytosolic leaflets of membranes, is expected to recruit such target proteins to these sites. In this way, ABA insensitive (ABI1), a protein phosphatase, is inhibited by PA, thereby preventing the dephosphorylation of target proteins in the cytoplasm, which promotes ABA signaling (Zhang et al. 2004; Mishra et al. 2006). ROS-producing NADPH oxidases

RbohD and RbohF are examples of PA targets already located at the PM but whose activity is enhanced and stabilized by PA (Zhang et al. 2009; Kong et al. 2024; Qi et al. 2024). RbohD and RbohF play essential roles in stress signaling and development (Zhang et al. 2009; Kadota et al. 2015; Chapman et al. 2019). Also activated by PA are various protein kinases, such as MPK6, MKK7, and MPK9, leading to the activation of SOS1, an Na⁺/H⁺ antiporter that transports Na⁺ out of the cell in response to salinity stress (Yu et al. 2010; Shen et al. 2019). SnRK2.4 and SnRK2.10 are 2 other PA-binding protein kinases related to salinity (McLoughlin et al. 2012, 2013; Julkowska et al. 2015). PA has also been suggested to play a role in the nucleus, by preventing CCA1, a circadian rhythm regulator, from binding its target promoters (Kim et al. 2019). Some of these PA responses may also be related to PLD signaling (Yao et al. 2024).

With so many PA pools and responses, the big question remains of how PA would generate any specificity. A similar question holds for Ca²⁺ signaling that is basically activated by any stress ever tested. In this field, specificity is thought to lie in so-called Ca²⁺ signatures, with differences in amplitude and frequency (Edel and Kudla 2015; Gilroy et al. 2016; Yuan et al. 2017). A much easier explanation, however, is that stress and developmental signals activate more than just 1 signaling pathway and that the combination of such pathways, plus what is specifically expressed in the particular cell or tissue as targets, together determine the specificity of the outcome. A big advantage of PA (and other lipid second messengers) is that it generates a spatio-temporal membrane-delimited signal, so that the whole process, that is, target activation and/or recruitment, complex formation, and response output etc., can occur at the same site where the signal is perceived and/or receptor is activated—for example, where a cell wall locally requires a reinforcement. Water-soluble messengers, like Ca²⁺ and the various IPPs, have other spatio-temporal advantages, such that they can warn and prepare the whole cell.

The PA signal can be switched off by dephosphorylation through PA phosphatases and metabolism into structural phospholipids, or by phosphorylating it into diacylglycerol pyrophosphate (DGPP) through PA kinase (PAK) (Munnik et al. 1996; Munnik 2001; van Schooten et al. 2006). Both routes would attenuate PA signaling, but with DGPP, a potential new signaling molecule would be generated, though research on PAK and DGPP targets is progressing slowly (den Hartog et al. 2001; Munnik 2001; van Schooten et al. 2006; Arisz et al. 2009; Graber et al. 2022).

PIP and PIP₂

PI4P and PI(4,5)P₂ are not only substrates for PLC, but they are also emerging as signaling molecules themselves (Fig. 1; Noack and Jaillais 2020; De Jong and Munnik 2021; Heilmann and Heilmann 2024), and as such, PLC may control their activity besides generating IPPs and PA (Munnik 2014).

Synthesis of these PPIs starts from phosphatidylinositol (PI), which is generated by PI synthase from CDP-DAG and *myo*-inositol (Lofke et al. 2008; Vermeer and Munnik 2013). PI comprises about 5% to 10% of all phospholipids, of which only a small percentage (5% to 10%) is phosphorylated into PI4P by PI4K and even a smaller percentage (2% to 3% of PIP) is phosphorylated into PI(4,5)P₂ by PIP5K (Munnik et al. 1994; Munnik et al. 1998a; Vermeer and Munnik 2013).

Phosphorylation can also occur at the D3 position of the inositol ring, creating distinct PPI isomers: PI3P, PI(3,5)P₂, and PI5P [the latter through dephosphorylation of PI(3,5)P₂] (Munnik and Vermeer

2010). While these PPIs play important roles in signaling too (Meijer et al. 1999; Hirano et al. 2017a; Noack and Jaillais 2017; Lee et al. 2018; Chung 2019; Hirano and Sato 2019; Liu et al. 2020a; Xing et al. 2021; Lin et al. 2022), they are not PLC substrates (Munnik et al. 1998a).

PI4P and PI(4,5)P₂ are implicated in various cellular processes, often involving PA too, including endocytosis and exocytosis through interaction with AP2, clathrin, EXO70, and pectin proteins (Naramoto et al. 2009; Zhao et al. 2010; Ischebeck et al. 2013; Noack and Jaillais 2017; Wu et al. 2017; Noack and Jaillais 2020; Doumane et al. 2021; Synek et al. 2021; Xing et al. 2021; Yperman et al. 2021; Lebecq et al. 2022). Similarly, these lipids are implicated in membrane contact sites (Brault et al. 2019; Ruiz-Lopez et al. 2021; Qian et al. 2022) and are important for (1) cell division, probably by recruiting target proteins to the cell plate during its formation (van Leeuwen et al. 2007; Vermeer et al. 2009, 2017; Lin et al. 2019); (2) cell polarity, by influencing PIN localization in cells (Mei et al. 2012; Tejos et al. 2014; Rodriguez-Villalon et al. 2015; Gujas et al. 2017; Marhava et al. 2020; Wang et al. 2023; Aliaga Fandino et al. 2024); and (3) tip growth, by localizing PIP₂ at the tip of root hairs and pollen tubes (Dowd et al. 2006; Helling et al. 2006; Sousa et al. 2008; Gagne and Clark 2010; Ischebeck et al. 2010; Zonia and Munnik 2011; Yoo et al. 2012; Ischebeck et al. 2013; Stanislas et al. 2015; Simon et al. 2016; Kato et al. 2019; Fratini et al. 2021; Song et al. 2021). Both PPIs (and PA) are involved in regulating the actin cytoskeleton as well (Yoo et al. 2012; Guo et al. 2020; Doumane et al. 2021; Fratini et al. 2021). Additionally, PI4P has been found to play a role in brassinosteroid signaling by interacting with BK1 and MAK1-4 proteins (Jaillais and Vert 2016; Simon et al. 2016) and is involved in plant immunity and cell death (Saile et al. 2021). Lastly, PIP₂ is emerging to regulate K⁺ channels and to control stomatal opening (Lee et al. 2007; Lee and Lee 2008; Ma et al. 2009; Zarza et al. 2020).

Several lipid-binding domains that specifically bind the head-group of PI(4,5)P₂ have been identified (De Jong and Munnik 2021). Target proteins containing such domains can be recruited to sites where PIP₂ is synthesized by activation of 1 of the 11 Arabidopsis PIP5Ks (De Jong and Munnik 2021; Kuroda et al. 2021; Verslues et al. 2023; Heilmann and Heilmann 2024). Additionally, PIP₂ and PI4P are implicated to play roles in membrane curvature, electrostatics, and nanodomain identity, which may further explain involvement in above pathways (Fig. 1) (Heilmann 2016a, 2016b; Simon et al. 2016; Gronnier et al. 2017; Colin and Jaillais 2020; Noack and Jaillais 2020; Fratini et al. 2021; Heilmann and Heilmann 2022, 2024), which PLC would attenuate upon activation. Recent studies also imply PIP₂ signaling in the nucleus (Dieck et al. 2012; Gerth et al. 2017; Heilmann and Heilmann 2024).

Difficulties of measuring PLC activity in vivo

Typical omics analyses are unable to measure PPI or IPP levels. The reason for this is that their concentrations are low and that isomers cannot be distinguished (Munnik 2014). PA is usually present in just sufficient quantities (1% to 4% of total phospholipids), but most of this represents a precursor role in glycerolipid synthesis at ER and plastids and not what is generated by DAG phosphorylation (Arisz et al. 2013).

To measure PPI and PA responses in plant tissues, in vivo metabolic labeling with radioactive tracers (³²Pi, ³³Pi) is commonly used. Extracted lipids can be separated by thin layer chromatography and visualized and quantified by phosphoimaging (Munnik and Zarza 2013). If necessary, PPI isomers can be separated by

HPLC-SAX analysis after removal of their fatty acids (Munnik 2013). For IPPs, tissue or seedlings are metabolically prelabeled with ^3H - or ^{14}C -myo-inositol and analyzed using HPLC-SAX analysis too. However, since concentrations of many are extremely low, they remain difficult to measure (Stevenson-Paulik et al. 2005; Laha et al. 2015; Zhang et al. 2018b; Laha et al. 2022).

With the discovery of various specific lipid-binding domains (de Jong and Munnik 2021), a number of genetically encoded-lipid biosensors have been developed by fusing encoded DNA to that of fluorescent proteins and expressing them in plants. As such, biosensors have been developed for DAG, PA, PI4P, and PI(4,5) P_2 , but also for PI3P, PI(3,5) P_2 , and PS (Vermeer et al. 2006; van Leeuwen et al. 2007; Vermeer et al. 2009; Vermeer and Munnik 2013; Simon et al. 2014; Platre and Jaillais 2016; Hirano et al. 2017b; Vermeer et al. 2017; Platre et al. 2018). Such biosensors visualize the in vivo dynamics and subcellular localization of these lipids but do not measure absolute levels.

PLC isoforms: protein structure, regulation, and localization

Arabidopsis contains 9 PLC genes (Hunt et al. 2004; Tasma et al. 2008). Several plant PLC gene families have been resolved meanwhile, including monocots maize (11), wheat (11), brachypodium (4), and rice (4); and dicots potato (4), tomato (6), tobacco (6) soybean (12), chickpea (6) cotton (12), peach (5), coffee (4), various orchids (~2–3), poplar (8), and rapeseed (27) (Das et al. 2005; Sui et al. 2008; Vossen et al. 2010; Singh et al. 2013; Zhang et al. 2014; Zhang et al. 2015; Wang et al. 2015; Zhang et al. 2018a; Gonzalez-Mendoza et al. 2020; Iqbal et al. 2020; Sagar et al. 2020; Wang et al. 2020a; Wang et al. 2020b; Zhu et al. 2020; Chen et al. 2021; Kanchan et al. 2021; Wang et al. 2021; Luo et al. 2022; Sun et al. 2022; Perk et al. 2023). The number of PLCs in rapeseed, an important seed oil crop and close family member of Arabidopsis, is quite remarkable, even taking into account that rapeseed (*Brassica napus* (AACC, $2n=38$) emerged from a cross between *B. rapa* (AA, $2n=20$) and *B. oleracea* (CC, $2n=18$) (Iqbal et al. 2020).

Phylogenetic analyses show that PLCs cluster into 5 clades, with 4 of them consisting of dicotyledonous species, and the monocotyledonous species grouping together into a single clade (Perk et al. 2023). Interestingly, Arabidopsis PLC8- and PLC9 appear to be outliers, as no homologues in other species are found. AtPLC8 and -9 differ from other PLCs by containing deletions in the Y-domain and 2 mutations in the catalytic center, which are associated with a strong reduction in enzymatic activity in rat PLC δ 1 (Ellis et al. 1998; Tasma et al. 2008). Whether PLC8 and PLC9 exhibit in vitro enzymatic activity is unknown; however, KO and OE mutants of PLC9 do exhibit reduced and increased thermotolerance, respectively (Zheng et al. 2012; Liu et al. 2020b), and OE of PLC9 has been shown to lead to increased drought tolerance, just like OE of AtPLC2, -3, -4, -5, and -7 (Van Wijk et al. 2018; Zhang et al. 2018b, 2018c; van Hooren et al. 2023, 2024). Hence, the enzymatic status of AtPLC8 and AtPLC9 remains unclear, let alone their precise role in Arabidopsis.

The catalytic activity of PLC rests on the X and Y domains, which together form a 3-dimensional structure, like a hollow barrel (TIM-barrel), of which the inside hosts the active catalytic sites (Box 1; Essen et al. 1996; Hunt et al. 2004; Katan and Cockcroft 2020). The X-Y linker connecting the 2 domains is a region with a high degree of structural disorder that is not conserved between plant PLCs and may have a role in regulating PLC's activity (Kopka et al. 1998; Hicks et al. 2008; Robuschi et al. 2024).

How plant PLCs are activated and regulated is still a big mystery. Prediction software identified potential sites for palmitoylation, phosphorylation, sumoylation, ubiquitination, and acylation (Pokotylo et al. 2014; Kumar et al. 2022), though in vivo, only phosphorylation and acetylation has been shown (Nuhse et al. 2007; Hemsley et al. 2013). In particular, the intrinsically disordered X-Y linker in AtPLC2 is susceptible to phosphorylation upon elicitation with flg22 or oligogalacturonic acid (Nuhse et al. 2003, 2007; Kohorn et al. 2016). Regulation through monomeric and trimeric G-proteins has been suggested (Misra et al. 2007; Khalil et al. 2011; Sun et al. 2011), but genetic and structural evidence is missing for this (Munnik 2014). Despite the scarce information available on the regulatory role of the extra-catalytic domains, both C2 domain and EF-hand motif confirm a role of Ca^{2+} for their activity (Otterhag et al. 2001; Hunt et al. 2004; Rupwate and Rajasekharan 2012).

Various Arabidopsis PLC genes (PLC1-3, -5, -7, and -9) are prominently expressed in vascular tissue, in particular in phloem and/or companion cells (van Wijk et al. 2018; Zhang et al. 2018b, 2018c; Van Hooren et al. 2023, 2024). Specific PLC expression has been reported for various other cell types, including guard cells (PLC2, PLC5), trichomes (PLC2, -3, -5, and -7), female gametophytes and early embryos (PLC2), and in pollen (PLC4) (Hunt et al. 2004; Kanehara et al. 2015; Di Fino et al. 2017; van Wijk et al. 2018; Zhang et al. 2018b, 2018c; van Hooren et al. 2023, 2024).

Several PLC fusions with fluorescent proteins confirmed localization at the PM, including AtPLC2, AtPLC3, AtPLC5, AtPLC9, PetPLC1, NtPLC3, VrPLC3, OsPLC1, and OsPLC3 (Kim et al. 2004; Dowd et al. 2006; Helling et al. 2006; Zheng et al. 2012; Kanehara et al. 2015; Li et al. 2017; Ren et al. 2017; Yu et al. 2021; van Hooren 2023). Some PLC fusions were found in the cytoplasm, such as OsPLC1 and OsPLC4 (Singh et al. 2013), or nucleus, including AtPLC3, OsPLC1, OsPLC3, and OsPLC4 (Singh et al. 2013; Ren et al. 2017; Yu et al. 2021), though it is unclear whether these reflect breakdown products of the fusion protein. Interestingly, our laboratories never managed to create N-terminal fusions, indicating the N terminus is crucial for PLC functionality.

Since breakdown of PIP and production of PA can already be witnessed within minutes of stress application, it is likely that most of the PLC regulation occurs at the protein level (Munnik et al. 2000; Meijer et al. 2001a, 2001b; Konig et al. 2007; Mishkind et al. 2009; Arisz et al. 2013; Meijer et al. 2017; Li et al. 2019). Thus, the PLC protein should already be there, expressed at basal conditions, and catalytically inactive. Often, treatments that activate PLC signaling also enhance its gene expression (or of other PLCs), maybe as a feedback mechanism to prime the cell/tissue for further stimulation (Hirayama et al. 1995; Hirt 1999), though it may also reflect a response that is important for acclimation later on. Such a strategy has been used to identify tomato PLCs involved in plant defense against *Cladosporium fulvum* (Vossen et al. 2010), *Botrytis cinerea* (Gonorazky et al. 2016; Perk et al. 2023), *Phytophthora infestans* (Perk et al. unpublished data), and during perception of pathogen derived molecules (Gonorazky et al. 2014).

Transcriptomic analysis has revealed stress-responsive expression of multiple PLC genes in all plant species studied. In most cases, transcript levels increased in response to stress, though substantial variation among PLC isoforms, type of stress, and plant species is observed. A large number of stress-responsive elements have been found in PLC promoters across plant species, including, but not limited to, DREB2A-responsive ABRE element, ethylene-responsive ERE element, and the stress-responsive MYB element (Tasma et al. 2008; Hsieh et al. 2013; Singh et al.

Table 1. Arabidopsis PI-PLC genes, mutants, and their phenotypes

PI-PLC	ATG nr.	Expression	Mutant	Phenotype	References		
PLC1	At5g58670	KD	Antisense	Reduced inhibition of ABA on germination and growth	Sanchez and Chua (2001)		
		KO	<i>plc1-1</i>	Increased trichome branching		Goldberg et al. (2024)	
		OE		Underdeveloped trichomes		Goldberg et al. (2024)	
PLC2	At3g08510	KD	amiR	Reduced stomatal MAMP-triggered immunity, reduced ROS production	D'Ambrosio et al. (2017)		
				Reduced <i>Botrytis cinerea</i> infection and proliferation		Robuschi et al. (2024)	
		KO	<i>plc2-2</i>	Problems in gametophyte and embryo development	Di Fino et al. (2017)		
				Unpaired auxin-modulated reproductive development	Li et al. (2015)		
				Unpaired auxin-modulated root development, gravitropism	Chen et al. (2019)		
CRISPR/Cas9	<i>plc2-1</i>	Unpaired auxin-modulated reproductive development	Li et al. (2015)				
PLC3	At4g38530	KD	OE	Unpaired endoplasmic reticulum stress responses	Kanehara et al. (2015)		
				Problems in female gametophyte development	Di Fino et al. (2017)		
				Reduced <i>Botrytis cinerea</i> infection and proliferation; Shorter leaf serration	Robuschi et al. (2024)		
		OE	<i>plc3-2, plc3-3</i>	Increased drought tolerance	van Hooren et al. (2024)		
				Defects on root development, lateral root formation, seed germination	Zhang et al. (2018a)		
PLC4	At5g58700	KO	<i>plc4-3</i>	Reduced sensitivity to ABA stomatal closure and germination	Zhang et al. (2018a)		
				Decreased heat resistance	Gao et al. (2014)		
		OE		Increased heat resistance	Gao et al. (2014)		
				Increased drought tolerance	Zhang et al. (2018a); van Hooren et al. (2024)		
				Hyposensitivity to salt; normal salt sensitivity	Xia et al. (2017); van Hooren et al. (2023)		
PLC5	At5g58690	KO	<i>plc5-1</i>	Increased drought tolerance	van Hooren et al. (2024)		
				Hypersensitivity to salt; normal salt sensitivity	Xia et al. (2017); van Hooren et al. (2023)		
		KD		Lethal	Zhang et al. (2018b)		
				Defects in primary root growth and lateral root formation	Zhang et al. (2018b)		
				Increased drought tolerance; shorter root hairs	van Hooren et al. (2024); Zhang et al. (2018b)		
PLC6	At2g40116	No	NA	NA	Müller-Roeber and Pical (2000); Hunt et al. (2004)		
				KO/KD	<i>plc7-3/ plc7-4</i>	Reduced stomatal closure by ABA; enhanced leaf serration, seed mucilage defect	van Wijk et al. (2018);
						Increased drought tolerance	van Wijk et al. (2018); van Hooren et al. (2024)
				OE		NA	Hunt et al. (2004); Tasma et al. (2008)
						Decreased heat tolerance	Zheng et al. (2012)
AtPLC8	At3g47290	NA	<i>plc9-1, 9-2</i>	Increased heat tolerance	Gao et al. (2014)		
				Increased drought tolerance	van Hooren et al. (2024)		

2013; Sagar et al. 2020; Wang et al. 2020a, 2020b; Zhu et al. 2020). Only a few PLCs were downregulated: *OsPLC3*, *CaPLC4* and *ZmPLC2* upon salt stress (Sagar et al. 2020; Zhu et al. 2020; Yu et al. 2021), *ZmPLC1* and *ZmPLC2* upon cold (Zhu et al. 2020), *GmPLC3* and *GmPLC9* upon ABA treatment (Wang et al. 2015), *GmPLC6* upon hyperosmotic stress treatment with PEG (Wang et al. 2015), *ZmPLC3* and *ZmPLC4* with heavy metal (copper) (Zhu et al. 2020), and *SIPLC1* during *Botrytis* infection (Gonorazky et al. 2016).

PLC in plant stress and development

Development and growth

KO and KD analyses of Arabidopsis PLCs have revealed roles for PLC in ABA and auxin signaling, lateral root formation, leaf serration, seed mucilage, and gametogenesis (Table 1). Silencing of *AtPLC1* decreased ABA sensitivity during seed germination and seedling growth (Sanchez and Chua 2001), while *Atplc3*-KO mutants revealed reduced ABA sensitivity in both seed germination and stomatal closure and displayed a reduction in lateral root

number (Zhang et al. 2018b). KO of *AtPLC5* turned out lethal, whereas *Atplc5*-KD plants grew more slowly and exhibited a reduced number of lateral roots too (Zhang et al. 2018c). *Atplc7*-KO plants are less sensitive to ABA during stomatal closure, and double KO mutant of *plc5 plc7* displayed defects in seed mucilage and leaf serration (van Wijk et al. 2018). In contrast, double *Atplc3 plc7* KOs were lethal (van Wijk et al. 2018). Single KO of *AtPLC2* is also lethal due to problems in female gametophyte and embryo development (Di Fino et al. 2017), of which parts are mediated through auxin (Li et al. 2015). A low proportion (0.8%) of *plc2-2* homozygous mutants escaped lethality and showed morphological defects in megagametogenesis (Di Fino et al. 2017) and auxin signaling, with severe phenotypes related to auxin and PIN distribution in root development and gravitropism (Chen et al. 2019).

Abiotic stress

Atplc3- and *plc9*-KO mutants lost part of their heat stress tolerance, which was additive in *plc3 plc9* double mutants (Zheng et al. 2012; Gao et al. 2014). *Atplc5 plc7* double mutants showed

decreased stomatal movement but, strangely, showed increased survival upon drought stress (van Wijk et al. 2018; Zhang et al. 2018c). For *Atplc4* mutants, an increase in salt tolerance was reported (Xia et al. 2017), though this was not reproduced (Van Hooren et al. 2023). Rice PLC-KO mutants *Osplc1* and *Osplc4* both showed reduced salt tolerance, with *Osplc4* also showing reduced drought tolerance and *Osplc1* plants having reduced grain size (Li et al. 2017; Yu et al. 2022). For *Osplc3*, reduced damage was found when treated with H₂O₂ (Yu et al. 2021).

Overexpression (OE) of PLCs clearly improves plant stress tolerance. OE of *AtPLC3* or *AtPLC9* increased heat tolerance in Arabidopsis (Zheng et al. 2012; Gao et al. 2014) and rice (Liu et al. 2020b). Numerous PLCs have been shown to promote drought tolerance when overexpressed. These include *ZmPLC1* in maize (Wang et al. 2008), *BnPLC2* in canola (Georges et al. 2009), and *AtPLC2*, *AtPLC3*, *AtPLC4*, *AtPLC5*, *AtPLC7*, and *AtPLC9* in Arabidopsis (van Wijk et al. 2018; Zhang et al. 2018b, 2018c; van Hooren et al. 2023, 2024). OE of wheat *TaPLC1* in

Arabidopsis or *NtPLCδ1* in tobacco improved both salt and osmotic stress tolerance (Tripathy et al. 2012; Wang et al. 2020b). OE of rice *OsPLC1* and *OsPLC4*, or soybean *GmPLC7*, increased the salt and drought stress tolerance too (Li et al. 2017; Deng et al. 2019; Chen et al. 2021). Two outliers of the above pattern have been reported: (1) inducible OE of *AtPLC4* was found to reduce salt tolerance of Arabidopsis seedling growth; and (2) OE of *OsPLC3* in rice displayed a reduction in tolerance to either salt or drought, though it must be said that the latter mRNA levels normally decrease under salt or drought stress (Xia et al. 2017; Yu et al. 2021).

Biotic stress

PLC signaling has been implicated in ROS production during PAMP (pathogen-associated molecular patterns)- and effector-triggered immunity (PTI and ETI) responses (van der Luit et al. 2000; Laxalt and Munnik 2002; den Hartog et al. 2003; de Jong et al. 2004; Andersson et al. 2006; Laxalt et al. 2007; Raho et al. 2011; Gonorazky et al. 2014; Abd-El-Haliem and Joosten 2017; D'Ambrosio et al. 2017; Fang et al. 2023), which is mainly based on instant ³²P-PA responses. Genetic evidence for the involvement of PLC came from several recent studies using KO and KD plants. In Arabidopsis, *AtPLC2/DGK5*-derived PA regulates the NADPH oxidase D (RbohD) activity during PTI response (Box 2; D'Ambrosio et al. 2017; Kong et al. 2024). By transient gene silencing or loss-of-function mutants generated by CRISPR/Cas9 in tomato, *SIPLC2* was shown to play a crucial role in the susceptibility to *Botrytis cinerea* (Gonorazky et al. 2016; Perk et al. 2023) and *Phytophthora infestans* (Perk et al. unpublished data) and, hence, in this context should be considered as a susceptibility gene (a gene utilized by the pathogen during colonization and infection). *SIPLC2*-KO plants exhibit normal phenotypic development and normal susceptibility to bacterial pathogen (Perk et al. 2023). *SIPLC4* is specifically required for the ETI during Avr4 perception, while *SIPLC6* is associated with responses to a wider range of pathogens (Vossen et al. 2010). In *Nicotiana benthamiana*, *NbPLC2* is required for PTI triggered by *Ralstonia solanacearum* or *Pseudomonas fluorescens* (Kiba et al. 2020). In rice, *OsPLC-1* expression is associated with the resistance response to the fungus, *Magnaporthe grisea* (Song and Goodman 2002).

Concluding remarks

Much progress has been made on PLC signaling over the last decade, yet many issues still remain to be resolved. Clearly, we have to let go of the animal paradigm and accept that plants PLC signaling has its differences. We still need to identify and characterize more downstream targets of PA and IPPs and obtain more knowledge about their spatiotemporal activation and/or recruitment in response to stimuli. The various lipid biosensors have revolutionized our ideas about the location and behavior of lipids, but it would even be better if FRET-based sensors were available to monitor concentration changes. Similarly, it would be great if biosensors for the various IPP isomers would become available to monitor their in vivo dynamics and also a new MS protocol that would measure their absolute levels; the latter also holds for the PPIs. A link to Ca²⁺ has already been known since the 1980s, but this field, unfortunately, has not made any progress in identifying any of these ligand-gated channel(s). Even though many potential regulators of PLC have been identified, actual evidence for regulation is still very limited, while this could greatly help understanding the function of PLCs. That many PLCs are predominantly

Box 2.

Case study. Role for Arabidopsis PLC2 and DGK5 in plant defence. In the early 2000s, various plant systems were shown to trigger a fast (minutes) PA response upon stimulation with PAMPs (then called elicitors). Biochemically, evidence was provided that the majority of this response was generated through phosphorylation of DAG and that this occurred upstream of the ROS burst (Van der Luit et al. 2000; De jong et al. 2004; den Hartog et al. Laxalt and Munnik, 2002). Recently, genetic evidence for this pathway was obtained for PLC2 and DGK5 in Arabidopsis. Constitutively, of all 9 *AtPLCs*, PLC2 exhibits the highest expression levels among tissues, with predominant expression in the vasculature (roots and leaves). PLC2 is associated with the plasma membrane and rapidly phosphorylated on Ser₂₈₀ upon treatment with flg22 and other elicitors (Nuhse et al. 2003; Nuhse et al. 2007; Kohorn et al. 2016). Silencing of PLC2 reduced PAMP-triggered immunity (PTI) by reducing RbohD-dependent ROS production, and consequently reduced disease resistance (D'Ambrosio et al. 2017). Recent studies identified DGK5 as key enzyme in the PA response upon flg22 treatment, with *dgk5*-KO mutants showing reduced ROS production and disease resistance (Kalachova et al. 2022; Kong et al. 2024; Qi et al. 2024). PA-binding of RbohD enhanced ROS production and increased protein stability, thereby augmenting the PAMP induced-ROS production (Kong et al. 2024; Qi et al. 2024). Upon flg22 recognition by FLS2, DGK5 is activated through phosphorylation of Ser₅₀₆ by the pattern recognition receptor (PRR)-associated kinase, BIK1, while MPK4 phosphorylation of Thr₄₄₆ deactivates DGK5, resulting in a local and transient PA response at the plasma membrane (Kong et al. 2024). These findings provide functional and genetic evidence for the role of PLC2-DGK5 action in producing ROS as a first layer of basal defense. The relevance of PLC2's phosphorylation and identity of the protein kinase are still unknown. Consequences of the subsequent increase in IP₂ remains unknown too, but likely plays a role in the production of IPPs implicated in plant defense (Murphy et al. 2008; Mosblech et al. 2011; Laha et al. 2015; Riemer et al. 2022). Meanwhile, several plant-pathogen systems have been shown to use this pathway.

expressed in deeper lying phloem tissues will be another challenge to functionally characterize their role in signaling. Nonetheless, with a good number of tools emerging in advanced imaging, omics, genetic screens, and data analyses with AI, PLC signaling will remain an exciting topic for future basic and applied sciences.

Outstanding questions box

- What controls PLC's activity status and how is the enzyme regulated at the molecular level?
- Is PLC in complex with DGK to boost PA levels directly?
- What is the effect of PLC phosphorylation on activity, localization, complex formation?
- Do changes in PLC gene expression eventually reflect changes in PLC activity?
- How does IP₆ activate a Ca²⁺ channel that releases intracellular Ca²⁺ upon IP₆ formation in guard cells but also elsewhere?
- While several PA-binding proteins have been identified, a genuine PA target "at work" remains to be shown. How does the PA-binding domain look like?
- Single KO mutants of PLC have only small or no phenotypic effect? Is this due to genetic or chemical redundancy?
- Which other receptors than FLS2 lead to a direct activation of a plant PLC-signaling cascade?
- Why is PLC so predominantly expressed in phloem and companion cells?
- What kind of protein modification regulates plant PLCs?
- Is there any difference in K_m and V_{max} values of PLC activity between PI4P and PI(4,5)P₂?
- Is PLC a bona fide attenuator of PI(4,5)P₂ signaling?
- Are PLC-generated IPPs required for functional auxin- and JA perception via their respective receptors, and if so, what triggers it?
- Similarly, are (part of) the IPPs that play a role in phosphate signaling generated through PLC?

Acknowledgments

We thank our funding sponsors and both reviewers for their valuable comments and corrections.

Author contributions

All 3 authors wrote the review and constructed the figures.

Funding

This work was supported by the Netherlands Organization for Scientific Research (NWO 867.15.020 to TM), the European Union (EPPN2020 grant 731013 to TM), and Agencia Nacional de Promoción Científica y Tecnológica (ANPCyT, PICT 2021 to AML).

Conflict of interest statement. None declared.

Data availability

The data underlying this article are available in the article and in its online supplementary material.

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