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Review

The plant non-specific phospholipase C gene family. Novel competitors in lipid signalling

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ABSTRACT

Non-specific phospholipases C (NPCs) were discovered as a novel type of plant phospholipid-cleaving enzyme homologous to bacterial phosphatidylcholine-specific phospholipases C and responsible for lipid conversion during phosphate-limiting conditions. The six-gene family was established in *Arabidopsis*, and growing evidence suggests the involvement of two articles NPCs in biotic and abiotic stress responses as well as phytohormone actions. In addition, the diacylglycerol produced via NPCs is postulated to participate in membrane remodelling, general lipid metabolism and cross-talk with other phospholipid signalling systems in plants. This review summarises information concerning this new plant protein family and focusses on its sequence analysis, biochemical properties, cellular and tissue distribution and physiological functions. Possible modes of action are also discussed.

Contents

Abbreviations: ABA, abscisic acid; BL, 24-epibrassinolide; BY-2, Bright Yellow 2; BODIPY, 4,4-difluoro-4-bora-3a,4a-diaza-*s*-indacene; D609, tricyclodecan-9-yl-xanthogenate; DAG, diacylglycerol; DGDG, digalactosyldiacylglycerol; DGK, diacylglycerol kinase; EDTA, ethylenediaminetetraacetic acid; GUS, β-glucuronidase; LPA, lysophosphatidic acid; LPC, lysophosphatidylcholine; LPE, lysophosphatidylethanolamine; MAG, monoacylglycerol; MGDG, monogalactosyldiacylglycerol; MeJA, methyl jasmonate; NPC, non-specific phospholipase C; PA, phosphatidic acid; PAP, phosphatidic acid phosphatase; PC, phosphatidylcholine; PC-PLC, phosphatidylcholine-specific phospholipase C; PE, phosphatidylethanolamine; PIP_2, phosphatidylinositol 4,5-bisphosphate; PI-PLC, phosphatidylinositol-specific phospholipase C; PKC, protein kinase C; PL, phospholipid; PLD, phospholipase D; PMA, phorbol 12-myristate 13-acetate; PS, phosphatidylserine; ROS, reactive oxygen species; SA, salicylic acid; SQDG, sulphoquinovosyldiacylglycerol; TDTMA, tetradecyltrimethylammonium bromide.

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1. Introduction

Phospholipases (Fig. 1) are now well recognised as key components of the regulatory systems of cellular growth and development in living organisms. They give rise to an array of second messenger molecules and lipid derivatives and are implicated in both metabolism and intracellular signalling. Recent research progress has made it possible to convincingly reveal an important role for phospholipases in mediation of stress responses directed to provide acclimation to ever-changing environmental conditions.

Phospholipases C (PLC) are able to cleave membrane phospholipids, facilitating release of water-soluble phosphorylated headgroups from hydrophobic diacylglycerols (DAG). PLCs in living systems can generally be divided into phosphatidylinositol-specific phospholipases C (PI-PLC) and phosphatidylcholine-specific phospholipases C (PC-PLC) according to substrate specificity range. The role of specific phosphatidylinositol 4,5-bisphosphate (PIP_2) cleaving PI-PLCs in cell metabolism regulation is fairly well studied in various organisms. Thus, multidomain animal PI-PLCs are G-protein activated enzymes that are notably responsible for intracellular calcium level regulation and protein kinase C (PKC) activation [1]. Despite a lack of identified inositol 1,4,5-trisphosphate receptors in plants [2], PI-PLCs are unquestionably implicated in the regulation of growth, development and stress responses in *Arabidopsis* and other plant species [3]. In turn, bacterial PI-PLCs belong to secreted pathogenicity factors that typically confer virulence [4].

PC-PLCs, in plants also known as non-specific PLCs (NPC), are characterised by broader substrate ranges that include abundant phosphatidylcholine (PC) (discovered in 1847 by a French chemist Theodore Nicolas Gobley as "lecithin" molecules), while their role in cell signalling and regulation in general remains far less understood. PC-hydrolysing phospholipases were first discovered under the name "lecithinase C" in bacteria [5] and later established as important bacterially secreted pathogenicity factors performing host membrane lysis and defence signalling interference [6]. PC-PLC activity was also identified in fungi [7] and was acknowledged to be an essential source of phospholipid-derived signal molecules in animal cells [8,9]. It was demonstrated that transient increases in DAG production occur in cellular membranes in response to various stimuli [10,11], whereas attributed PC-PLC activity appears to be involved in a number of intracellular regulatory events (see section 3). However, the current lack of molecular and genetic characterisation of PC-PLCs in animals hampers the progress of research.

Although putative PC-PLC activity in plants was observed as early as 1955 [12], PC-PLC functions in plants have long remained vague and their role elusive. Some supporting clues for PC-hydrolysing PLC occurrence were identified in plant organs and tissues such as peanut seeds [13], rice grains [14], tomatoes [15] and others [16]. However, this data lacked sufficient enzymatic characterisation [17]. Eventually, in 2002, fluorescently labelled PC was shown to be directly cleaved to produce DAG in parsley and tobacco cells, suggesting the presence of NPC (PC-PLC) as a novel type of phospholipase in plants with putative signalling functionality [18]. Later, six NPC genes were identified in the *Arabidopsis* genome based on sequence similarities with bacterial PC-PLCs [19]; nine NPC genes were identified in soybean plants [20]. DAG production via PC hydrolysis was also observed in *Petunia hybrida*, suggesting the omnipresence of NPCs in the plant kingdom [21]. A subsequent increase in research interest in dissection of NPC's roles in plants over the recent years has promoted the identification of NPC

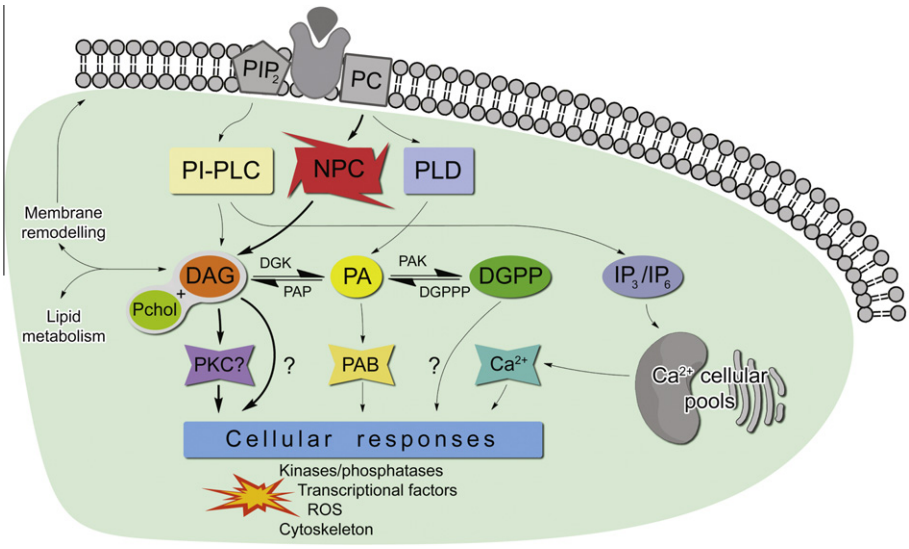

Fig. 1. Phospholipase C- and phospholipase D-dependent signalling in plants. A schematic diagram depicts contemporary model of metabolism regulation carried out by plant cell phospholipases. Various augmenting signalling pathways are shown, demonstrating synergistic interactions between phospholipases and lipid second messenger molecules in excitation of cell responses. PIP_2, phosphatidylinositol 4,5-bisphosphate; PC, phosphatidylcholine; NPC, non-specific phospholipase C; PI-PLC, phosphatidylinositol-specific phospholipase C; PLD, phospholipase D; Pchol, phosphocholine; DAG, diacylglycerol; PA, phosphatidic acid; DGPP, diacylglycerol pyrophosphate; IP_3/IP_6, inositol 1,4,5-trisphosphate/inositol hexakisphosphate; PKC, protein kinase C; DGK, diacylglycerol kinase; PAP, phosphatidic acid phosphatase; PAK, phosphatidic acid kinase; DGPPP, diacylglycerol pyrophosphate phosphatase; ROS, reactive oxygen species; PAB, PA-binding proteins.