Short Conceptual Overview

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Plant phospholipase A: advances in molecular biology, biochemistry, and cellular function

Abstract: Plant phospholipase As (PLAs) are a complex group of enzymes that catalyze the release of free fatty acids from phospholipids. Plant PLAs can be grouped into three families, PLA_1, PLA_2, and patatin-like PLA, that catalyze the hydrolysis of acyl groups from the *sn-1* and/or *sn-2* position. Each family is composed of multiple isoforms of phospholipases that differ in structural, catalytic, and physiological characteristics. In this review, recently acquired information on molecular, biochemical, and functional aspects of plant PLAs will be discussed.

Keywords: lipid biosynthesis; phospholipase; plant development; signal transduction; stress response.

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Introduction

Enzymes of the phospholipase A (PLA) family catalyze the hydrolysis of acyl groups from phospholipids to produce free fatty acids and lysophospholipids. PLAs represent one of the earliest enzymes to be characterized, which traces back to the identification of lytic actions of snake venom at the end of the 19th century (1). Plants possess a complex and diverse set of PLA enzymes that differ in nucleotide sequence, protein structure, enzymatic properties, cellular functions, and anthropocentric applications (2–7). Here, we review the functions of plant PLAs, with particular focus on information acquired in the past 3 years.

Plant PLA genes and proteins

Defined by the bond that they work on, plants have three families of PLAs. PLA_1 and PLA_2 enzymes catalyze the hydrolysis of acyl groups from the *sn-1* and *sn-2* position, respectively, and patatin-like PLAs (pPLAs) exhibit activity toward both positions (Figure 1). It should be noted that this generally accepted classification system is convenient, but is neither very accurate nor broad enough to cover all enzymes with PLA activity. For instance, oleosin has recently been shown to be a bifunctional enzyme with both monoacylglycerol acyltransferase and PLA activities (8). Also, a lecithin:cholesterol acyltransferase (LCAT)-like PLA, which is not a pPLA, shows both PLA_1 and PLA_2 activities, with a preference for acyl groups at the *sn-2* position (9). In this review, this LCAT-PLA will be included in the discussion of the PLA_1 family, as it is the closest homologue of LCAT-PLA_1. Oleosin and other multifunctional enzymes with PLA activities will not be included in this review.

Fourteen genes encoding PLA_1s have been identified in *Arabidopsis*, which can be divided into five classes based on the presence of particular N-terminal stretches and sequence similarities in the catalytic region (Table 1). All known plant PLA_1s have molecular masses of 45–50 kDa, contain a conserved GXSXG motif, and have a catalytic triad composed of a serine, an aspartic acid, and a histidine residue (3). In contrast, their cellular localizations are diverse (4, 10–12). AtPLA_1-Iα1 is localized to cytoplasmatic lipid bodies that are often associated with chloroplasts, whereas the other six class I PLA_1s are targeted to plastids (10–14). All four class II PLA_1s are predicted to be localized to the cytosol, which has been demonstrated experimentally for AtPLA_1-IIγ and AtPLA_1-IIδ (4, 15, 16). AtPLA_1-III and AtPA-PLA_1 are localized to the mitochondria and vacuolar membranes, respectively (17, 18). The transcription of *PLA_1* genes can be diverse as well. *PLA_1* transcripts can generally be detected in almost all plant organs, but the individual isoforms vary considerably in their temporal or tissue specificity (11–15, 19). For example, *AtPLA_1-III* is highly expressed in seedlings.

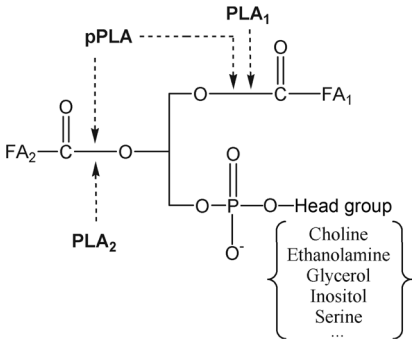

Figure 1 Positional specificity of plant phospholipase As (PLAs) on phospholipids. FA, fatty acyl chain; pPLA, patatin-like PLA. Some plant PLAs can also use glycolipids, lysophospholipids, and neutral glycerolipids as substrates (Table 1).

The carnation *PLA_1-II* is expressed in 4- to 5-day-old roots, whereas *LCAT-PLA* is expressed in both roots and developing siliques (9, 17, 19).

Plants have a relatively much simpler and less complex pool of 'real' PLA_2s (phospholipases that have only PLA_2 activity but no PLA_1 activity) compared with plant PLA_1s, and those from animals and other sources. Only four soluble PLA_2s have been identified in *Arabidopsis* (AtPLA_2-α, -β, -γ, and -δ) (6). Similar to animal secretory PLA_2s (sPLA_2s), all four of these PLA_2s have low molecular masses of 13–18 kDa. All of these plant sPLA_2s also contain a catalytic site DACCxxHDxC motif with a well-conserved histidine-aspartate dyad, and a calcium-binding loop (YGKYCGxxxxGC) (20). Regarding protein localization, AtPLA_2-α is localized to the Golgi, AtPLA_2-β and AtPLA_2-δ are localized to the endoplasmic reticulum, and AtPLA_2-γ is localized to both the endoplasmic reticulum and the Golgi (21–23). A recent study indicates that AtPLA_2-α can also be localized to the nucleus in the presence of AtMYB30 (24). The transcripts of *AtsPLA_2*s are tissue specific: *sPLA_2-α* is expressed in most tissues with the exception of siliques; the expression of *sPLA_2-β* can be detected in flowers and siliques but not in maturing seeds; *sPLA_2-δ* and *-γ* are only expressed in floral tissues (20, 25, 26). Recently, Kim et al. (23) used RT-PCR to compare the expression profiles of all four *AtsPLA_2*s in pollen. *AtsPLA_2-β*, *-γ*, and *-δ*, but not *AtsPLA_2-α*, were expressed in pollen, potentially indicating an important role for class II but not class I sPLA_2s in pollen development. Environmental conditions can also affect *sPLA_2* expression. For example, the expression of *Citrus sinensis sPLA_2-α* and *sPLA_2-β* exhibited diurnal rhythmicity in leaf and fruit tissues, suggesting accompanying daily cycle changes in second messengers (27).

Patatins are a group of vacuolar non-specific lipid hydrolases in tubers of solanaceous plants with combined PLA_1, PLA_2, and galactolipase activities. *Arabidopsis* has 10 pPLA enzymes that can be divided into three classes based on their genomic sequences (Table 1). AtpPLA-I has a molecular mass of 156 kDa, which is much larger than the other AtpPLAs (averaging 45 kDa) (28). Class I and II pPLAs have a catalytic dyad, composed of a typical serine hydrolase motif of GXSXG, and a conserved aspartic acid within a patatin domain. The class III pPLAs, conversely, have a hydrolase motif sequence of GXGXG (5, 29, 30). The localizations of the six AtpPLAs have all been identified. AtpPLA-I is localized in the chloroplasts; pPLA-IIδ, ε, and γ are localized to the cytoplasm and associate with membranes such as plasma or endoplasmic reticulum membrane. pPLA-IIIβ associates with the plasma membrane, and pPLA-IIIδ is localized to both the plasma and intracellular membranes (28, 29, 31, 32). Similar to *sPLA_2*s, *pPLA*s have a range of expression profiles among different plant tissues (Table 1). For instance, *AtpPLA-IIγ* is expressed preferentially in flowers and siliques, but *AtpPLA-IIε* is mainly expressed in roots (28). *AtpPLA-IIIα* has the highest expression level in siliques, whereas the other three *AtpPLA-IIIs* are expressed predominantly in roots (31).

Enzymatic properties of plant PLAs

The enzymatic properties of several plant PLAs have been studied through recombinant expression in yeast or *Escherichia coli*. These enzymes exhibit a broad range of calcium dependencies, substrate specificities, and pH and temperature optimums.

In general, all the characterized PLA_1s are calcium independent, can use phosphatidylcholine (PC) as substrate, and prefer a pH in the range of 5.0–7.5. Individual PLA_1s, however, exhibit different catalytic properties. For instance, all AtPLA_1-Is and AtPLA_1-III can use monogalactosyldiacylglycerol (MGDG), digalactosyldiacylglycerol (DGDG), and triacylglycerol (TAG) as substrates in addition to PC; however, AtLCAT-PLA_1 cannot catalyze the hydrolysis of non-phospholipid substrates (11, 17, 33). AtLCAT-PLA, a homologue of animal lysosomal PLA_2 (group XV), can use phospholipids but not lysophospholipids as substrates (9, 34).

The catalytic properties of the four AtsPLA_2s have been extensively characterized. As shown in Table 1, AtsPLA_2-α, -β, -δ, and -γ are all calcium dependent and can use PC and phosphatidylethanolamine (PE) as substrate; however, their optimal pH vary from 8.5 to 9.0, 6.0 to 7.0, 7.0 to 9.0, and 8.0 to 9.0, respectively (20, 35). Recently, sPLA_2s have also been characterized in other

Table 1 *Arabidopsis* phospholipases (AtPLAs).

Family[a]	Class	Gene ID (name)	Tissue-specific transcripts[b]	Protein location[c]	Substrate preference[d]	Representative physiological roles	References
PLA_1	I	*At1g05800* (*AtPLA$_1$-Iα1*)	L>Sd>St>F	LB	DAG>PC>MAG,TAG	Jasmonate formation, stress	(10–12, 49)
	I	*At2g31690* (*AtPLA$_1$-Iα2*)	F>St>Sd, no L	P	DAG>MAG>PC>TAG	Senescence, stress	(10, 11, 14, 49)
	I	*At2g44810* (*AtPLA$_1$-Iβ1*)	F>>St,L,Sd	P	PC>DAG>MAG>TAG	Jasmonate formation, stress	(10, 11, 13)
	I	*At4g16820* (*AtPLA$_1$-Iβ2*)	F>Sd>>L>St	P	DAG>TAG>MAG>PC	Stress	(10–12, 49)
	I	*At1g06800* (*AtPLA$_1$-Iγ1*)	L>Sd>F>St	P	TAG>DAG,MAG,PC	Jasmonate formation, stress	(11, 12, 49)
	I	*At2g30550* (*AtPLA$_1$-Iγ2*)	St>L>Sd>F	P	TAG,DAG,MAG,PC	Stress	(11, 12, 49)
	I	*At1g51440* (*AtPLA$_1$-Iγ3*)	F>L>>St>Sd	P	MAG>DAG>TAG>PC	Stress	(11, 12, 49)
	II	*At1g06250* (*AtPLA$_1$-IIα*)	–	*c*	–	–	(4)
	II	*At2g31100* (*AtPLA$_1$-IIβ*)	–	*c*	–	–	(4)
	II	*At4g18550* (*AtPLA$_1$-IIγ*)	St,Sd,Si>>F	C	DAG>MAG>LPC>>MGDG>PC>TAG	Storage oil metabolism	(4, 16)
	II	*At2g42690* (*AtPLA$_1$-IIδ*)	–	C	PC>MAG>TAG	UV-B, Se	(4, 15)
	III	*At1g30370* (*AtPLA$_1$-III*)	Sd	M	LPC>MAG,PA>PC,PE>MGDG,DGDG >TAG, DAG	Seed germination, root development	(17)
		At1g31480 (*AtPA-PLA$_1$*)	Rt>St,Sd,L>F	VM	–	Shoot gravitropism	(18, 44)
		At3g03310 (*AtLCAT-PLA$_1$*)	–	*es*	PC>PE>PA>LPC	–	(33)
		At4g19860 (*AtLCAT-PLA*)	Rt>Si>L>St>F	C	PC>PA>PE>PG>PS	–	(9)
$sPLA_2$	I	*At2g06925* (*AtsPLA$_2$-α*)	F,L,St,Rt	G,N	PE>PC	Protein trafficking, root	(20, 22, 24, 35)
	II	*At2g19690* (*AtsPLA$_2$-β*)	F,Si	ER	PE>PC	Auxin signaling	(20, 21, 35)
	II	*At4g29460* (*AtsPLA$_2$-γ*)	F	ER,G	PE>PC	Pollen development	(20, 23, 35)
	II	*At4g29470* (*AtsPLA$_2$-δ*)	F	ER	PE>PC	Pollen development	(20, 23, 35)
pPLA	I	*At1g61850* (*AtpPLA-I*)	Sh>Rt,F>>L	CHL	MGDG>DGDG>PG>>PI>PC	Jasmonate formation, stress	(28, 39)
	II	*At2g26560* (*AtpPLA-IIα*)	Rt>>F,L	*mem*	MAG>DAG>PE>PC	Oxylipin formation, stress	(30, 32)
	II	*At5g43590* (*AtpPLA-IIβ*)	–	*n*	–	–	
	II	*At4g37050* (*AtpPLA-IIγ*)	F>Rt,St>L	PM,ER	PG>MGDG,DGDG>PC>PI	Root development, stress	(28, 32, 40)
	II	*At4g37070* (*AtpPLA-IIε*)	Rt	PM,ER	PG>MGDG>DGDG>PI>PC	Root development, stress	(28, 32, 40)
	II	*At4g37060* (*AtpPLA-IIδ*)	Rt,L	PM,ER	PG>MGDG,PI>DGDG>PC	Root development, stress	(28, 32, 40)
	III	*At2g39220* (*AtpPLA-IIIα*)	Si>Rt>F,St,L	–	–	–	(31)
	III	*At3g54950* (*AtpPLA-IIIβ*)	Rt>L>St>>F,Si	PM	PG,DGDG>PS,PA,MGDG,PE,PC	Cell elongation, cellulose, lipid	(31)
	III	*At4g29800* (*AtpPLA-IIIγ*)	Rt	–	–	–	(31)
	III	*At3g63200* (*AtpPLA-IIIδ*)	Rt>F>Si>>St	PM,IM	PC	Lipid synthesis	(29, 31)

[a]$sPLA_2$, secretary PLA_2; pPLA, patatin-related PLA.

[b]F, flower; L, leave; Rt, root; S, seed; Sd, seedling; Sh, shoot; Si, silique; St, stem.

[c]Enzyme locations demonstrated experimentally were labeled with capital letters. Predicted locations were marked with italic lowercase letters. C, cytosol; CHL, chloroplast; ER, endoplasmic reticulum; ES, extracellular space; G, Golgi apparatus; IM, intracellular membranes; LB, lipid bodies that are often associated with chloroplasts; M, mitochondria; MEM, membranes; N, nucleus; P, plastids; PM, plasma membrane; VM, vacuolar membranes.

[d]Substrate specificity may vary in different reactions conditions. Please check the references for the detailed reaction conditions. DAG, diacylglycerol; DGDG, digalactosyldiacylglycerol; LPC, lysophosphatidylcholine; MAG, monoacylglycerol; MGDG, monogalactosyldiacylglycerol; PA, phosphatidic acid; PC, phosphatidylcholine; PE, phosphatidylethanolamine; PG, phosphatidylglycerol; PI, phosphatidylinositol; PS, phosphatidylserine; TAG, triacylglycerol.

plants, including tobacco, soybean, and wheat (36–38). Interestingly, a purified tobacco class II $sPLA_2$, Nt1-PLA_2, showed both PLA_1 and PLA_2 activities (37). The authors used non-radiolabeled substrates in their enzyme assays, and then labeled the released fatty acids with 9-anthryldiazomethane for high-performance liquid chromatography analysis. As PLA_1 activity has never been reported for other plant $sPLA_2$s, it would be interesting to verify this result directly using radiolabeled substrates.

All three classes of pPLAs are capable of catalyzing the hydrolysis of phospholipids and other glycerolipids at both the *sn-1* and *sn-2* positions (3, 5, 29). AtpPLA-I, the only class I pPLA, preferentially catalyzes the hydrolysis of phosphatidic acid (PA) and phosphatidylserine (PS) at the *sn-2* position, and phosphatidylinositol (PI), PC, PE, and phosphatidylglycerol (PG) at the *sn-1* position. Furthermore, AtpPLA-I catalyzes the hydrolysis of MGDG four times faster than PG (39). Surveying class II pPLAs, AtpPLA-IIα showed strong PLA_1 activity toward PC and PE; strong PLA_2 activity toward PG, PI, PA, and PS; and strong hydroxylase activity toward other membrane glycolipids, including MGDG, DGDG, and even oxidized glycolipids (30). AtpPLA-IIγ, -IIε, and -IIδ can act on glycolipids and phospholipids, but not on TAG (40). To describe class III pPLAs, AtpPLA-IIIβ can catalyze the hydrolysis of phospholipids and glycolipids but not neutral lipids, and PA is the preferred substrate. AtpPLA-IIIδ has five times greater PLA_2 activity than PLA_1 activity when PC is used as a substrate. Although its activity toward other lipid classes has not been described, it would not be surprising if this enzyme could catalyze the hydrolysis of glycolipids and other phospholipids. Interestingly, both AtpPLA-IIIβ and -IIIδ have thioesterase activity (29, 31).

Biological roles of plant PLAs

PLAs are involved in a wide range of cellular processes, many of which are believed to be linked to the accumulation of free fatty acids and lysophospholipids as either signaling molecules or building blocks in lipid metabolism (3, 4, 41). Here, we summarize the physiological aspects of plant PLAs with a focus on their recently identified roles (Table 1). Although some animal PLAs also have functions in signaling transduction and lipid metabolism, we cannot find similar biological roles of plant PLAs and their animal counterparts [for the functions of animal PLAs, please see ref. (42)].

During the past decade, substantial advances have been made toward understanding the biological functions of plant PLA_1s. Among class I PLA_1s, $AtPLA_1$-Iα1, $AtPLA_1$-Iβ1, and $AtPLA_1$-Iγ1 are important for jasmonic acid production (10, 12, 13). Class II PLA_1s have numerous important roles, including ultraviolet B-induced defense signaling ($AtPLA_1$-IIδ), onset of senescence (*Dianthus caryophyllus* PLA_1-IIδ), seedling establishment ($AtPLA_1$-IIγ), and also cell development and tissue growth (*Capsicum annuum* PLA_1-IIγ) (15, 19, 43). The sole class III $AtPLA_1$, $AtPLA_1$-III, plays an important role in seed viability and longevity. Also, *$AtPLA_1$-III*-overexpressing lines possess significantly longer roots than the *$atpla_1$-iii* knockout or wild-type seedlings. Also, $AtPLA_1$-III may help protect and/or maintain seed contents that are important for germination, as *$AtPLA_1$-III*-overexpressing seeds showed a strong tolerance to accelerated-aging treatments (17). Regarding other PLA_1s, AtPA-PLA_1 plays an important role in the early phases of shoot gravitropism (44). Although the enzymatic properties of AtLCAT-PLA_1 and AtLCAT-PLA have been reported, their functions in plants remain to be explored (9, 33).

Compared with other plant PLAs, $sPLA_2$s have been most extensively studied. To date, $sPLA_2$ enzymes have been shown to be involved in numerous developmental processes (4, 21, 22, 24, 26). For example, $AtsPLA_2$-α is required for the trafficking of PIN-FORMED proteins (auxin efflux transporters) to the plasma membrane, and may negatively regulate AtMYB30-mediated pathogen defense (22, 24). $AtsPLA_2$-β produces second messengers to enhance light-induced stomatal opening and also contributes to cell elongation and shoot gravitropism through the auxin signaling pathway (21, 26, 45). Additionally, all three class II $sPLA_2$s play critical roles in pollen development and pollen tube growth, most likely by modulating membrane deformation and enabling membrane trafficking (23).

Recent studies with transgenic plants indicate that the 10 plant pPLAs have unique yet overlapping functions. AtpPLA-I contributes to basal, but not pathogen- or wound-induced jasmonic acid production (39). Class II pPLAs modulate oxylipin formation (AtpPLA-IIα), water loss (AtpPLA-IIα), root development (AtpPLA-IIγ and AtpPLA-IIε), and stress responses (AtpPLA-IIα, AtpPLA-IIα, and AtpPLA-IIγ) (30, 40, 46–48). None of these pPLAs, however, are involved in providing free fatty acids for jasmonic acid biosynthesis (39). Among class III pPLAs, AtpPLA-IIIβ was found to be involved in cell elongation, cellulose accumulation, and lipid metabolism (31). In T-DNA insertional knockout mutants of the four pPLA-IIIs, only the *ppla-iiiδ* knockout mutant seeds had significantly lower oil contents. Conversely, when *pPLA-IIIδ* was overexpressed in *Arabidopsis*, the mutant had increased TAG

content, without detrimental effect on overall seed yield per plant (29). As AtpPLA-IIIβ and AtpPLA-IIIδ have been reported to be involved in seed acyl lipid biosynthesis, further functional studies of lipid-hydrolyzing enzymes from other plants, particularly class III pPLAs, could better our understanding of lipid metabolism.

Conclusions and perspectives

Our understanding of plant PLAs has increased substantially over the past decade. A comprehensive and complex collection of PLAs have been identified, and further shown to exhibit a broad range of catalytic properties and biological functions. Some important questions, however, still remain. Further studies are necessary to elucidate the precise role(s) of each individual PLA in the phospholipid signaling networks, the upstream and downstream targets of lipid products generated by plant PLAs, and the functions of PLAs in lipid metabolism.

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