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How Phospholipase C Regulates Stress Tolerance and Development in Plants?

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Lipid signaling pathways regulate many cellular processes in eukaryotes [1]. PLCs are the major players in lipid signaling, triggered by numerous environmental cues in plants. PLC signaling module is well established in animal system where, upon perception of a stimulus, PLC hydrolyze the membrane bound PI [2-5] P2 lipids to produce DAG and IP3. After hydrolysis, DAG remains attached to the membrane and activates protein kinase C (PKC) while IP3 moves to the cytoplasm to bind ligand gated Ca^{2+} channels (IP3 receptors) resulting in the release of Ca^{2+} from the intracellular reservoirs. This model doesn't hold completely true and still debatable in plant system, as the level of PI [4,5] P2 in plant membrane is very low, and no IP3 receptors, and equivalents of animal PKC have not been identified till date in plants. Instead, the phosphorylated products of DAG and IP3 i.e. PA, diacylglycerol pyrophosphate (DGPP) and IP6 are thought to function as second messenger in plants [2].

Based on their affinity towards different lipid substrates, two major type of PLCs namely; phosphatidylinositol-specific PLCs (PI-PLCs) and phosphatidylcholine-PLC (PC-PLC, or non-specific PLC; NPC) are known to hydrolyze the membrane lipids in plant cells, to initiate the signaling. Both PI-PLCs and NPCs are encoded by multi-gene families in *Arabidopsis* and rice genomes [3]. PI-PLCs could be divided further into two distinct types; cytosol localized or soluble, and the membrane bound. Availability of Ca^{2+} is the major determinant of activity of both the PI-PLC groups [4]. However, Ca^{2+} requirements may vary with their preferred substrate type. Cytosolic PI-PLCs use phosphatidylinositols (PtdIns) as substrate and act optimally at the millimolar Ca^{2+} concentration range whereas, membrane bound PI-PLCs act upon phosphatidylinositol 4-phosphate (PtdIns4P) and PtdInsP2 efficiently, in the physiologically optimum micromolar range of Ca^{2+} concentration. Besides Ca^{2+} ion, different post-translational modifications including, phosphorylation, SUMOylation, Ubiquitination and Palmitoylation are known to regulate the activity of plant PLCs [5].

Like in animals, G-protein coupled receptors (GPCRs) and G-proteins have been implicated in regulation of plant PI-PLC. Interaction of PI-PLC and G protein has been found in Lilium daviddi and Pisum sativum [6,7]. However, these are the early reports and consequences of these interactions and regulations will provide new insights in PI-PLC response mechanism. Epigenetic regulation of PI-PLCs has been reported in humans. The expression of human PI-PLC beta1 was found to be negatively regulated by the DNA methylation at its promoter [8]. Since DNA methyltransferases (DNMTs) play a major role in depositing and protection of DNA methylation in both mammals and plants [9,10], and some histone modifiers are also involved in the maintenance of DNA methylation [11], the expression of PLC might be directly regulated by these enzymes. Al^{3+} might control the activity of plant NPCs as indicated by hampered PC hydrolysis by high $Al3^{+}$ (≥ 100 μ M AlCl3) concentration [12]. No specific pharmacological agent/inhibitors of NPC activity are known in plants till date; however, inhibitors have been identified for animal and bacterial PC-PLC activity [13]. Functional relevance of PLC mediated lipid signaling has been recognized by wide range of studies across the spectrum of plant species. Multiple PLC members are reported to participate in abiotic stress triggered signaling events. For instance, maize and tobacco PLCs conferred high degree of drought and salt stress tolerance upon overexpression in transgenic plants [14,15]. Heat stress leads to PI-PLC proteins accumulation in pea plants [16], and activity of PI-PLC protein enhanced in pea cell membranes within 40 minutes of stress [17]. Similarly, Arabidopsis AtPLC9 has been implicated in heat stress responses [18]. PI-PLCs generate abiotic stress related response by their influence on crucial cellular processes including, activation of mitogen activated protein kinases (MAPKs) and generation of reactive oxygen species (ROS) in soybean, Tubby like proteins (transcription factors) in *Arabidopsis*, regulation of gene expression of PEP carboxylase kinase1 in sorghum [5]. Through mutant and overexpression transgenic analyses, significant role of *Arabidopsis* NPC4 has been demonstrated in ABA mediated hyperosmotic and salt stress responses [19].

PLCs are important enzymes to control plants biotic stress responses too. PLCs are shown to mediate pathogen induced hypersensitive response (HR), systemic acquired resistance (SAR) and induced systemic resistance (ISR) in plants [20]. Tomato PI-PLCs; SlPLC4 and SlPLC6 showed differential expression in *Cladosporium fulvum* resistant Cf-4 tomato. SlPLC4 silencing led to decreased Avr4/Cf-4 induced hypersensitive response and increased accumulation of Avr4 expressing *C. fulvum* on Cf-4 tomato plants [21]. Remarkably, PI-PLC signaling not only control plants function, but also regulates functions of pathogen. Bacterial pathogens activate PI-PLC enzymes during their pathogenesis mechanism [22]. Thus, slight shift in the delicate balance of two defense mechanisms (plants versus pathogens) will lead to either plant resistance or disease. Therefore, researchers should be mindful of this fact while developing disease resistant plants. Recent studies have revealed that various plant NPC genes are differentially expressed upon pathogen treatment, which is indicative of their probable involvement in biotic stress response mechanism. NPCs are relatively novel class of plant PLCs, thus, exploration of their functional behaviour could promise the identification of key players to mitigate abiotic stress from plants.

Some progress has been made by identifying the role of NPCs in phosphate starvation condition in plants. Under phosphate starvation, NPCs are believed to facilitate the mobilization of organic phosphate from membrane phospholipids by cleaving the phosphate head group from phosphatidylcholine and other phospholipids. Notably, the removal of phosphate does not upset the membrane integrity and compactness, because DAG produced from NPC activity serves as the precursor for sulfolipids and glycolipids production, which generally

replace the phosphate deficient phospholipids. Investigation of entire *Arabidopsis* NPC family revealed that some of the NPC genes are readily inducible under low phosphate condition [23]. Moreover, higher expression level corresponds to higher PC-phospholipase activity and greater DAG accumulation.

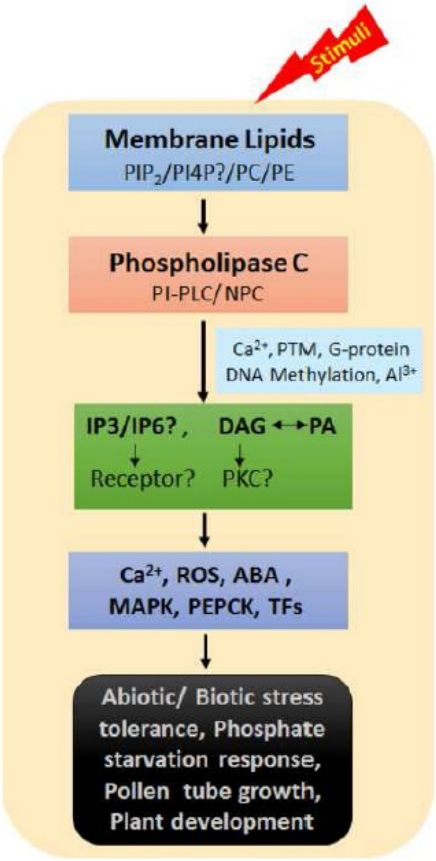

Figure 1: PLC signaling pathway in plants showing the series of events after perception of stimuli. Various regulators of PLC activity, second messengers produced downstream effectors molecules and consequent physiological responses of plant are depicted.

Another vital role of PI-PLC enzymes has been detected in pollen tube growth. Expression and promoter analyses indicated the production of PI-PLC in *Arabidopsis* pollen [24]. Pollen tube in seed plants, functions as channel for passage of male gamete cells from pollen grains to the ovules. During elongation, PI-PLCs are known to localize at the plasma membrane of pollen tube while, its substrate PI (4,5) P2 exclusively accrues at the tip of pollen tube [24,25]. During polarized pollen tube growth, PI (4,5)P2 is proposed to be linked with cytoskeleton remodeling membrane trafficking and apical pectin deposition [5]. Moreover, PI-PLCs are reported for their crucial roles in other development related processes [26]. Constitutively overexpression of BnPI-PLC2 resulted in early alteration from vegetative to reproductive phases, shorter maturation period accompanied by significant alteration in hormonal distribution in various tissues of Brassica plant [27]. Our recent study of entire rice PLC family also indicated their possible role in plant reproductive development, as several PLCs expressed differentially during reproductive developmental phases including, stages of panicle and seed development [3]. Major events of lipid Signaling mediated by PLCs in plants are summarized in Figure 1.

Even though good amount of knowledge has been accumulated from these important studies, lacunae are still there in comprehension of molecular properties and functional aspects of PLC enzymes in plants. Detail functional studies are to be undertaken to completely understand the PI-PLC signaling in plants, as their real substrate is yet to be identified. Moreover, PI [4,5] P2 is present in minute quantity in plant cell membranes in comparison to PI-4-P [5]. Thus, it is speculated that PI-4-P could be the real *in vivo* substrate of PI-PLC. The role of PA and IP5/IP6 has been established in PI-PLC signaling but other molecules could also be the part of the cascade. It would be interesting to investigate the underlying epigenetic mechanisms associated with the initiation and activation of the lipid signaling pathways in stress tolerance and plant development. As far as NPCs are concerned, some progress is made in recent times in terms of understanding their role in different aspects of plant physiology, but a lot is yet to be explored. Detail exploration of their protein structure, biochemical properties will help to understand their molecular basis of functions.

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