The roles of chloroplast membrane lipids in abiotic stress responses

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Abstract

Plant chloroplasts have complex membrane systems. Among these, thylakoids serve as the sites for photosynthesis and photosynthesis-related adaptation. In addition to the photosynthetic membrane complexes and associated molecules, lipids in the thylakoid membranes, are predominantly composed of MGDG (monogalactosyldiacylglycerol), DGDG (digalactosyldiacylglycerol), SQDG (sulfoquinovosyldiacylglycerol) and PG (phosphatidylglycerol), play essential roles in shaping the thylakoid architecture, electron transfer, and photoregulation. In this review, we discuss the effect of abiotic stress on chloroplast structure, the changes in membrane lipid composition, and the degree of unsaturation of fatty acids. Advanced understanding of the mechanisms regulating chloroplast membrane lipids and unsaturated fatty acids in response to abiotic stresses is indispensable for improving plant resistance and may inform the strategies of crop breeding.

Keywords: lipids, fatty acids, lipid metabolism, lipid transport, abiotic stress.

Introduction

Plants often need to cope with a variety of stressful environments that are not conducive to growth and development, such as drought, salt and temperature stress [1, 2]. Drought stress can hinder protein synthesis, while reducing the rates of plant cell division and the efficiency of photosynthesis [3, 4], ultimately resulting in slower plant growth [5-7]. Salt stress can alter the membrane lipid composition [8, 9], inhibit seed germination [10-13], and disrupt ion homeostasis [14, 15], and lead to oxidative stress [16-18]. Continuous temperature stress can destroy the structure of plant cells [19, 20], disturb the physiological and biochemical metabolisms [21, 22], reduce crop yield [4], and limit the geographical distribution of plants [23].

Chloroplasts are the special organelles executing photosynthesis in plants and eukaryotic algae, and contain a complex membrane system [19, 24]. The photosynthetic membranes (also called thylakoid membranes) accommodate photosynthetic pigment-protein complexes and electron transport chains [25-27]. When plants are subjected to abiotic stress, photosynthetic organs are susceptible to environmental influences and undergo structural and metabolic regulations [28-31]. As a result, the integrity and fluidity of the chloroplast membranes may be destroyed, and the chloroplasts in the entire plant may be deactivated [32-34]. Membrane structure and fluidity are affected by lipid composition and fatty acid desaturation [35]. The fluidity of the lipid membrane is determined by the variable unsaturated fatty acid content [36]. Changes in unsaturated fatty acid content can improve the plant's tolerance to environmental stresses, such as cold, high temperature and drought [37]. The glycerolipids of thylakoid membranes in cyanobacteria and plant eukaryotes chloroplasts have a glycerol skeleton, where two fatty acid molecules are bonded to sn-1 and sn-2, and have phosphorus (phospholipid) or sugar at the sn-3 position (Glycolipid) molecule [38]. The lipid bilayer is mainly composed of four unique lipids, including monogalactosyldiacylglycerol (MGDG), digalactosyldiacylglycerol (DGDG), sulfoquinoxayldiacylglycerol (SQDG) and phosphatidylglycerin (PG) [39]. MGDG and DGDG are uncharged galactolipids, which form the main body of thylakoid membrane lipids, and provide a lipid bilayer matrix as the main component for photosynthetic complexes [40]. Glycolipid SQDG and phospholipid PG are anionic lipids with negatively charged head groups [41, 42]. This review summarizes a series of physiological changes in chloroplast membrane lipids under abiotic stress. Changes in the composition and content of chloroplast membrane lipids and unsaturated fatty acids have physiological impacts on the structure of chloroplasts and thylakoid membranes, and thereby affecting photosynthesis and plant growth.

Biosynthesis and transportation of fatty acid and membrane lipid

The production of chloroplast lipids begins with the synthesis of fatty acids in chloroplast intermediates. **Figure 1** shows the whole process of membrane lipid synthesis and transport. The fatty acids are derived entirely from chloroplast FA synthase (FAS), while phosphatidic acid (PA) can be produced in both chloroplast and endoplasmic reticulum (ER), depending on the plant species [43]. Fatty acid synthesis is catalyzed by acetyl-CoA carboxylase (ACC) and FAS [44]. Most de novo synthesized fatty acids assemble into phospholipids and neutral lipids in the ER, so fatty acids must be transported from the plastid to the endoplasmic reticulum [45]. Fatty acids are synthesized through repeated cycles of condensation, dehydration, and reduction on acyl carrier proteins [46]. The acyl chain grows and attaches to the acyl carrier protein (ACP). The newly synthesized acyl-ACP (acyl-ACP) is hydrolyzed by acyl-ACP thioesterases to release free fatty acids or perform the next cycle of fatty acid chain extension [47]. Free fatty acids synthesize C16 and C18 long-chain fatty acids under the action of Long-chainacyl-COA synthetase (LACS) [44]. 40% of fatty acids are left in the plastids to synthesize plastid lipids. This pathway is called the prokaryotic pathway for lipid synthesis [48]. The eukaryotic biological process is that 60% of fatty acids are transported out of the plastid in the form of acyl-COA and then transported to the endoplasmic reticulum for extension and processing [49]. About half of the lipids were transported back to the plastid for further modification [50]. Such as Pea (*Pisum sativum*) and rice (*Oryza sativa* L.), which only use the eukaryotic pathway for chloroplast glycolipid assembly, and these plants have a high proportion of α-linolenic acid (C18:3) in chloroplast lipids, giving rise to their designation “18:3 plant” [51]. Such as *Arabidopsis thaliana* and spinach (*Spinacia oleracea* L.), these two pathways are involved in the biosynthesis of chloroplast lipids [52]. Their chloroplast lipids contain a large amount of hexadecanoic acid (C16:3), so they are called “16: 3 plants” [53]. The prokaryotic pathway directly generates MGDG, DGDG, SQDG and PG from newly synthesized FA [54]. Diacylglycerol (DAG), as a precursor of MGDG and DGDG, can be synthesized through eukaryotic and prokaryotic pathways [55]. Part of the DAG that synthesizes chloroplast lipids comes from the chloroplast，and the other part is synthesized using phospholipid synthesized by endoplasmic reticulum as a precursor [56].

In the eukaryotic pathway of lipid synthesis, fatty acids synthesized in plastids are transported out of the plastids for the synthesis of phospholipids and triacylglycerols (TAG) [57]. FAX1 (fatty acid export1) transporter can regulate lipid transport between chloroplast and endoplasmic reticulum [58]. FAX1 is a new *Arabidopsis* Tmemb_14 family transporter located in the inner membrane of the chloroplast, which mediates the output of free fatty acids in the chloroplast [59]. The ATP binding cassette (ABC) protein located in the endoplasmic reticulum mediates the transport of cytoplasmic acyl-COA or fatty acids to the endoplasmic reticulum in *Arabidopsis* [60]， and the protein family has a transmembrane domain and a nucleotide binding domain [61]. ABCA9 regulates the transport of fatty acyl-COA or fatty acids in the cytoplasm to the endoplasmic reticulum to provide lipid raw materials for the synthesis of TAG [62].

Fatty acids enter into the ER and are incorporated through the Kennedy pathway. The fatty acid in the form of fatty acyl-COA is catalyzed by glycerol-3-phosphate acyltransferase (GPAT) to esterify the fatty acid to the sn-1 position of glycerol-3-phosphate (G3P), preferably 18:1 acyl-ACP. Lyso-phosphatidic acid acyltransferase (LPAAT) esterifies the second fatty acid to the glycerol backbone at the sn-2 position. The resulting PA is phosphorylated by phosphatidic acid phosphatase (PAP) to generate DAG. DAG is incorporated into various lipids, including phosphatidylcholine (PC) [63, 64]. The second pathway is called as “acyl-editing”. In this pathway, fatty acids are added directly to lyso-PC to regenerate PC, which is cycled back into lyso-PC [65]. Lipid transport from the endoplasmic reticulum to the chloroplast requires *Arabidopsis* thalactosyl diglyceride trigalactosyldiacylglycerol (TGD) to regulate lipid across the chloroplast inner and outer membranes into the chloroplast. Lipids transported through the TGD protein complex can include PC, PA or DAG, each TGD protein complex specifically binds PA [66]. TGD1 is the first identified protein located on the outer membrane of the chloroplast, and this protein mutation promotes the accumulation of DGDG [67]. Three proteins TGD1, TGD2 and TGD3 all inhibited the transport of *Arabidopsis* endoplasmic reticulum lipids to the chloroplast [68]. TGD4 is a transmembrane lipid transfer and plays a more direct role in lipid transfer from the ER to the outer plastid envelope [69]. TGD5 facilitates lipid transfer from the outer to the inner plastid envelope by bridging TGD4 with the TGD1,2,3 transporter complex [70]. LACS can not only catalyze the formation of fatty acid-CoA from free fatty acids to participate in the synthesis of long-chain fatty acid derivatives, but also regulate the transport of fatty acids from the endoplasmic reticulum to the chloroplast [71]. Studies have shown that LACS9 localized on the outer membrane of chloroplasts is involved in regulating the input of chloroplast fatty acids [72]. MGDG is synthesized by MGDG synthetase, which catalyzes the transfer of galactose from Uridine diphosphate galactose (UDP-Gal) to the DAG backbone. DGD synthase then transfers a second galactose from UDP-Gal to MGDG to form DGDG, where the contents of MGDG and DGDG are regulatable under stress conditions (**Figure 2**) [73, 74].

The effect of abiotic stress on chloroplast structure in cellular level

Abiotic stress can cause irreversible damage to the structure of the chloroplast. Maintaining structural stability under adverse conditions and reducing damage to chloroplasts may play an important role in improving plant stress resistance [75]. The plasma membrane is considered to be the main barrier between the organism and the external environment, and is a substance that overcomes pressure damage [76].

Chloroplasts are usually the earliest abiotic damage sites visible in the ultrastructure of plants. The degradation of chloroplasts in plants leads to a decrease in net photosynthetic rate and growth retardation [77]. Temperature, drought and salt stress can cause irreversible damage to the structure of the chloroplast, such as the reduction of the aspect ratio and area of the chloroplast, and the phase change of the chloroplast membrane [78, 79]. The thylakoid membrane system is essential for photosynthesis. Once the system is disturbed, the number and size of plastid spheres change. After being treated at 4°C for 20 days, the thylakoid membrane of the sweet pepper swelled and deformed and the thylakoid of the grain split, and at the same time the starch grains increased. [80]. Chloroplasts gradually expanded from ellipsoids to larger spheres. Studies have shown that chloroplast swelling could lead to an increase in cell matrix permeability and low temperature could cause chloroplast degradation [81, 82]. When the Chinese cabbage Wucai (*Brassica campestris* L.) was exposed to high temperature, the chloroplast envelopes were degraded, the thylakoids were inflated, and the grana lamellae were loosely arranged. The osmiophilic particles in the chloroplasts were increased in both number and size [83]. Treatment of Rice salt-sensitive (IR-29) varieties with 100mMNaCl showed that the chloroplast structure was damaged, which was manifested in the cracking of the existing grana stacks, the increase of the existing grana stacks, and the expansion of the thylakoid membranes, which ultimately led to a decrease in photosynthetic activity [84].

Maintaining structural stability under adverse conditions and reducing damage to chloroplasts may play an important role in improving plant stress resistance. Changes in lipid composition and structure in the plasma membrane under ambient pressure are essential to maintain the stability and function of the membrane. When plant organelles experience stress, chloroplasts respond most rapidly and with the most sensitivity [85, 86]. Changes in the ultrastructure of chloroplasts result in a series of adaptive and evasive responses [87, 88]. Expression of the chloroplast targeting protein *SlCOR413IM1* in tomato (*Solanum lycopersicum* L.) increased rapidly under low temperature, causing minimal damage to the chloroplast membrane system and maintaining the integrity of the chloroplast ultrastructure [89]. In the dry state, AtCOR15 protein could interact with the galactose head group of chloroplast lipid MGDG in *Arabidopsis thaliana*. The decrease of the gel-liquid crystal transition temperature depends on the unsaturation of the fatty acyl chain and the structure of the lipid head group. FTIR (Fourier-transforminfrared) spectra from membranes containing MGDG showed evidence for increased fatty acyl chain mobility in the gel phase in the presence of the COR15 proteins [90]. In cucumber (*Cucumis sativus* L.), exogenous spermine (Spm) can prevent chloroplast and thylakoid membrane structural changes induced by salt stress, and maintain a complete internal layering system. Spm can also prevent chlorophyll degradation in cucumber leaves caused by salt stress, and protect the light harvesting complex (LHC) and PSII from salt-induced damage [91].

The functions of chloroplast membrane lipids during abiotic stress

The thylakoid membrane is the site of photo-driven photochemical reactions and electron transfer in plants, and it also plays an important role in maintaining the stability of photosynthesis (Table 1) [92, 93]. Membrane lipids are also part of the thylakoid complex [94]. For example, DGDG and PG are involved in the binding of extrinsic proteins, thereby stabilizing the manganese cluster in PSII [95]. Plants resist abiotic stress and protect themselves by changing the synthesis and composition of thylakoid membrane lipids [74, 96-98].

Variations in the DGDG/MGDG ratio could modify the stability of chloroplast membranes [99, 100]. When plants were subjected to drought stress, MGDG was most sensitive to drought [101]. In the MGDG synthetic gene knockout *Arabidopsis* mutant *mgd1*, the expression level of MGDG was reduced and had no effect on PSII activity [102]. However, in the *mgd1* mutant, the electrical conductivity of the thylakoid membrane increased, thereby weakening the photoprotective effect of the thylakoid membrane [103]. Studies have shown that drought stress increases the ratio of DGDG / MGDG in spring wheat, and a decrease in PG content is observed. The author believes that it may be that PC or PC-derived lipids are directly or indirectly transported to galactolipid biosynthetic plastids, or that DAG is phosphorylated into PA for synthesis of DGDG [104, 105]. In the process of drying and recovery, the content of chloroplast membrane lipid and the expression of related genes of desiccation-tolerant plants (*Craterostigma plantagineum* and *Lindernia brevidens*) and desiccation-sensitive plants (*Lindernia subracemosa*) must change. In desiccation-tolerant plants, the total lipid content remains constant, but the membrane lipid composition changes and the MGDG content decreases. One of the ways to reduce MGDG is the synthesis of phospholipids by DAG, and the other is the conversion of MGDG to the DGD1/DGD2 pathway, followed by the formation of oligogalactolipids from SFR2 (**Figure 2**)[106]. The reduced MGDG / DGDG ratio helps maintain the bimolecular conformation of membrane lipids and greatly improves the stability of the chloroplast membrane [106].

In the halophyte *Thellungiella*, increasing the content of PG and SQDG in membrane lipids and the ratio of MGDG/DGDG under salt stress could alleviate PSII photoinhibition [107]. Under salt stress, there are decreases in the content of SQDG, the ratio of MGDG/DGDG in the chloroplast membranes of peanut (*Arachis hypogaea* L.), the expression of ω-3 FAD gene, and unsaturated fatty acid content. Increasing the unsaturated fatty acid content of peanut leaf membrane lipid reduced the photoinhibition of PSII and PSI and improved salt tolerance [108, 109]. By contrast, *Arabidopsis* and rice have different lipid synthesis pathways. *Arabidopsis* is a “16:3 plant” with both eukaryotic and prokaryotic lipid synthesis pathways, while rice is an “18:3 plant” with only a eukaryotic lipid synthesis pathway. Under low temperature, *Arabidopsis* contains higher levels of galactolipid than those in rice. The higher double bond index and lower average acyl chain length make *Arabidopsis* chloroplast membranes more fluidic at low temperatures [110]. Two varieties of Fabaceae: Sulla carnosa and Sulla coronaria, treated with 200mM NaCl for 20 days. The experimental results show that (a) maintaining a constant MGDG/DGDG ratio and fatty acids unsaturation level, (b) increasing unsaturation level in MGDG, DGDG and PG may contribute to some degree in the adaptation to salt stress and could protect chloroplast membrane integrity against salt stress effects [111].

Roles of fatty acid composition in abiotic stress response

Plants can adjust the fluidity of membrane lipids, by changing the degree of saturation of polyunsaturated fatty acids, to cope with stress conditions [112, 113]. The levels of the unsaturated FAs (those that carry double bonds between carbons) 18:1, 18:2, and 18:3 are particularly important in plant defense [114]. Analysis of fatty acids in thylakoid membrane lipids revealed the presence of the saturated fatty acids palmitic acid and stearic acid, and unsaturated fatty acids palmitoleic acid and oleic acid (18:1), linoleic acid (18:2) and linolenic acid (18:3) [115]. In the neutral membrane lipids (MGDG and DGDG) of the photosynthetic membrane, the two fatty acyl chains are mostly unsaturated linolenic acid [116]. The negatively charged DGDG is mainly unsaturated linolenic acid and saturated palmitic acid, or a mixture of PG [117]. Fatty acid desaturase (FAD) is an important enzyme that introduces double bonds into fatty acids during the synthesis of glycerolipids [118]. For example, the ω-3 FAD is based on the first carbon atom at the methyl terminus being the ω-1 position, with a C=C double bond at the ω-3 position, and consists of at least two C=C double bonds [119]. According to different electron donors, there is one type of omega-3 FAD in the endoplasmic reticulum, which mainly acts on PG or other phospholipids, while the other type exists in the plastid and acts on phosphatidylglycerol or galactosyl [120].ω-3 FAD and two plastid enzymes, FAD7 and FAD8, are the key enzymes that catalyze the conversion of 16:2 or 18:2 into 16:3 or 18:3, respectively (**Figure 3A**) [121]. The increase of unsaturated fatty acids can enhance plant resistance to stress [122, 123]. Therefore, the regulation of fatty acid saturation by FAD is an important way for plants to adapt to abiotic stress.

Under low temperature stress, the PSII D1 protein is the target of photoinhibition. Fatty acids in PG through over-expression of *LeGPAT* can alleviate PSII photoinhibition [124]. The increase of unsaturated fatty acids in PG reduces the formation of ROS and damage to photosynthetic complexes, thereby improving the low-temperature tolerance of tomato plants [125]. At lower temperatures, an increase of unsaturated fatty acid content was observed in the transgenic lines. The CaHSP26 protein protects PSII by reducing photooxidation, maintaining antioxidant enzyme activity and increasing the fluidity of the thylakoid membrane [126]. Under heat stress, the relative amount of one triacylglycerol species (54:9) containing α-linolenic acid (18:3) increased. Heat stress could induce an increase in TAG levels in *Arabidopsis* leaves, which acts as an intermediate in lipid turnover and leads to a reduction in membrane polyunsaturated fatty acids [127].

Sui et al. [124] found that the increase of unsaturated fatty acids in the membrane lipids of *Suaeda salsa* increases the protection of PSII under high salinity, and that unsaturated fatty acids in membrane lipids can protect PS from NaCl stress. Under salt treatment of the halophyte *Thellungiella*, 18:3 unsaturated fatty acids increased significantly, whereas 18:1, 18:2, and 18:3 decreased greatly in the non-halophyte Arabidopsis [107]. This may be due to the ion channel or Na^+/H^+ reverse transport system that are located on the plasma membrane. The increased unsaturated fatty acids in the membrane lipids could improve the fluidity of the membrane, thereby activating the ion channel and protecting the photosystem [107, 128]. In tomato, *LeFAD3* overexpression can enhance the tolerance of early seedlings to salt stress. It could increase the level of 18:3 in plants to remove excess active oxygen, and promote the repair of PSII, finally reduce the damage to membrane lipids (**Figure 3B)** [129-131]. Under drought stress, the proportion of saturated fatty acids in thylakoid membranes increased, and mature leaves elevated the heat tolerance of plants by increasing the levels of saturated fatty acids, thereby increasing the melting temperature of the plasma membrane [129]. A smaller reduction in the index of unsaturated fatty acids under drought stress is beneficial to thylakoid membrane stability [132]. In rice LYPJ varieties, linoleic acid (18:2) increased significantly at 28 days [133]. The increase in linoleic acid can enhance the fluidity of thylakoid membranes, thus improving the PSII repair rate in crops under severe drought stress [133]. High temperature causes changes in the lipid profile of wheat, and plants respond to high temperature stress by remodeling lipids and reducing the level of lipid unsaturation [134]. The lower lipid unsaturation level under high temperature stress is mainly due to lower levels of 18:3 fatty acyl chains and higher levels of 18:1 and 16:0 fatty acyl chains [135].

Conclusions and perspectives

The structure and composition of chloroplast membrane lipids are vital for maintaining the normal physiological activities in plants. Abiotic stress could induce changes in the content and ratio of the components of chloroplast membrane lipids. The regulation of the corresponding genes has become a hot topic in molecular biology. As transcriptome sequencing and gene editing technologies become increasing popular, we are now able to analyze more comprehensively the key genes that are involved in regulating membrane lipid biosynthesis under abiotic stress, to provide new insight into the expression and regulatory mechanism of these genes.

The observations of the ultrastructures of chloroplasts and thylakoids enable us to study the organ damage under environmental stress. However, the development of molecular probes is needed to decipher the accurate positions of individual lipid molecules in membranes and membrane integral complexes, so that changes in chloroplasts and thylakoids can be seen more intuitively and dynamically [95]. Given that the regulation of membrane lipid fatty acids in chloroplasts depends largely on FAD activity, it is imperative to seek how to regulate the genes in other organelles and tissues. Under abiotic stress, changes in membrane lipids may be accompanied by the effects of plant hormones or some signal proteins. A profound understanding of their mutual regulatory relationship will pave the way for improving plant resistance.

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Author Contributions

Jinlu Li prepared the manuscript. Na Sui, Hai Fan, Qingwei Meng and Lu-Ning Liu conceptualized the idea and revised the manuscript. All authors read and approved the final manuscript.

Conflict of Interests

The authors declare that they have no competing interests.

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Table 1 Typical functions of membrane lipids

Lipid species	Description	Related references
MGDG	In the *mgd1* mutant, the electrical conductivity of the thylakoid membrane increased, thereby weakening the photoprotective effect of the thylakoid membrane.	101,102,103
DGDG	DGDG confers thermotolerance to plants due to its bilayer-stabilizing properties as demonstrated by the failure of DGDG-deficient *dgd1* mutant plants to adapt to high growth temperatures.	104,105
SQDG	SQDG is a negatively charged glycolipid, composed of more saturated fatty acids, and contains different numbers of eukaryotic and prokaryotic species according to plant species.	107,108,109
PG	PGs are the major phospholipid in thylakoid membranes of higher plants and can be used as a precursor of cardiolipins located on the inner mitochondrial membrane that are required for proper functioning of the oxidative phosphorylation enzymes.	117,120

Abbreviations: MGDG, monogalactosyldiacylglycerol; DGDG, digalactosyldiacylglycerol; SQDG, sulfoquinovosyldiacylglycerol; PG, phosphatidylglycerol.

Figures

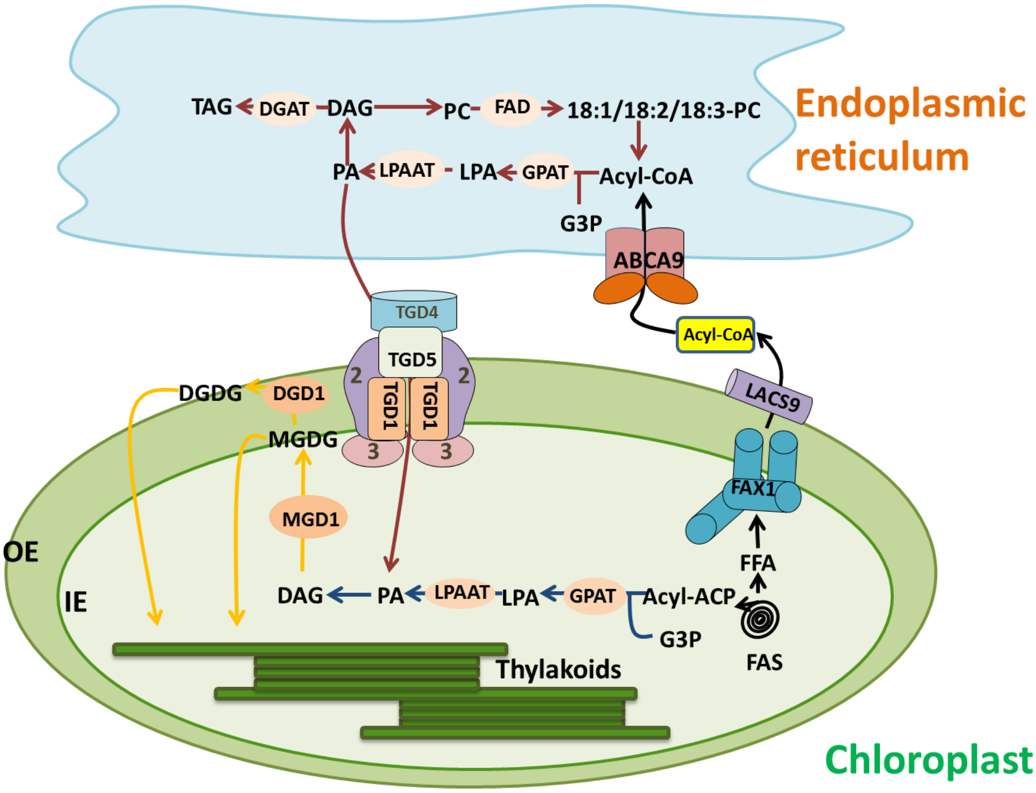

Figure 1 ER-chloroplast interacts in the process of lipid biosynthesis, including: exporting fatty acids from plastids, thylakoid lipid biosynthesis. Acyl-ACP is released from the fatty acid synthase complex (FAS) and hydrolyzed into free fatty acids (FFA), using the FAX1/LACS mechanism to export FFA, reactivated into the acyl-CoA in the outer membrane of the chloroplast, through the Kennedy pathway or acyl .The editing approach incorporates acyl-CoA into the ER lipid. TGD regulates the transport of lipids (mainly PA) across the inner and outer chloroplast membranes into the chloroplast. MGDG is synthesized from chloroplast-derived lipids and ER-derived lipids, which can then be desaturated by chloroplast-specific FAD. The blue arrow shows the lipid assembly reaction of the plastid pathway, the red arrow shows the ER pathway reaction, and the yellow arrow shows the common reaction, mainly the biosynthesis of MGDG and DGDG. The biosynthesis of MGDG occurs on the surface of the inner envelope, and the biosynthesis of DGDG occurs on the cytoplasmic surface of the outer envelope. FADs fatty acid desaturases, DGD1 digalactosyldiacylglycerol synthase 1, MGD1 monogalactosyldiacylglycerol synthase

1, PAP phosphatidic acid phosphatase, LPAAT lyso-phosphatidic acid acyltransferase, GPAT glycerol-phosphate acyltransferase, DGAT diac glycerol acyltransferase, TGD trigalactosyldiacylglycerol, LACS long-chain acyl-CoA synthetases, FAX1 fatty acid export 1, PA phosphatidic acid, PC phosphatidylcholine, MGDG monogalactosyldiacylglycerol, DGDG digalactosyldiacylglycerol.

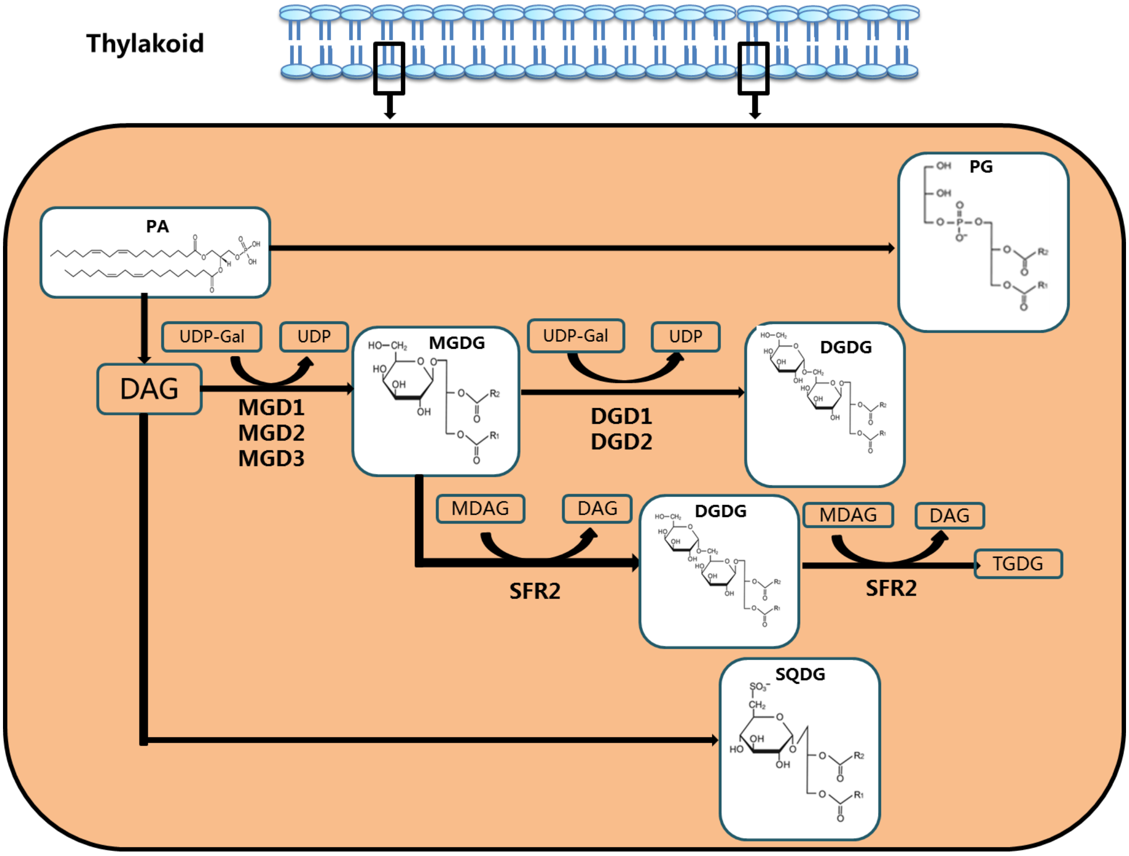

Figure 2 In thylakoids, MGDG, DGDG, SQDG and PG are synthesized by PA through different pathways. MGDG is synthesized by MGD synthetase, which catalyzes the transfer of galactose from UDP-Gal to the DAG. DGD synthase transfers a second galactose from UDP-Gal to MGDG to form DGDG; MGDG synthesizes DGDG through DGD1/DGD2 pathway, and then forms TGDG from

SFR2.

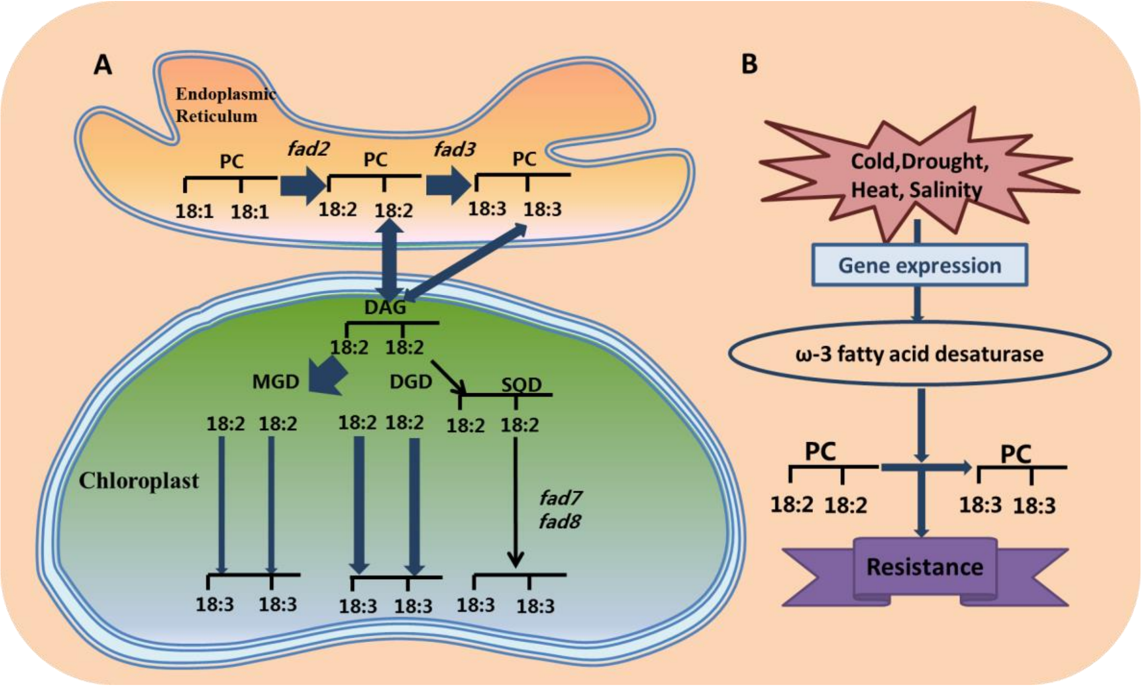

Figure 3 (A) Fatty acid biosynthetic pathway and regulating mechanism of fatty acid desaturases in response to stress. (B) Under abiotic stress, the ω-3 fatty acid desaturase gene FAD3 catalyzes 18:2 to 18:3 in phospholipids, giving plants resistance to stress.