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Review Article

Lipids: A Key Regulatory Hub in Plant Stress Adaptation

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Abstract

The plants exert rapid responses to environmental stresses to adapt with the stress. Plants respond in many ways to different abiotic and biotic stresses. The first cellular component to sense stress signals is cell membrane. Cell membrane is a biological membrane, and its main constituents are Lipids that can sense conditions outside the cell. Remodeling of cellular membrane lipids is one of the critical mechanisms in the plant cells to withstand stresses. Lipids play a critical role in triggering and regulating cellular hormonal signaling cascades. There is a close correlation between ABA-dependent signaling and lipid metabolic pathways to maintain the integrity and the viability of cellular membranes. Phosphatidic acid, lysophospholipid, inositol phosphate, fatty acid, oxylipins, diacylglycerol, and sphingolipid are considered as the signaling molecules. Lipids also act as a stress reliever to lower the negative effects of stress. This review highlights the key regulatory roles of lipids in plant adaptation against the environmental stresses.

Keywords: Homeostasis, Lipids remodeling, Lysophospholipid, Oxylipins, Phosphatidic acid, Signal lipids, Sphingolipid

Introduction

The pace of world population, the increment in food consumption per capita and the need for renewable resources inferred from plants have driven to an increment in the need for crop products (Singer et al., 2020). Despite this, crop yields are decreasing because of abiotic pressures such as heat, cold, drought, and salinity - which are increasing due to climate change (van Zelm et al., 2020). As sessile organisms, plants develop partial metabolic and physiological ways of adapting and living under these harsh conditions of stress (Van Wallendael et al., 2019). Despite our huge knowledge of these processes, many questions remain due to the negative impact of abiotic and biotic pressures on plants. Therefore, there is always an urgent need to understand and study the stress response on a large and continuous basis. It is nearly certain that such information will be fundamental to enhance stress tolerance, hence keeping up or expanding crop yields within the light of future climate change (Lu et al., 2020).

Cell membranes are the first cellular components to sense stress signals. Lipids are the main components of biological membranes that can sense conditions outside the cell. Remodeling of cellular membranes lipids is one of the basic mechanisms within the plant cells to resist stress (Liu et al., 2019). Lipids play a critical role in triggering and regulating cellular hormonal signaling cascades. Also, there is a close correlation between ABA-dependent signaling and lipid metabolic pathways to maintain the integrity and the viability of cellular membranes (Golldack et al., 2014). Phosphatidic acid, lysophospholipid, inositol phosphate, fatty acid, oxylipins, diacylglycerol, and sphingolipid are considered as signaling molecules (Hou et al., 2016). Other than their roles as signal molecules, lipids act as a stress reliever to reduce the negative impacts of stress. Lipids are a major regulatory center in plant adaptation to the environmental stresses (Lu et al., 2020). This review highlights the regulatory roles of lipids in stress adaptation in plants.

Effect of Plant stress on Lipid Content

Various plant stresses like drought stress, salinity stress, oxygen deficit stress and heat stress affect the lipid content in plants. A notable decrease in the entire amount of DGDG (digalactosyl diacyl glycerol) and MGMD (monogalactosyl diacyl glycerol) was reported under hypoxia stress in *Arabidopsis* (Xie et al., 2015: Wang et al., 2016). However, hypoxia studies in *Arabidopsis* have reported a significant increase in the polyunsaturated molecular species of phosphatidyl choline (PC), phosphatidyl ethanolamine (PE), and phosphatidyl inositol (PI) and a decline in saturated and monounsaturated molecular species which shows hypoxia promoted the lipid desaturation (Klecker et al., 2014; Xie et al., 2015). Total net leaf lipid contents of *Arabidopsis thaliana* decreased gradually during drought (Gigon et al., 2004). Rape seed galactolipid and phospholipid content levels were significantly reduced by drought stress, but their neutral lipids increased. The composition of fatty acid of rapeseed leaf was also affected under water-deficit stress. The linolenic acid (18:3) percentages decreased mainly in monogalactosyl diacyl glycerol and that of linoleic acid (18:2) in phospholipids (Benhassaine et al., 2002). Mueller et al. (2017) reported a decrease of phospholipids diacylglycerol acyltransferase 1 (PDAT1) in seeding that lowers the accumulation of TAGs under heat stress when compared to wild-type plants, showing significance of PDAT1 in heat stress.

Lipids as Signal Molecules

The signaling role of lipids as auxiliary signaling molecules is of great importance. In common, lipid signaling molecules account less than 1% of total lipids (Huo et al., 2016). The role of lipids in signaling pathway in plants under abiotic stress is discussed in the following section.

Phosphatidic acid

Phosphatidic acid (PA) is a minor membrane phospholipid. Its role as a signal transduction molecule under different stress conditions in plants has taken a great attention. Beside its important role as a signal transduction molecule, PA is an essential compound in the structural lipid biosynthesis. In plants, PA can be produced by lysophosphatidyl acyltransferases from the Gro3P pathway-derived LPA pool, in both the endoplasmic reticulum (Kim et al., 2005) and the chloroplast (Yu et al., 2004), where it acts as a precursor for the biosynthesis of phospho- and galactolipids (Arisz, 2010).

Under stress conditions, the PA can be produced through different routes, the first PA can be produced through the action of Phospholipase D (PLD) on the structural lipids (phosphatidylcholine (PC) and phosphatidylethanolamine (PE) (Pappan et al., 1998). The other pathway is through the synergetic action of phospholipase C (PLC) and diacylglycerol kinase (DGK) as the diacylglycerol (DAG) produced by the activity of PLC on phosphatidylinositol lipids (PPIs) is then undergo phosphorylation with the action of diacylglycerol kinase (DGK) (Arisz et al. 2009).

PA is considered as a membrane-localized signal. It plays a role in signaling pathways through the association with a specific target protein such as phosphatase, protein kinases, and other proteins involved in vesicle smuggling (Raghu et al., 2009). PA controls the activity of these binding proteins, either simply through the recruitment, or directly through stimulating conformational changes (Testerink & Munnik, 2005). Another study shows that PA activates the transfer of transcription factor MYB into the nucleus in *Arabidopsis* (Yao et al., 2013). Various studies indicated that binding of PA to proteins can either activate or deactivate protein function. For example, PA binds to a passive regulator of the ethylene pathway, the constituent of triple response kinase (CTR1) in Arabidopsis and inhibits its activity, while PA binding to the sphingosine kinase induces its activation (Testerink et al., 2007; Guo et al., 2011).

Another role of PA under stress conditions is that the local increase in PA affects the membrane curvature and surface charge (Kooijman & Testerink, 2010). PA makes the membranes positively charged which causes the fission and fusion of the membrane, that affects the formation of the signal transduction vesicle (Hou et al., 2016).

Phosphoinositides

Phosphoinositides (PIs) are a type of cell signaling lipid derived from phosphatidylinositol (PtdIns) through the enzymatic activity of lipid kinases and phosphatases. PIs are one of the regulatory membrane lipids found in eukaryotic cells. PIs are present in low content, unlike most structural membrane lipids. PIs importance is more common in animal cells than in the plants. Its role in treating diseases such as cancer has been proven. However, in recent years, PIs have been shown to have critical roles in plant development and function (Heilmann, 2016).

Numerous studies confirmed the presence of changes in PI content in plants exposed to different stresses, indicating the roles of PIs in adapting to plant stress. For example, different PIs change in abundance and localization in response to excessive osmotic stress in plants (Meijer & Munnik, 2003). It has been found that PIs participate in adaptive processes to saline stress by stimulating cell endocytosis and membrane uptake. The biochemical and cellular biological evidence illustrates additional roles for PIs to combat salt stress such as formation of clathrin-coated vesicles and possibly uptake of the stress-induced plasma membrane. In the group of PI pathway, enzymes play an important role in regulating stress responses (Gillaspy, 2013). The ability of PI can be summarized by the various mechanisms. For example, they can act as intact lipids, bound to target proteins, or they can influence the properties of the membrane in which they are included. Alternatively, they can serve as precursors to form soluble IPPs (Heilmann, 2016).

Sphingolipids

The sphingolipids are three building blocks: a long-chain sphingoid backbone amide (LCB) bound to an N-acylated fatty acid (FA), which binds to a polar head group (Pata et al., 2010). The sphingolipids contain a heterogeneous group of compounds because each of the three building blocks is different. Dihydrosphingosine and phytosphenogenesine are the main LCBs in yeast and plants (Hanoun & Obaid, 2008). Sphingolipids are abundantly present in the cytoplasm and interstitial membranes, especially with sterols that form membranous micro-domains (lipid rafts), which have an active role in cell surface activities and protein smuggling into the plasma membrane. Thay have an important and effective role in plants growing under stress. Besides being influential structural elements in plant membranes, their special structure has an active role in fluidity and biophysical system. Sphingolipids also contribute to many cellular and regulatory processes including vesicle smuggling, plant development and defense (Huby et al., 2020). The participation of sphingolipids in drought-induced stomatal closure was demonstrated, as sphingozin kinase (SPHK) was found to have an important role in the ABA-enhanced stomatal response (Guo et al., 2012). Sphingolipids have an important and effective role in plant response to chilling, as it was found that plants whose membranes especially chloroplast membranes contain sphingolipids can grow efficiently under low temperature (Zhou et al., 2016). The plant experiences a state of hypoxia when growing under flood conditions, which has a great impact on the vital cellular and physiological processes in plants. Sphingolipid signals under these conditions are not well evident. Despite this, the remodeling of sphingolipids in plant systems under conditions of hypoxia has recently been reported as a new preventive strategy for plants to improve tolerance to environmental stresses such as floods. Hypoxia causes a significant increase in the levels of ceramides and hydroxy ceramides (Xie et al., 2015).

Interestingly, sphingolipids are involved in the plant's response to salt stress. It has been found that the activity of the ceramide stimulating enzyme, ceramidase (AtACER), in ER and Golgi, significantly contributes to salt tolerance in Arabidopsis (Wu et al., 2015a,b). Also, Zheng et al. (2018) confirmed the role of AtACER against nutrient stress, oxidation and salinity in Arabidopsis. These studies ensured the effective role of sphingolipid signaling in tolerating plant salt stress. However the advances reached in the information about the role of the sphignolipids in the signal transduction during stress in plants are still very limited compared with those in animals. Receptors, targets, and the mediators of the sphingolipid signaling pathway are almost completely unknown in plants, which considered a great opportunity to investigate plant sphingolipids and their signaling roles (Huby et al., 2020).

Lysophospholipids

Lysophospholipids like sphingosyl phosphoryl choline, sphingosine-1-phosphate (S1P), lysophosphatidyl choline (LPC), and lysophosphatidic acid (LPA) are phospholipids that consist of one fatty acyl chain (D'Arrigo & Servi, 2010). Lysophospholipids are found in various tissues and fluid as minor membrane components and signalling elicitors (Sheng et al., 2015). Lysophospholipids can be produced through the hydrolysis of the membrane associated lipids into the extracellular space where they are recognized by certain receptors to induce specific signal pathways. The lysophospholipids can be recognized by the receptors through the position of the acyl chain on the glycerol, degree, length, and saturation of the fatty acyl chain as well as the phosphate head group (Huo et al., 2016). In animals, the lysophospholipids effects are induced with specific G protein coupled receptors (GPCRs) (Meyer zuHeringdorf & Jakobs, 2007). In plants, the existence of GPCRs and associated pathways is still unclear. However, it is found that LPCs activate the H^+-transporting ATPase of the plasma membrane affecting auxin responses, which is considered as evidence that H^+-ATPases can be considered potential receptors for lysophospholipids in plants (Wielandt et al., 2015).

Oxylipins

Oxylipins are an important lipid signaling molecules that regulate the development, growth, and stress responses in living organisms. The oxylipins are biosynthesized in plants through a few parallel pathways as peroxygenase, epoxy allene oxide synthase, alcohol synthase, hydroperoxidelyase, divinyl ether synthase, and others. Oxylipins are also formed non-enzymatically through fatty acids oxygenation with free radicals and reactive oxygen species. These oxylipins are known as phytoprostanes (Savchenko et al., 2014). Oxylipins play an important role in stress signal transduction either directly through the regulation of stress genes expression or participate in other signaling pathways (Lopez et al., 2011; Yang et al., 2012). Generation of reactive oxygen species (ROS) is a common characteristic feature under various stresses. These ROS induced the formation of phytoprostanes in high levels. These phytoprostanes involve in the activation of MAP-kinase signalling system and the induction of the secondary metabolism genes such as phenylalanine ammonialyase (Thoma et al., 2003).

Membrane Lipids Remodeling Role in Enhancing Plant Abiotic Stress Tolerance

Remodeling of membrane lipids is one of the effective adaptation mechanisms for plants to protect against diverse abiotic stresses. Hence, studying the response of membrane lipids to diverse abiotic stresses is considered as critical need to improve the ability of plants to adapt to different stresses (Liu et al., 2019).

Membrane fluidity protection

Alterations in fatty acid saturation are important in plant response to different stresses. The 16: 3 and 18: 3 fatty acids are the basic polyunsaturated fatty acids in the membrane lipids and any change in the levels of those fatty acids greatly controls the fluidity of the membrane (Wang et al., 2010). It is found that dehydration leads to decreasing the fatty acid desaturation. Zhang et al. (2005) reported that tolerant tobacco plants to drought or osmotic stress there is an over expression of two ω-3 desaturases which result in fatty acid desaturation induction. The same was reported by Chen et al. (2018) as they found that under drought the desaturated fatty acids were higher in the tolerant maize than in sensitive cultivar. Hence, maintaining a huge degree of de-saturation with fatty acids can allow plants a high ability to stabilize membrane fluidity, thus relieving membrane harm from abiotic stresses (Liu et al., 2019).

Correctly stack the thylakoid membrane

Photosynthetic membranes are dynamic structures, which require both lipid biosynthesis and circulation during diurnal contrast and life cycles. In photosynthetic organisms, monogalactosyl diacyl glycerol (MGDG), digalactosyl diacyl glycerol

(DGDG) are the common thylakoid lipids and their presence plays a crucial role in photosynthesis (Kobayashi, 2016). In grana stacks composition MGDG is crucial (Lee, 2000). Under stress conditions the protection of the chloroplast structure is controlled with the lipid membranes which primarily related to the hyperstacking of grana (Wang et al., 2014). Du et al. (2018) reported that the change in the abundance of MGDG in *Chlamydomonas*, through its degradation with specific lipase PGD1 (Plastid Galactoglycerol lipid Degradation1) resulted in a hyperstacking phenotype of the thylakoid grana and chloroplast destruction. Hence, the plentitude of MGDG and DGDG is highly imperative for the wellbeing of the thylakoids and the chloroplasts (Liu et al., 2019).

Membrane stability protection through regulation of DGDG/MGDG ratio

The regulation of DGDG/MGDG ratio has been shown to play an important role in plant stress response. In Arabidopsis, a high DGDG/MGDG ratio contributed to high temperature stress tolerance (Chen et al., 2006). Similarly, a high DGDG/MGDG ratio in tobacco shows less susceptible to salt stress (Wang et al., 2014). In maize, the drought-tolerant cultivar has a high DGDG/MGDG ratio than that in drought-sensitive cultivar, which may be associated with the retarded drought-induced leaf senescence (Chen et al., 2018). Under stress conditions, the relatively high abundance of bilayer lipid could contribute to facilitating the stability of lamellar membrane, and possibly reducing the level of saturation of glycerolipids (Nakamura & Li-Beisson, 2016). It is known that MGDG and DGDG are readily interconvertible, and the DGDG/MGDG ratio was correlated with the stage of development of plants (Sanjay et al., 2006). Therefore, it is considered that the DGDG/MGDG proportion may not be a determinant of plant stress tolerance, but plant might improve their membrane stability through controlling the DGDG/MGDG ratio, at least partially, when adapt with stresses (Liu et al., 2019).

Conclusion

Various lipids help in physiological process of Plant growth and development. Also, lipids are a major regulatory center in plant adaptation to stress. They can act as signal molecules and help in the membrane's stability under stress conditions. However, the advances reached in the study of the lipids role in the plant adaptation to stress, there are many issues needs for investigation such as the molecular mechanisms regulating the lipids signal pathways and the receptors involved in these pathways. Lipids have potential to overcome the plant stress and can helps in crop improvement. So progressive understanding of the lipids signaling mechanism to the environment stress is needed to improve plant resistance quality that help to provide more food for present growing population.

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