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Role of phospholipid signalling in plant environmental responses

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ABSTRACT

Despite the fact that all plants follow strict developmental programmes, they also have intrinsic mechanisms to monitor the environment and activate appropriate responses at the (sub-)cellular level, facilitating adaptation to abiotic and biotic fluctuations. The functionality of plant adaptive systems always relies on the sum of signalling machineries that control their transition from the resting state. Phosphoglycerolipids play a role in such signalling mechanisms. These structural components of cell membranes can be converted into multiple bioactive lipids, but also into soluble molecules. Together they shape cell metabolism via binding to downstream protein targets, thus affecting enzymatic activities, vesicle trafficking and ion fluxes. The conversion of lipids is catalysed by the hydrolytic activity of phospholipases and by the action of lipid-kinases and lipid-phosphatases. These activities are strictly regulated in plant cells and are highly reactive to various environmental signals. While phospholipases have been shown to be essential for plant growth and adaptability, many aspects of phosphoglycerolipid signalling at the molecular level remain unknown. Here, we summarise the latest concepts and challenges associated with phosphoglycerolipid signalling in relation to environmental responses in plants.

1. Introduction

Production of biologically active lipids, such as phosphatidic acid (PA), results from the action of phospholipases and/or lipid-kinases (Fig. 1). Phospholipases are found in all living organisms and typically constitute single-polypeptide multi-domain hydrolytic enzymes acting on (phospho)ester bonds of phospholipids. They are classified according to the site of phospholipid cleavage, and consistently, to the nature of their products, into phospholipases A_1, A_2, C and D (PLA_1, PLA_2, PLC and PLD; Fig. 2) (Wang et al., 2012). Some phospholipases are characterised by their strict substrate preference. For instance, PLCs are either phosphoinositide-specific PLCs (PI-PLCs) or non-specific PLCs (NPCs). The latter hydrolyse membrane structural phospholipids such as phosphatidylcholine (PC) or phosphatidylethanolamine (PE). Several types of lipid-kinases are found in plants. One can distinguish kinases acting on diacylglycerol (DAG) – the DAG-Kinases (DGK) – from those acting on phosphatidylinositol (PI), – the PI-kinases (*e.g.* phosphatidylinositol 4-kinase, PI4K) – and those acting on phosphorylated PI (PIP) – the PIP-kinases (*e.g.* phosphatidylinositol-4-phosphate 5-kinase, PI4P5K). In plant genomes, many lipid-processing enzymes are encoded as multigenic families. For instance, the genome of *Arabidopsis thaliana* encodes 12 PLDs, 9 PI-PLCs, 6 NPCs and 7 DGKs and 3 PI4Ks. It is not uncommon that each isogene codes for an enzyme with unique regulatory properties, organ localisation or stress-induced expression patterns (Pinosa et al., 2013; Zheng et al., 2012). Moreover, the activity of phospholipases can be rapidly altered by post-translational regulation (*e.g.* G-protein-mediated activation, protein phosphorylation), granting them a role in rapid signalling events. Phospholipases and lipid-kinases are also functionally connected to other plant signalling systems including nitric oxide (NO; Lanteri et al., 2008), reactive oxygen species (ROS; Zhang et al., 2009) and Ca^{2+} (Parre et al., 2007).

2. Plant phospholipases and lipid processing enzymes

2.1. Phospholipase D

PLD (EC 3.1.4.4) hydrolyses structural membrane phospholipids (PC, PE and phosphatidylglycerol, PG) into phosphatidic acid (PA) and the corresponding soluble headgroup. Only two PLD genes are known in mammals (Exton, 2002). In contrast, plant PLDs are encoded by large multigenic families. Twelve PLD genes were identified in *A. thaliana* (Qin and Wang, 2002), 17 in rice (Li et al.,

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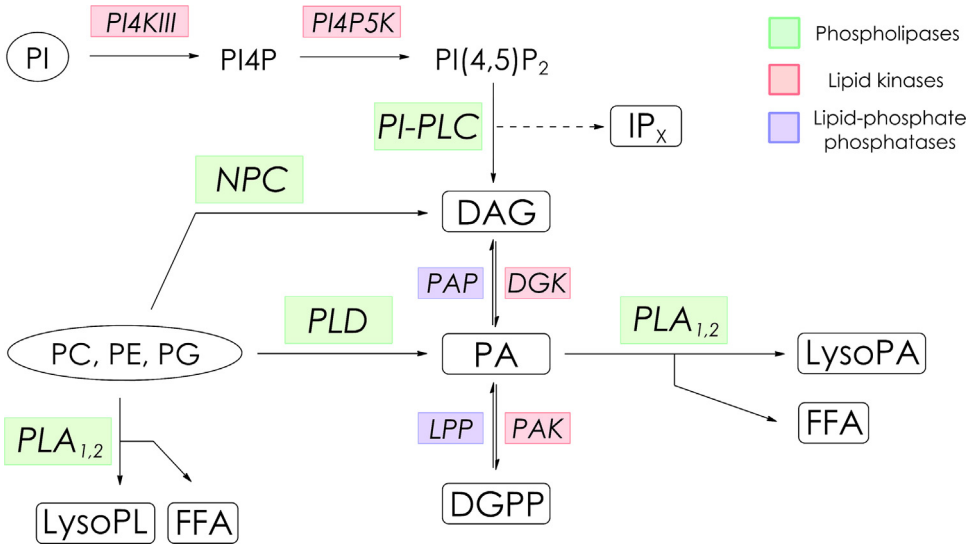

Fig. 1. Phospholipid signalling pathways in plants. Lipid processing enzymes are shown in red. DAG, diacylglycerol; DGK, diacylglycerol kinase; DGPP, diacylglycerol pyrophosphate; FFA, free fatty acids; IP_x, inositol polyphosphate; LysoPA, lysophosphatidic acid; LysoPL, lysophospholipids; LPP, lipid phosphate phosphatase; NPC, non-specific phospholipase C; PA, phosphatidic acid; PAK, phosphatidic acid kinase; PAP, phosphatidic acid phosphatase; PE, phosphatidylethanolamine; PC, phosphatidylcholine; PG, phosphatidylglycerol; PI, phosphatidylinositol; PI4K, phosphatidylinositol 4-kinase; PI4P5K, phosphatidylinositol-4-phosphate 5-kinase; PI4P, phosphatidylinositol 4-phosphate; $PI(4,5)P_2$, phosphatidylinositol 4,5-bisphosphate; PI-PLC, phosphatidylinositol-specific phospholipase C; PLA, phospholipase A; PLD, phospholipase D.

2007), 18 in soybean (Zhao et al., 2012), 17 in poplar and 11 in grape (Liu et al., 2010). Plant PLDs are characterised by a complex domain structure. They facultatively contain C2, PH, PX and DRY regulatory domains (Fig. 3) (Kolesnikov et al., 2012). The differences in primary structure, together with differences in enzymatic properties, distribute plant PLDs into α, β, γ, δ, ε and ζ sub classes. In particular plant species, PLD isoforms named κ and φ (the latter bearing a signal peptide sequence) are also present (Li et al., 2007). The majority of PLDs are thought to be membrane-associated and require Ca^{2+} for their activity (Pappan et al., 1997). The stress-induced, calcium-dependent PLD allocation to membranes is considered as a key mechanism of PLD activation (Ryu and Wang, 1996). Among other post-translational regulators of PLD activity in plants are G-proteins (Munnik et al., 1995), lipids (such as phosphatidylinositol-4,5-bisphosphate, $PI(4,5)P_2$) and protein-kinases (Novotná et al., 2003). The different classes of plant PLDs have distinct modes of regulation. For instance, PLDα activity is $PI(4,5)P_2$-independent and calcium-dependent, and that of PLDζ is calcium-independent and $PI(4,5)P_2$-dependent. PLDs can participate in a characteristic transphosphatidylation reaction with primary alcohols leading to a production of non-metabolisable phosphatidylalcohol (Rainteau et al., 2012). This reaction is used both to inhibit PA production and monitor PLD activity *in vivo* (Munnik and Laxalt, 2013). The primary alcohol most commonly used for these experiments is *n*-butanol. Tertiary-butanol, which is not a substrate of PLD, is used as a control. PLDs have long been considered as the main contributors to PA signalling. However their hegemony is now being challenged by the PLC/DGK pathway.

2.2. Phosphoinositide-specific phospholipase C

Phosphoinositides, such as phosphatidylinositol-4-phosphate (PI4P) or $PI(4,5)P_2$, are minor constituents of plant membranes. PI-PLC (EC 3.1.4.11) selectively hydrolyses phosphoinositides into diacylglycerol (DAG) and phosphorylated-*myo*-inositol. When compared to animal PI-PLCs, the plant PI-PLC structure (close to that of animal ζ isoform) is relatively simpler, with X and Y catalytic domains, C2 domain and truncated EF hand regulatory domains (Fig. 3) (Pokotylo et al., 2014a). Nine PI-PLC genes were identified in *A. thaliana* (Hunt et al., 2004) and rice (Singh et al., 2013) and six in tomato (Vossen et al., 2010). In animals, it is well established that DAG activates proteins, such as protein kinases C (PKC), while inositol trisphosphate (IP_3) binds calcium channels and thus triggers the release of the cation from internal reservoirs. However in plants, the mode of action of PI-PLCs is different. Identification of gene(s) encoding a receptor protein of IP_3 in plant cells has not been successful (Krinke et al., 2007a) and no plant proteins orthologous to mammalian PKCs have been found. In plants, IP_3 might be phosphorylated into inositol hexakisphosphate (IP_6) – a putative signalling molecule (Lemtiri-Chlieh et al., 2003). DAG on the other hand is phosphorylated into PA and thus contributes to PA-dependent plant stress responses (Arisz et al., 2013).

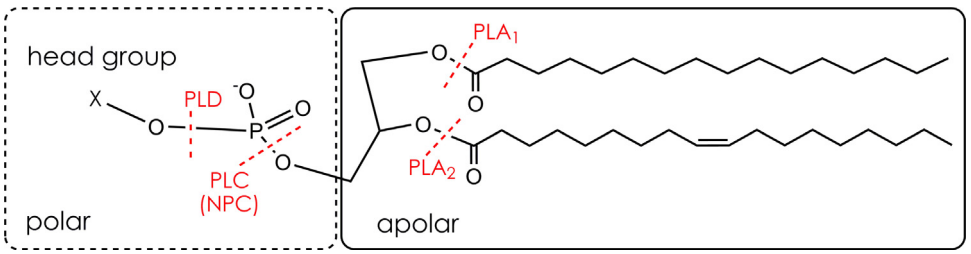

Fig. 2. Diversity of phospholipases. A generalised representastion of the structure of phospholipid molecule with an arbitrary fatty acid composition is shown with the sites of phospholipid cleavage indicated. The polar and apolar regions of the phospholipid and corresponding lipid products are marked. PLA_1, phospholipase A1; PLA_2, phospholipase A2; PLC, phospholipase C; PLD, phospholipase D.