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REVIEW

Emerging role of phospholipase C mediated lipid signaling in abiotic stress tolerance and development in plants

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Abstract

Environmental stimuli are primarily perceived at the plasma membrane. Stimuli perception leads to membrane disintegration and generation of molecules which trigger lipid signaling. In plants, lipid signaling regulates important biological functions however, the molecular mechanism involved is unclear. Phospholipases C (PLCs) are important lipid-modifying enzymes in eukaryotes. In animals, PLCs by hydrolyzing phospholipids, such as phosphatidylinositol-4,5-bisphosphate [PI(4,5)P_2] generate diacylglycerol (DAG) and inositol- 1,4,5-trisphosphate (IP_3). However, in plants their phosphorylated variants i.e., phosphatidic acid (PA) and inositol hexakisphosphate (IP_6) are proposed to mediate lipid signaling. Specific substrate preferences divide PLCs into phosphatidylinositol–PLC (PI–PLC) and non-specific PLCs (NPC). PLC activity is regulated by various cellular factors including, calcium (Ca^{2+}) concentration, phospholipid substrate, and post-translational modifications. Both PI–PLCs and NPCs are implicated in plants' response to stresses and development. Emerging evidences show that PLCs regulate structural and developmental features, like stomata movement, microtubule organization, membrane remodelling and root development under abiotic stresses. Thus, crucial insights are provided into PLC mediated regulatory mechanism of abiotic stress responses in plants. In this review, we describe the structure and regulation of plant PLCs. In addition, cellular and physiological roles of PLCs in abiotic stresses, phosphorus deficiency, aluminium toxicity, pollen tube growth, and root development are discussed.

Keywords Phospholipase C · Structure · Regulation · Signaling · Abiotic stress · Root development

Introduction

Lipid signaling is triggered by different external stimuli and it regulates diverse cellular processes in plants (Katan and Cockcroft 2020). PLC, an important class of phospholipases has been involved in lipid signaling. In plants, based on their substrate specificity PLCs have been classified into two classes: phosphoinositide (PI) specific PLCs (PI–PLC) that hydrolyses phosphoinositides and non-specific PLCs (NPCs) that cleave common phospholipids, such as phosphatidylcholine (PC) and phosphatidylethanolamine (PE) (Singh et al. 2015). The favoured substrate for PLC is PI(4,5)P_2, followed by phosphatidylinositol phosphate (PIP) and phosphatidyl inositol (PI) (Bill and Vines 2020). Impressively phospholipases can also bind to various regulatory proteins, such as sphingosine kinase and G protein subunits thereby, displaying their modulating action (Guo et al. 2012; Pandey 2016). Upon perception of external stimuli, such as abiotic stresses PLC cleaves the glycerophosphate-ester bond of the phospholipids at the glycerol side thereby, generating DAG and IP_3. NPCs are found exclusively in higher plants and bacteria, and they have a wide range of substrate preferences. NPCs hydrolyse the common phospholipid, such as PC, PE, phosphatidylserine (PS) and some other phospholipids (Heilmann 2016). The activity of NPCs also results in DAG production.

In animal systems, while membrane-bound DAG activates protein kinase C (PKC), IP_3 is found in soluble form and binds to its receptors i.e., ligand-gated Ca^{2+} channels in the cytoplasm to release Ca^{2+} from cellular reservoirs (Vossen et al. 2010). However, this model has been debatable in plant systems because the level of PI(4,5)P_2 is much lower in plant membranes than animals and equivalents of animal PKC and IP_3 receptors are missing in plant cells (Singh et al. 2015). Rather, PA, diacylglycerol pyrophosphate (DGPP), and IP_6,

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respectively the phosphorylated variants of DAG and IP_3 are proposed as the second messenger in plants (van Leeuwen et al. 2007; Xue et al. 2007). Nevertheless, several PLCs have been implicated in plant's response to biotic and abiotic stresses and plant development (Hong et al. 2016; Takáč et al. 2019). This review provides the details of the structure and regulation of plant PLCs and discusses their emerging role in abiotic stress responses, phosphorus deficiency, aluminium toxicity, pollen tube growth and root development.

Plant PLC family and protein structure

PLCs constitute a multigene family both in animal and plants. In mammals, 13 PLC members have been identified which are categorised into six different isoforms, including PI–PLCβ, γ, δ, ε, η, and ζ (Bunney and Katan 2011). Plant PI–PLCs are structurally similar to animal PI–PLCζ. Like animals, plant PLCs display great diversity as the *Arabidopsis thaliana* genome encodes for nine PI–PLC and six NPCs (Tasma et al. 2008; Nakamura et al. 2005). PI–PLCs and NPCs have been identified in several plant species, including *Oryza sativa* (rice) (Singh et al. 2013), *Triticum aestivum* (wheat) (Khalil et al. 2011) *Solanum lycopersicum* (tomato) (Vossen et al. 2010), *Glycine max* (soybean) (Wang et al. 2015), *Zea mays* (maize) (Wang et al. 2008), *Gossypium spp.* (cotton) (Zhang et al. 2018a, b, c) and *Cicer arietinum* (chickpea) (Sagar et al. 2020).

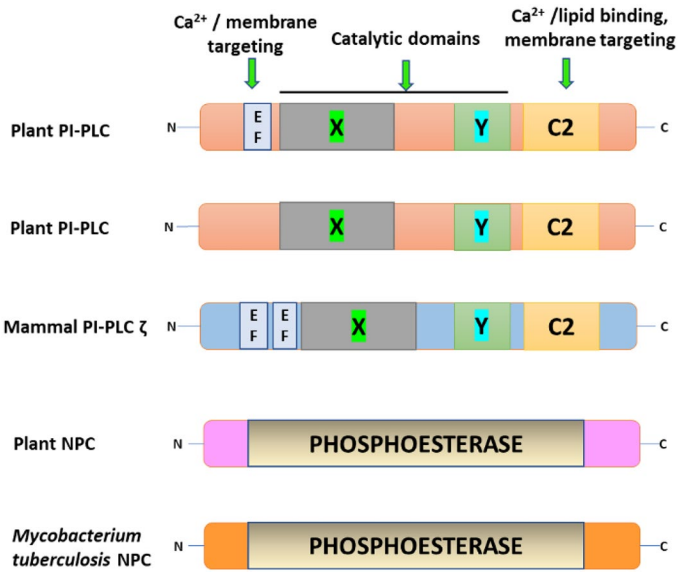

Fig. 1 Domain structure of PLCs. Plant PI–PLCs contain X and Y domain at the catalytic centre and C2 domain towards C-terminus. In some plant species PI–PLCs may have an additional EF domain towards N terminal. Most plant PI–PLCs are structurally similar to mammalian PI–PLCζ. Plant NPCs are structurally similar to bacterial NPC and contain a single phosphoesterase domain

Plant PI–PLCs are comprised of catalytic X and Y domains which have phosphoesterase activity. An EF hand motif is located at the N-terminal, whereas at the C-terminal a C2 domain is present which facilitates binding of PI–PLC with Ca^{2+}/phospholipids (Fig. 1) (Chen et al. 2011). EF hand motifs facilitate the interaction of PLCs with its substrate by targeting them to the plasma membrane (PM). Though, the crystal structure of a plant PLC has not been deciphered yet, the X-ray crystallography structure of mammalian PLCδ1 provided insight into their catalytic mechanism. The X and Y catalytic domains form a TIM-barrel structure with α-helices and β-sheets and contain two catalytically important histidine residues (His311and His356) (Essen et al. 1996). These His residues are conserved and have been found in plants also (Tasma et al. 2008). According to mammalian model, PI–PLC activity involves two steps. Firstly, PLCδ1 binds with its substrate $PI(4,5)P_2$ via PH domain that supports the attachment of PLC to the membrane. In the second step, C2 domain in presence of Ca^{2+} brings the catalytic domain in a desired confirmation which in presence of conserved His residues complete the catalysis. Since, plants PLCs lack PH domain, other mechanisms might be involved during the first step which needs investigation.

NPCs have a single phosphoesterase domain with esterase activity and are devoid of membrane-spanning domain in their structure (Singh et al. 2013). Though the structure of plant NPCs is not well defined, alignment with their bacterial orthologs has provided some crucial details (Pokotylo et al. 2013). Some *Arabidopsis* NPCs (NPC1, NPC2, and NPC6) contain a putative signal peptide at the N-terminal close to the start of phosphoesterase domain, followed by a short variable region and highly conserved ENRSFDxxxG motif. The phosphoesterase domain contains highly conserved TxPNR, DExxGxxDHV, and GxRVPxxxxxP motifs which could be critical for NPC activity. Towards the C-terminal, 50–100 amino acids constitute the most variable region. This region possibly imparts functional diversity to NPCs by mediating variable subcellular localizations and interactions with diverse proteins.

Regulation of PLC activity

Ca^{2+} plays a prominent role in PLC activity by regulating not only catalysis but also its substrate preference and subcellular localisation. Plant PI–PLCs are found either in soluble form in the cytosol or in membrane-bound form (Nomikos et al. 2011). Generally, the soluble PI–PLCs preferentially act on PI, PI(4,5)P_2, and PI(4)P at millimolar Ca^{2+} level. Whereas, membrane-bound PI–PLCs use PI(4,5)P_2 and PI(4)P as preferred substrates at micromolar Ca^{2+} level (McMurray and Irvine 1988; Drøbak 1992). The activity of a wheat PI–PLC is inhibited towards PI(4,5)P_2 but enhanced towards PI(4)P by millimolar Ca^{2+} levels (Melin et al. 1992). Similarly, *Physcomitrella Patens* (moss) PpPLC1 prefers PI(4,5)P_2 as substrate at micromolar Ca^{2+} level whereas, at millimolar Ca^{2+} level PpPLC2 but not PpPLC1 uses PI as substrate (Mikami et al. 2004). The hydrolysis of PI(4,5)P_2 by potato StPLC1, StPLC2 and StPLC3 has been promoted at 10 mM Ca^{2+} level, but inhibited by Al^{3+} (Pan et al. 2005).

Plant NPCs exhibit differential affinity to different phospholipids substrates. Both NPC4 and NPC5 preferably act upon PC and PE, however, activity of NPC4 is 40 times higher than NPC5 (Peters et al. 2010, 2014). Remarkably, NPC3 exhibits phosphatase activity on lysophosphatidic acid (LPA) while displaying negligible activity towards other phospholipids (Reddy et al. 2010). Notably, in vitro activity of NPC4 is independent of Ca^{2+}, rather it increases fractionally by addition of EGTA, probably due to its chelating effect on inhibitory cations, including Co^{2+}, Mn^{2+} or Zn^{2+}(Nakamura et al. 2005). The activity of plant PLCs is also regulated by its interaction with G-proteins. In *Pisum sativum* (pea), Gα1 binds to the C2 domain of PI–PLC whereas, wheat PI–PLC interacts with GA3, the Gα subunit of the heterotrimeric G protein (Mishra et al. 2007; Khalil et al. 2011). Pharmacological studies showed that in *Lilium daviddi* (Lily) pollen protoplast, a G protein stimulates PI–PLC activity against cholera toxin while suppressed by G protein antagonist pertussis toxin (Pan et al. 2005). Emerging evidence indicate that post-translational modifications may be crucial in regulation of PLC activity in plants. Mass spectrometry analysis revealed multiple phosphorylation sites in *Arabidopsis* PI–PLC (Durek et al. 2010). Phosphorylation sites were detected within EF hand motif and catalytic X and Y domains of AtPLC2 and AtPLC7 (Nühse et al. 2004; Chen et al. 2010). Similarly, a role of SUMOylation, ubiquitination and palmitoylation has been proposed in regulation of PLC activity in plants (Ren et al. 2008; Park et al. 2011; Pokotylo et al. 2014). Thus, along with Ca^{2+} various factors regulate the PLC activity and their fine-tuning will achieve the optimum PLC activity in different plant functions.

PLCs regulate abiotic stress tolerance in plants

Osmotic, drought and salinity stresses

Numerous genome-wide expression analyses indicated the involvement of PLCs in abiotic stress response in diverse plant species (Sagar et al. 2020; Singh et al. 2013; Tasma et al. 2008; Iqbal et al. 2020). Consequently, functional analyses of several plant PLCs by reverse genetic approaches have strongly supported their role in abiotic stress signaling. For example, overexpression of maize *ZmPLC1*, *Brassica napus* (Rapeseed) *BnPLC2* and *Nicotiana tabacum* (tobacco) *PLCδ* conferred enhanced drought tolerance in plants (Wang et al. 2008; Georges et al. 2009; Tripathy et al. 2012). Similarly, improved heat tolerance in *Arabidopsis* was associated with the function of both AtPLC3 and AtPLC9 (Zheng et al. 2012; Gao et al. 2014). Recently, constitutive expression of *AtPLC3* and *AtPLC5* led to reducing stomatal aperture that prevented excessive water loss, thereby provided drought tolerance in *Arabidopsis* (Zhang et al. 2018a, b). Overexpression of AtPLC7 also results in enhanced drought tolerance, however, unlike AtPLC3 and AtPLC5 stomata aperture remains unaffected in these plants (van Wijk et al. 2018). The level of PI(4,5)P_2 was found to be higher in all three overexpression plants which could be associated with an improved drought stress response. Under osmotic stress, concomitant higher levels of IP_3 and PI(4,5)P_2 have been observed in the plant cell, which indicates towards a concurrent activity of a PI–PLC and phosphoinositide kinase (Darwish et al. 2009; Pokotylo et al. 2014). Emerging evidences have established the crucial role of PLCs in salt stress response. AtPLC4 overexpression plants exhibit hypersensitivity whereas, *atplc4* mutants are insensitive to salt stress, thus, AtPLC4 negatively regulates salt tolerance in *Arabidopsis*. This response is linked with the salt-induced enhanced Ca^{2+} level and expression of salt stress-responsive genes, such as *RD29B, MYB15,* and *ZAT10* (Xia et al. 2017). Recently, a rice PLC, OsPLC1 was implicated in salinity stress tolerance. Under salt stress, OsPLC1 was translocated from cytoplasm to plasma membrane where it preferentially hydrolysed PI4P substrate. OsPLC1 mediates salt stress-induced Ca^{2+} signaling which is evident from the enhanced expression of Ca^{2+} dependent stress-related genes, such as *OsMSR2, OsRab16* and *OsCDPK7* in OsPLC1 overexpression plants (Li et al. 2017). OsPLC1 mediated Ca^{2+} signaling prevents the Na^{+} accumulation in the leaf blades, thereby improves plants salt tolerance. Importantly this study established a connection between PI and Ca^{2+} signaling via a PLC. Similarly, OsPLC4 by modulating PA and Ca^{2+} signaling pathways positively regulates salinity and dehydration tolerance in rice seedlings (Deng

et al. 2019). Thus, PI–PLC regulate salinity stress tolerance in plants by controlling stress-induced PI and Ca^{2+} signaling.

Like PI–PLCs, some of the NPCs have also been implicated in plants' abiotic stress responses. *Arabidopsis* seedlings overexpressing NPC4 are relatively more resilient and viable under salt and drought stresses (Peters et al. 2010). In another study, root tip localized NPC4 was highly induced and produced DAG under salt stress. Abrogation of NPC4 function renders plants salt stress-sensitive in terms of seed germination and root elongation (Kocourková et al. 2011). Thus, an important role of NPC4 is proposed in hyperosmotic stress tolerance. While, NPC4 helps to tolerate a higher level of salt stress, NPC5 helps to tolerate a mild level of salt stress by regulating the number of lateral roots (Peters et al. 2014). Thus, different NPCs might regulate plant tolerance at variable intensities of salt stress and could be utilized to engineer crop plants of agricultural zones with varying levels of soil salinity. The activity of NPC1 increases in tobacco BY-2 under heat stress. In addition, its role in heat stress tolerance has been established by gain- and loss-of-function analysis in *Arabidopsis* (Krčková et al. 2015). The role of PLC-mediated signaling in the regulation of various abiotic stress responses is depicted in Fig. 2.

PLCs in phosphate deficiency

NPCs have been implicated in phosphate (P) deficiency responses in plants. NPCs participate in membrane lipid remodelling during P deprivation. They produce DAG which is a precursor for the synthesis of non-phosphorus-containing lipids digalactosyldiacylglycerol (DGDG) that substitute the membrane lipid to mobilise inorganic phosphate (Pi) under P deficiency (Nakamura2013). NPC5 has been recognised as a major regulator of DGDG synthesis as it produces a substantial amount of DAG under P starvation in leaves (Gaude et al. 2008; Peters et al. 2014). NPC3 has been shown to regulate lateral root development under low P conditions possible via regulation of auxin signalling (Wimalasekera et al. 2010; Krčková et al. 2015). In the earliest analysis, *NPC4* was highly induced under P deprivation however, its KO mutant show no change in PC or DGDG content under low P conditions (Nakamura et al. 2005). Nevertheless, recent studies indicate a crucial role of NPC4 in P deficiency tolerance. NPC4 mediates the lipid changes mainly in roots during early periods of P deficiency. NPC4 functions along with PLDζ2, and genetic analysis revealed that PLDζ2 positively regulates the primary root growth and negatively regulates root hair density and length, whereas

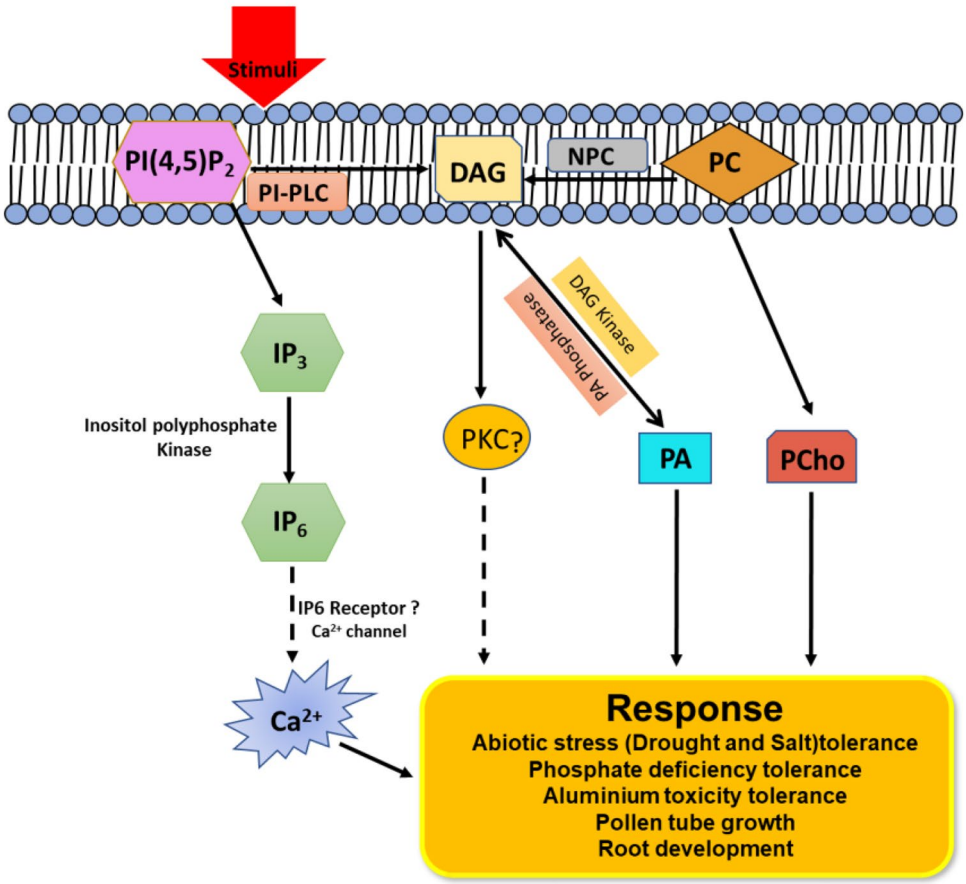

Fig. 2 PLC mediated signaling in diverse biological processes in plants. Upon perception of stimuli at the plasma membrane PLCs are activated. PI–PLCs act on the $PI(4,5)P_2$ and generates DAG and IP_3. Inositol polyphosphate kinase may convert IP_3 to IP_6 which might bind to IP_6 receptor like a Ca^{2+} channel and release Ca^{2+} from cellular reservoirs. NPCs act on PC/PS/PE to produce DAG and free head groups. These molecules activate the downstream signaling leading to adaptive

NPC4 positively regulates root hair length, under P deficiency (Su et al. 2018). DAG and PA generated by NPC4 and PLDζ2 are speculated to have a signaling role in this response, as NPC4 and PLDζ2-generated PA is known to promote primary root elongation (Li et al. 2006; Peters et al. 2010). Recently, instead of common lipids, NPC4 is shown to hydrolyse the most abundant sphingolipid in *Arabidopsis*, glycosyl inositol phosphoryl-ceramide (GIPC), during P starvation. NPC4 mediated sphingolipid remodelling promotes root growth under P deficiency (Yang et al. 2021). Thus, NPC4 via membrane lipid remodelling regulate RSA and helps plant to tolerate P deficiency. Differential expression of several *Gossypium hirsutum* (Mexican cotton) *NPCs* under P deficient conditions also support the role of *NPCs* in P deficiency response in plants (Song et al. 2017).

PLC in aluminium toxicity stress

In agricultural areas with acidic soils, low pH causes the release of toxic Aluminium ions (Al^{3+}) from fixed forms in soil minerals. The first and immediate symptom of Al^{3+} toxicity is the rapid cessation of root growth, whereas the long-term Al^{3+} toxicity causes root morphology changes, including root thickening, bursting, modification of cell wall structure, and cell death (Panda et al. 2009). However, the exact mechanism of rapid Al^{3+} mediated root growth arrest is unclear, it has been to some extent attributed to the loss of PM fluidity and suppression of endocytosis (Illéš et al. 2006; Krtková et al. 2012). It has been found that Al^{3+} targets PLCs and modulate their activity in plants. The treatment of pNPC4:GUS seedlings with $AlCl_3$ reduces GUS expression in apical meristem and partly in the elongation zone of the primary and lateral root, indicating that Al^{3+} suppresses NPC4 expression (Pejchar et al.2015). The NPC activity in terms of DAG formation has been found to decline in $AlCl_3$ treated WT seedlings. This inhibitory effect on NPC activity was alleviated by NPC4 overexpression. Interestingly, effect of Al^{3+} on NPC4 activity is neither due to direct inhibition of NPC4 enzyme nor due to NPC4 translocation, as in-vitro activity and NPC4 localization remained unaffected. Remarkably, the extent of Al^{3+} stress-mediated root growth arrest was similar in WT, NPC4-OE and *npc4* KO mutants. Thus, it could be speculated that either NPC4 is not involved in Al^{3+} toxicity mediated root growth arrest or other NPC isoforms are redundantly involved in the compensatory effect. Previously, Al^{3+} ions suppressed NPC-mediated DAG production that results in inhibition of pollen tube growth in tobacco (Pejchar et al. 2010) and this phenotype could be partially rescued by over-expression of AtNPC4 (Pejchar et al. 2015). Thus, NPC4 is crucial for mitigating early and long-term responses of Al^{3+} toxicity.

Recently, multiple *Coffea arabica* (Coffee) *PLCs* were differentially induced in response to $AlCl_3$. Moreover, the in-vitro activity of CaPLC4 was increased whereas, that of CaPLC2 was reduced in presence of $AlCl_3$ (González-Mendoza et al. 2020). To minimize the adverse effect of Al^{3+} toxicity, and protect the sensitive root tips plants secrete organic acids (OA) e.g., malate, citrate, and oxalate (Liu et al. 2009), however the exact mechanism of secretion is unknown. These organic acid anions chelate Al^{3+} externally and prevent Al^{3+} from binding to root cells thereby, detoxify Al^{3+} outside the cells (Ma et al. 2001; Ryan et al. 2001) Recently, phosphatidylinositol metabolism is shown to be involved in Al^{3+} induced malate secretion in *Arabidopsis*. Al^{3+} triggered early induction of aluminium activated malate transporter (*AtALMT1*) and other aluminium responsive gene e.g., *ALS3* and *MATE* is suppressed by inhibitors of PI4K (PAO) and PLC (U73122) (Wu et al. 2019). CAMTA2 and WRKY46 TFs, respectively activate and repress Al^{3+} induced expression of *AtALMT1* in the late phase of Al^{3+} exposure (Ding et al. 2013; Tokizawa et al. 2015). PAO and U73122 significantly suppress the expression of *CAMTA2* whereas, up-regulate *WRKY46*, after 24 h of Al^{3+} treatment PLC signaling lipid mediators, such as PA might act upstream of Ca^{2+} regulated kinases, including CIPKs or CDPKs in regulating Al^{3+}-responsive *AtALMT1* expression as PA is known to activate CDPKs in plants (Farmer and Choi 1999) and expression of Ca^{2+} dependent *CAMTAs* is regulated by downstream of PI4K pathway (Doherty et al. 2009; Gierczik et al. 2017). Thus, PI metabolism and Ca^{2+} signaling might play important roles in the transcriptional regulation of *AtALMT1*. Moreover, inhibitors of PI3K and PI4K suppress Al^{3+} induced malate transport by AtALMT1. Overall, PI4K–PLC metabolic pathway regulates the early and late phase of Al^{3+} induced AtALMT1 activity, and both PI3K and PI4K metabolic pathways control Al^{3+} induced malate secretion.

PLCs regulate plant development

PLCs in pollen tube growth

Pollen tube growth involves asymmetric cell expansion, and it's governed by some key cellular process, including Ca^{2+} signaling, vesicular trafficking, and cytoskeleton rearrangement (Singh et al. 2015). PLCs have been known to regulate these critical processes during pollen tube development. During elongation, PI–PLC localize at the plasma membrane near the tip of tobacco pollen tube while its substrate PI(4,5)P_2 localize right at the tip (Dowd et al. 2006; Helling et al. 2006). Impaired PLC activity led to lateral spreading of PI(4,5)P_2, and disturbed Ca^{2+} gradient and cytoskeleton organization at the tip that causes delocalized growth and swollen tip (Dowd et al. 2006; Helling et al. 2006; Stenzel et al. 2020). PI(4,5)P_2 is proposed to be involved in cytoskeleton remodelling, membrane trafficking and apical pectin

deposition during polarized pollen tube growth (Zhao et al. 2010; Ischebeck et al. 2011). Recently, NPC mediated lipid remodelling has emerged as a crucial regulatory mechanism of pollen tube development. NPC2 and NPC6 are highly expressed in developing pollen tubes. Gain- and loss-of-function genetic analysis revealed that NPC2 and NPC6 participate in lipid remodelling where they hydrolyse phospholipids to produce triacylglycerol (TAG) which is essential for pollen tube growth (Bose et al. 2021). A summary of the functional role of different plant PLCs in diverse plant processes in provided in Table 1.

PLCs regulate root development

Emerging evidences have established an important role of PLCs in root development. PI–PLCs express ubiquitously in different plant organs, but PLC2 and PLC5 are preferentially and highly expressed in root tips (Kanehara et al. 2015; Zhang et al. 2018b). PLC2 modulates the polar distribution of auxin efflux carrier PIN2 and thus, regulate auxin response and root development (Fig. 3). The *PLC2* mutants exhibit several altered root phenotypes due to auxin defect, including short primary root, impaired root gravitropism, and impaired root hair growth (Chen et al. 2019). PLC3 and PLC5 localized at root phloem differently regulate root development. While, PLC3 is involved in the regulation of lateral root growth, PLC5 regulates primary root growth and lateral root numbers (Zhang et al. 2018a, b). Interestingly, transgenic *Arabidopsis* ubiquitously expressing PLC5 had hampered primary and secondary root growth and stunted root hairs. These changes are possibly due to higher PLC activity as lower PI4P and PI(4,5)P_2 levels and higher PA level were observed in PLC5 OE plants. Moreover, lower PI(4,5)P_2 level and stunted root hair growth could be reverted upon overexpression of a root hair specific PIP 5-kinase, PIP5K3 (Zhang et al. 2018b). As discussed earlier, NPC3 and NPC4 regulate root hair growth under P deficiency (Su et al. 2018), and brassinolide-mediated primary and lateral root growth (Wimalasekera et al. 2010). Furthermore, NPC4 positively regulates root elongation via ABA signaling whereas, NPC5 is promoting lateral root formation possibly by stimulating auxin signaling (Peters et al. 2010). NPC2 and NPC6 have been involved in gametophyte development and their double knockout produces a gametophyte-lethal phenotype (Ngo et al. 2018). Therefore, their knock-down mutants were generated to avoid the lethal affect during gametogenesis. These mutants display significantly retarded root growth with abnormal root columella cell architecture. The retarded root phenotype could be rescued by exogenous application of phosphocholine (PCho), a product NPC hydrolysis of phosphatidylcholine (Ngo et al. 2019). PCho is produced from PEtn by the activity of phospho-base *N*-methyltransferase 1 (PMT1) and is known to be involved in root growth (Cruz-Ramírez et al. 2006; Liu et al. 2019). The expression of *PMT1* is induced in NPC2 and NPC6 knock-down mutants but it was suppressed after PCho supplementation. These results suggest that NPC and PMT pathways interact in PCho production for regulating root growth.

Conclusions and future perspective

The Discovery of PLCs in different organisms, understanding of their structure, regulation and functional role has been achieved somewhat in last two-decade. Their ability to produce second messenger in plants has been recognised however, several questions still need to be answered. The regulation of PI–PLCs catalytic activity is understood but the information is scanty for NPCs. The activation of different PLCs in response to multiple stresses is unclear. Understanding the activation PLCs under multiple stresses by the signal crosstalk will provide deep insights into PLC function in plants. It is well known that PLC produce DAG and IP_3 but what is the exact fate of these molecules is debatable in plants. Their higher phospho-derivatives like PA and IP_6 are thought to function in plants, which indicates a coordinated action of PI–PLC and DGK or inositol phosphate kinase in plants. Determination of substrate preferences and how these substrates are presented to PLCs at the membrane, cytosol and other cellular compartment can add to the clear understanding of PLC activity in plants. In addition, deciphering the complete structure of PLCs in active and inactive forms, their interacting partners, activators, and repressor will clearly delineate PLC signaling pathway in plants. Presently the techniques involved in studying the localisation and enzymatic activity of the PLCs in living cells are costly and time-consuming. New technology that allows high power and rapid visualisation of PLCs, protein–protein and protein -lipid interaction at the membrane is the need of the hour. These can help in utilising the information garnered from PLC research for biotechnological modification of crops towards stress resilience.

Table 1 Summary of different functional roles PLCs in plant

Gene/protein	Plant	Response	Mechanism	References
Abiotic stress response				
CaPLCs	*Cicer arietinum*	Abiotic stress tolerance	Abiotic stress response differential gene regulation	Sagar et al. (2020)
ZmPLC1	*Zea mays*	Drought stress response	Enhanced grain yield	Georges et al. (2009)
BnPLC2	*Brassica napus*	Drought stress response	Enhanced grain yield	Tripathy et al. (2012)
AtPLC3	*Arabidopsis thaliana*	HEAT stress tolerance	Higher survival and chlorophyll content	Zheng et al. (2012)
AtPLC9	*Arabidopsis thaliana*	Heat stress tolerance	Upregulation of AtPLC9	Gao et al. (2014)
AtPLC3	*Arabidopsis thaliana*	Drought stress response	Reduced stomatal response to prevent water loss	Zhang et al. (2018a)
AtPLC5	*Arabidopsis thaliana*	Drought stress response	Reduced stomatal response to prevent water loss	Zhang et al. (2018b)
AtPLC7	*Arabidopsis thaliana*	Drought stress response	Stomatal aperture remains unaffected	Van Wijk et al. (2018)
AtPLC7	*Arabidopsis thaliana*	Osmotic stress response	Increased IP_3 and $PI(4,5)P_2$	Pokotylo et al. (2014)
AtPLC4	*Arabidopsis thaliana*	Salt stress response	Negatively regulates salt stress tolerance mediated enhanced Ca^{2+} signaling and expression of *RD29B*, *MYB15* and *ZAT10*	Xia et al. (2017)
OsPLC1	*Oryza sativa*	Salinity stress tolerance	Translocates from cytosol to plasma membrane to hydrolyse PI4P. Enhanced expression of *OsMSR2, OsRab16, OsCDPK*	Li et al. (2017)
OsPLC4	*Oryza sativa*	Salinity, dehydration stresstolerance	Modulate PA and Ca^{2+} signaling	Deng et al. (2019)
NPC4	*Arabidopsis thaliana*	Salinity stress tolerance	Abrogation of NPC4 render plant salt stress sensitive in seed germination and elongation	Kocourkova et al. (2011)
NPC5	*Nicotiana*	heat stress tolerance	Gain and loss of function mutants concluded the involvement in heat stress tolerance	Krčková et al. (2015)
Phosphate deficiency				
NPC5	*Arabidopsis thaliana*	P starvation in leaves	INCREASED DAG production	Gaude et al. (2008), Peters et al. (2014)
NPC3	*Arabidopsis thaliana*	P stress tolerance	Regulate lateral root growth via auxin signaling	Wimalasekera et al. (2010), Krčková et al. (2015)
NPC4	*Arabidopsis thaliana*	P stress tolerance	Modulate lipid level	Su et al. (2018)
NPC4	*Arabidopsis thaliana*	P stress tolerance	Sphingolipid remodeling promote root growth	Yang et al. (2021)
GhNPCs	*Arabidopsis thalliana*	P stress tolerance	Differential expression pattern	Song et al. (2017)
Aluminium stress				
NPC4	*Arabidopsis thaliana*	Aluminium stress response	Aluminium suppresses NPC4 expression	Pejchar et al. (2015)
CaPLCs	*Coffea arabica*	Aluminium sensitive response	Differential regulation of genes	González-Mendoza et al. (2020)
CaPLC4	*Coffea arabica*	Aluminium sensitive response	*CaPLC4* expression level increases under Al^{3+} stress	González-Mendoza et al. (2020)
CaPLC2	*Coffea arabica*	Aluminium sensitive response	*CaPLC2* expression level decreases under Al^{3+} stress	González-Mendoza et al. (2020)
Pollen tube growth				
NPC4	*Arabidopsis thaliana*	Pollen tube growth	Hydrolyses phospholipid to TAG	Bose et al. (2021)
NPC6	*Arabidopsis thaliana*	Pollen tube growth	Hydrolyses phospholipid to TAG	Bose et al. (2021)
Root development				
PLC2	*Arabidopsis thaliana*	Root development	Highly expressed in root tip	Kanehara et al. (2015)
PLC5	*Arabidopsis thaliana*	Root development	Highly expressed in root tip	Zhang et al. (2018b)

Table 1 (continued)

Gene/protein	Plant	Response	Mechanism	References
PLC2	*Arabidopsis thaliana*	Root development	Altered root phenotype, short primary root	Chen et al. (2019)
P LC3	*Arabidopsis thaliana*	Root development	Regulate lateral root growth	Zhang et al. (2018a)
PLC5	*Arabidopsis thaliana*	Root development	Regulate lateral root growth	Zhang et al. (2018b)
NPC3, NPC4	*Arabidopsis thaliana*	Root development	Regulate root growth under P deficiency	Su et al. (2018)
NPC3, NPC4	*Arabidopsis thaliana*	Root development	Brassinolide-mediated primary and lateral root growth	Wimalasekera et al. (2010)
NPC5	*Arabidopsis thaliana*	Root development	Promote lateral root growth formation by auxin signaling	Peters et al. (2010)
NPC2, NPC6	*Arabidopsis thaliana*	Gametophyte development	Promote gametophyte development	Ngo et al. (2018)

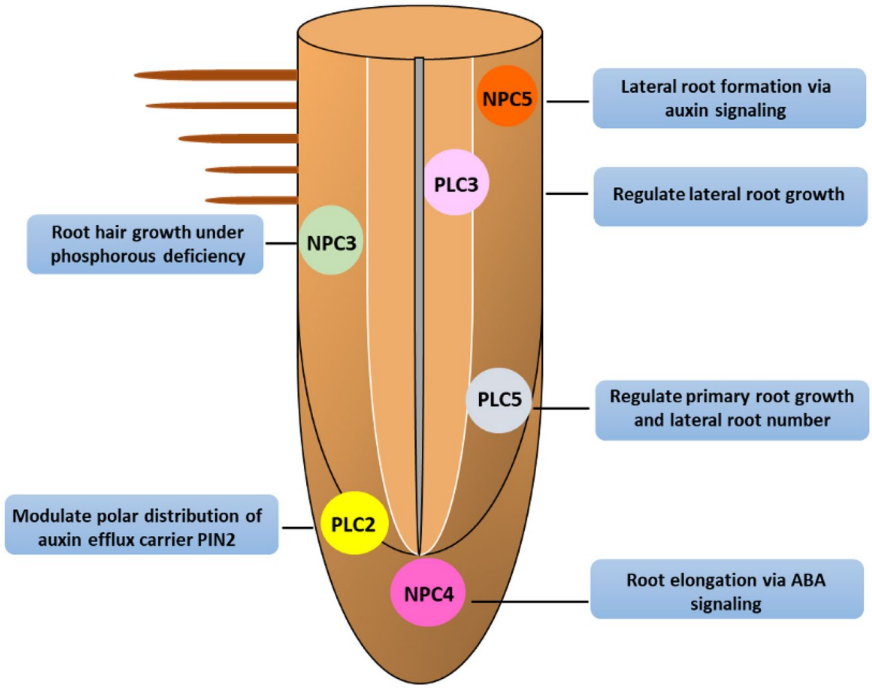

Fig. 3 Role of PLCs in root development. PI–PLCs and NPCs localizes at different parts of plant root and regulate various facets of root development

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Declarations

Conflict of interest The authors declare that there is no conflict of interest.

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