NEW ERA AGRICULTURE
MAGAZINE

Lipids and it's role in Plant–Pathogen Interactions

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Abstract: -

Lipids are vital organic molecules that serve not only as structural and energy-storage components in plant cells but also play crucial roles in signaling and defense mechanisms during plant–pathogen interactions. This review explores the biochemical diversity of plant lipid like glycerolipids, sphingolipids, sterols, polyketides and prenol lipids along with their multifaceted roles in immunity. Structural lipids such as cuticular waxes and cutin form the first line of defense by limiting pathogen entry, while lipid-derived signals like free fatty acids and phytooxylipins mediate antimicrobial responses and immune signaling. Fatty acid derivatives including oxylipins, jasmonates, and azelaic acid as signaling molecules that regulate systemic acquired resistance (SAR), hypersensitive responses (HR) and the expression of defense-related genes. Lipid transfer proteins and certain phospholipids also play supporting roles in recognizing threats and moving defense signals where they're needed. Together, these lipids not only protect plants but also help them communicate and respond quickly to attacks. Understanding how lipids work in plant immunity opens up new possibilities for growing crops that are better equipped to resist disease.

Keywords: Lipids, PR proteins, Phytooxylipins, Systemic acquired resistance etc.

1. Introduction to Lipids:

A lipid is any of various organic compounds that are insoluble in water. They include fats, waxes, oils, hormones, and certain components of membranes and function as energy-storage molecules and chemical messengers. Together with proteins and carbohydrates, lipids are one of the principal structural components of living cells. Lipids formed by esterification process between fatty acid molecules and glycerol. Fatty acid is a carboxylic acid with an aliphatic chain, which is either saturated or unsaturated.

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Generally aliphatic chain contains 4 to 28 carbon atoms. Fatty acids are classified into four major groups like short-chain fatty acids (up to 5 or even 7 carbons), medium-chain fatty acids (6–8 up to 12–14 carbons), long-chain fatty acids (13–18 up to 22 carbons) and very-long-chain fatty acids (VLCFAs, longer than 22 carbons).

Lipids play many roles in plants such as structural components (Cutile and plasma membrane), storage (TAG ex: chloroplast plastoglobules), defensive functions (poylketides), signaling (oxylipins). In plants, Fatty acids with **16** carbon atoms represent about **30%** of total fatty acids and those with **18** carbons about **70%**. The most abundant fatty acids species are **linoleic acid (C18:2) and α-linolenic acid (C18:3)**, representing about **80% of 18C** and nearly 55% of total FAs. Considerable amounts of **hexadecatrienoic acid** (C16:3) are present in the leaves of *Arabidopsis thaliana* and other 16:3 plants, where they represent about **14%** of the total fatty acid content.

2. Lipids classification

Lipids are classified into glycerolipids, sphingolipids, sterols, polyketides, prenol. **Glycerolipids** are composed of diacylglycerol (DAG) with esterified at sn-1 and sn-2 positions of a glycerol backbone. Based on the functional group attacted sn-3 position glycerolipids are divided into phospholipids (PLs), galactolipids (GLs), triacylglycerols (TAGs), sulpholipids (SLs).

Phospholipids (PLs) PLs phospholipids are composed of diacylglycerol (DAG), i.e., two fatty acids (FAs) esterified to the sn-1 and sn-2 positions of a glycerol backbone, and an alcohol-modified phosphate head group attached to the sn-3 position. Ex: Phosphatidylcholine (PC), Phosphatidylethanolamine (PE), Phosphatidylglycerol (PG), Phosphatidylserine (PS), Phosphatidylinositol (PI), Phosphatidic acid (PA).

Galactolipids are glycerolipids with one or two galactose molecules attached to the sn-3 position of the glycerol backbone. Ex: Monogalactosyldiacylglycerol (MGDG), Digalactosyldiacylglycerol (DGDG).

Triacylglycerol (TAG) comprises a glycerol backbone bearing three esterified FAs. Sulpholipids (SLs) are characterized by the presence of a sulfur-containing functional group. In plants, they are represented mainly by sulphoquinovosyldiacylglycerol (SQDG), an anionic glycolipid composed of sulphoquinovose (6-deoxy-6-sulphoglucose) linked to the sn-3 position of the glycerol backbone in DAG.

Sphinogolipids have a backbone of sphingoid bases. The classes of ceramides (Cers), glycosylceramides (GCers), glycosyl inositol phosphoceramides (GIPCs), free LCB (long chain base) are included in Sphinogolipids.**Phytosterols** are isoprenoids formed by a cylco-pentaperhydrophenantren moiety; this is a structure made up of four rigid rings which is hydroxylated at position 3. Phytosterols can occur in free forms or conjugated ones such as sterol glucosides (SGs). **Polyketides** are polymers composed of acyl residues synthesized by polyketide synthases. Prenol lipids (terpenoids) are synthesized from the 5-carbon precursors, namely, isopentenyl diphosphate and dimethyl diphosphate, which are mainly produced via the mevalonic acid pathway. They contain one or more isoprene units in their structure.

Note: Plasma membrane lipids contain glycerolipids (30–50%), sphingolipids (5–40%) and sterols (20–50%). Majorly glycerolipids in plasma membrane are represented by PC (25–45%) and PE (30–40%), and the less abundant classes are PS (3–12%), PG (2–15%), PI (2 11%), and PA (0–20%). Chloroplast membranes are characterized by a high amount of galactolipids. Thylakoids and the inner chloroplast envelope contain approximately 49% MGDG, 30% DGDG, 5% SQDG, and 8% PG. The outer envelope is composed of 17% MGDG, 29% DGDG, 6% SQDG, 10% PG, and 32% PC(Kuźniak and Gajewska, 2024).

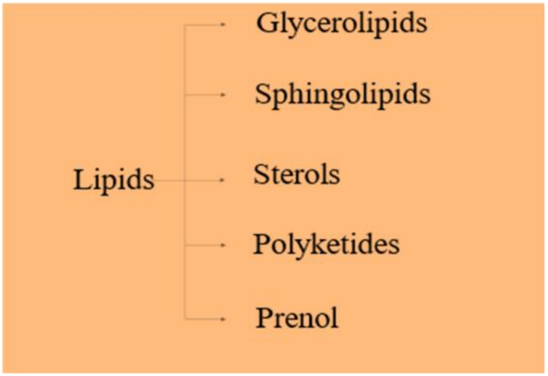

Figure 1: Classification of plant lipids

3. Plant defence and Plant lipids–Pathogen Interactions

Plant have first line of induced defense which are activated by membrane's pattern recognition receptors i.e., PRR (PAMPs, DAMPs and MAMPs), leading to pattern-triggered immunity (PTI), providing basal immunity against entire classes of pathogens. While, the second line of immune defense (ETI) is triggered by interaction of avirulence (Avr) genes-coded pathogen effectors and plant resistance (R) gene products. It is activated upon recognition of pathogen effectors by intracellular nucleotide-binding domain leucine-rich repeat-containing receptors (NLRs) and involves the local hypersensitive response (HR), often followed by systemic resistance in the host plant.

Plant response to induced defense response can be seen in cells through increased levels of intra cellular Ca2+, reactive oxygen species (ROS) generation, synthesis of phytoalexins, activation of mitogen-activated protein kinases (MAPKs) cascades, transcriptional induction of defence genes, and hormone signalling with SA, JA, and ethylene, comprising the backbone of plant immunity.

Plant lipid interaction can be broadly divied into plant surface lipids in plant–pathogen interactions, free fatty acids and phytooxylipins in plant–pathogen interactions and other lipids and lipid-related mediators involved in plant–pathogen interactions.

3.1 Plant Surface Lipids in Plant–Pathogen Interactions

Plant surface lipids include waxes and cuticles. Cuticular waxes are a mixture of aliphatic 20C to 40C VLCFA derivaties and variable amounts of triterpenoids and phenylpropanoids. Whereas, cutin is the core structural polymer, and it is composed of hydroxy and epoxy C16 and C18 FAs and glycerol.

Plant surface waxes have self-cleaning mechanism known as the “lotus effect” due to its hydrophobic nature. Removing the epicuticular wax layer in some plant–pathogen systems influenced the defense response against pathogens. Example, in interaction of *Brassica napus* X *Sclerotinia sclerotiorum* infection, the resistant lines with wax devoid mutants shown more intense sympotoms then other non-resistant lines, proving the role of waxes in plant defence (Cavaco *et al*.,2021).

On other hand wax aldehydes and wax primary alcohols enhance plants susceptibility. the studies on Barley and *Blumeria graminis* f.sp. *hordei* interaction revealed that n-hexacosanal compound helps the pathogen in germination and differentiation in a dose and chain-length-dependent manner in vitro. Cuticle primarily limits pathogen attachment, invasion, and infection. The studies involving on cuticle mutants of crops such as *Arabidopsis and Solanum lycopersicum* with Cuticle-degrading pathogens reveled that cuticle permeability has increased which is accompanied by a constitutive production of ROS. It has been proposed that the changes in the diffusive properties of the cuticle induced by infection may allow the early perception of MAMPs/DAMPs (cutin monomers) generated at the plant–pathogen interface and pathogen effectors, thus allowing faster and more efficient activation of PTI and ETI, respectively. Ex: Cutinases (RcCUT1) from *Rhizoctonia cerealis* acts as an effector triggering necrosis, H2O2 accumulation. But, on other hand the cutin monomers can promote expression of fungal inducible cutinase genes, facilitate the formation of specialized fungal infection structures and cuticle penetration and sometimes used as carbon and energy source.

3.2 Free Fatty Acids and Phytooxylipins in Plant–Pathogen Interactions

Free fatty acids (FFA) exhibit antimicrobial activity by penetrating and disrupting biological membranes. They mainly target bacterial cell membranes, increasing membrane permeability, disrupting the electron transport chain, interfering with oxidative phosphorylation, and inhibiting membrane-associated enzymes and nutrient uptake. For long-chain unsaturated FFAs, the antimicrobial activity increases with the chain length and degree of unsaturation. FFAs with medium (8–12 carbon atoms) to longer (>12 carbon atoms) chains are particularly effective against Gram-positive bacteria, whereas those containing six carbons or fewer affect Gram-negative bacteria. Saturated FA exerted antifungal activity towards devastating phytopathogenic fungi, namely, *Alternaria solani*, *Colletotrichum lagenarium*, and *Fusarium oxysporum*, by inhibiting spore germination and mycelium growth (Wang *et al.*,2021).

Trienoic acids (TAs) derived from fatty acid desaturases especially C18:3 derived from chloroplasts, act as effective **activators of NADPH oxidase**. Which inturn lead to response like HR, SA accumulation, PR genes (biotrophic pathogens). Ex.: Δ-9 stearoyl acyl carrier protein desaturase (SAD) and ω-3 fatty acid desaturases FAD7 and FAD8

Phytooxylipins are synthesized from Polyunsaturated fatty acid (PUFA) such as C18:2 and C18:3. These compounds can be synthesized through enzymatically pathways (13- and 9-LOX-dependent oxylipin biosynthesis) like Acrolein production which upregulates PR4 and through nonenzymatic pathways by oxygen-dependent oxidation (ROS) like phytoprostanes production.

Oxylipins are at the front line of plant–pathogen interactions due to their signaling role in both local and systemic defense and mediate a reciprocal cross-talk between plant and pathogen. Oxylipins involve in various mechanisms like quorum sensing, trigger gene expression (PR-4), interaction with the plant cell redox network (synthesis of superoxide dismutase, catalase, thioredoxins, glutaredoxins and redox target proteins like CYP20-3) along with regulate growth and reproduction of pathogen acts as antimicrobial agents. For example, plant oxylipins from peanut seeds alter sporulation and mycotoxin synthesis in invading Aspergillus.

Phytooxylipins production from 13-Lipoxygenase include C6 green leaf volatiles (GLVs) and C5 pentyl leaf volatiles (PLVs) which induce antagonistic biological effects.GLVs promoted this disease progression through induction of JA. Ex. (Z)-3-Henenol. PLVs are suggested to activate resistance to biotrophic and hemibiotrophic pathogens. Ex.:3-pentanol triggered resistance to *P. syringae* pv *lachrymans* in cucumber.

Phytooxylipins production from 9-Lipoxygenase pathway like Azelaic acid, generated by oxidative cleavage of C18 unsaturated fatty acids with a double bond at

C9, which was suggested to be a general oxidative stress signal implicated in SAR. Azelaic acid precursors are derived from the MGDG and DGDG galactolipids of the chloroplast membrane.

DGDG helps in accumulation of salicylic acid and nitric oxide (NO)- signaling molecules during SAR and also involved in retrograde signaling between the chloroplast and the nucleus by inducing the expression of nuclear genes, including SLD2 and EDS5 genes involved in SA biosynthesis and transport, respectively. Whereas, MGDG helps in biosynthesis of azelaic acid and glycerol-3-phosphate and down streaming of NO. Ex.: In cultured potato cells, treatment with *Phytophthora infestans* elicitor preferentially stimulated the 9-LOX pathway, which led to the accumulation of divinyl ether colneleic acid.

Jasmonates: Unsaturated fatty acid when reacted with 9 LOX and 13 LOX produces fatty hydro-peroxidase which further undergo reaction with allene oxide cyclase produces 12-oxo-phytodienoic acid (OPDA) and subsequently to jasmonates. Jasmonates play essential roles in regulating plant responses to environmental stimuli, including pathogens and insects and generally involved in plant resistance against necrotrophic pathogens. Jasmonates and its isoleucine conjugate (JA Ile) trigger massive reprogramming of the gene expression required to activate defense responses.

OPDA is responsible for callose accumulation (preventing the cell-to-cell spread), phytoalexins, involved in long distance signalling along with ketol-octadecadienoic acid (KODA) are two xylem-mobile oxylipins (ex.: Maize against *C. graminicola*). OPDA was found to occur not only as a free acid but also as esters with galactolipids, such as MGDG and DGDG. They are synthesized during the HR response triggered by bacterial effectors, act directly as antimicrobial substances inhibiting pathogen growth, and function as storage compounds allowing the slow release of free OPDA, which is then converted to JA (Mehta *et al*.,2021).

3.3 Other Lipids and Lipid-Related Mediators Involved in Plant–Pathogen Interactions

PR14 (pathogenesis related protein - 14) i.e., LTP (Plant lipid transfer proteins) expression is inducible by infection with pathogens and transgenics. In transgenic mediated PR-14 expression, the expression of gene may be induced or upregulated. Ex.: Transgenic rice plants expressing a nonspecific LTP gene secreted to the apoplast space exhibited enhanced resistance to *M. grisea*, *R. solani*, and *X. oryzae*

LTPs can inhibit the growth of bacterial and fungal pathogens, and this antimicrobial effect may result from the permeabilization of cell membranes. They also contribute to pathogen resistance by regulating epicuticular wax accumulation and maintaining adhesion integrity between the cuticle and the plant cell wall. LTPs are involved in transferring long-distance SAR signals via the phloem. SAR establishment in Arabidopsis requires long-distance translocation of LTPs, namely, AZI1 (Azelaic Acid Induced 1) and DIR1 (Defective in Induced Resistance 1) in conjunction with glycerol-3-phosphate. Moreover, the nonspecific LTP (PR14) interacts with PR1 in the apoplastic space to increase the antimicrobial activity of PR1 in an ROS-dependent manner and thus, increases pathogen resistance

Phospholipid helps in defense protein sorting in plants (subcellular compartments) which is essential for pathogen recognition and activation of the immune system. Example phosphatidyl-inositol-3-phosphate [PtIns(3)P] vesicle transport is necessary for the secretion of defense PR1 proteins to the apoplastic space where they exhibit their antimicrobial activity. Phosphatidic acid (PA) binds and stabilizes the NADPH oxidase, regulating ROS production in plant PTI and ETI. Helps in internalization of ligand-receptor complex from plasma membrane which is formed after pathogen recognition, PRRs bind to bacterial or fungal PAMP through process called endocytosis. This internalization is facilitated by PA and phosphatidylinositol-4,5-bisphosphate [PtIns(4,5)P2] targeting the PRR-PAMP complex. PA as an important secondary messenger role in plant defence mechanisms against microbial pathogens. Ceramides (**Cers)**, a class of sphingolipids induces SA-dependent plant cell death during ETI against biotrophic and hemi-biotrophic pathogens. Cers function's as signaling molecules that regulated programmed cell death which limits the spread of pathogen. Pathogens developed the virulence strategy against Cers by production of mycotoxins that inhibit acyl-CoA-dependent Cer synthase, leading to Cer depletion. Example: mycotoxin secretion by necrotrophic fungi like *A. alternata* and *Fusarium* species.

Conclusion

Lipids, traditionally recognized for their roles in energy storage and structural integrity, have emerged as key players in plant defense mechanisms against pathogens. Their diverse biochemical structures enable them to participate in multiple layers of plant immunity. Surface lipids such as cuticular waxes and cutin act as the initial physical barrier to pathogen invasion, while lipid-derived signalling molecules (oxylipins, jasmonates, and azelaic acid) perfrom complex defense responses such as systemic acquired resistance (SAR), hypersensitive response (HR) and modulation of defense gene expression. Moreover, free fatty acids and phytooxylipins not only exhibit direct antimicrobial activity but also function as messengers that fine-tune plant responses to various classes of pathogens. Lipid transfer proteins (LTPs) and phospholipids further amplify these responses by mediating the transport and localization of defense signals and proteins. Sphingolipids, particularly ceramides, serve critical functions in signaling cell death to contain pathogen spread, and are themselves targets of pathogen virulence strategies. Understanding the dynamic roles of lipids in plant–pathogen interactions underscore their potential in developing disease-resistant crops. Future advances in lipidomics and genetic engineering could enable precise manipulation of lipid pathways to strengthen crop immunity, offering sustainable solutions for global food security in the face of increasing biotic stress.

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