



Review

Plant lipid remodeling in response to abiotic stresses

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ABSTRACT

Plants are easily exposed to a wide range of adverse environmental conditions. Lipids, as one of the most crucial components of biological membranes in all plant tissues, have stoked great attention recently, especially in response to stresses. It has been shown that membrane lipid remodeling is one of the effective adaptation strategies for plants to defense against various abiotic stresses, including drought, salt, chilling, heat, nutrient deficiency and heavy mental stresses etc. Characterizing the response of membrane lipids to different abiotic stresses becomes crucial for improving plant acclimatization ability to different environmental adversities. The present review gives the holistic alteration of plant lipid in response to a series of abiotic stresses based on the meta-analysis. The possible underlying mechanisms of membrane lipid remodeling in mediating abiotic stress tolerance, and the role of lipids or its' intermediates as signaling molecules under abiotic stresses are discussed.

1. Introduction

Most of the time, the conditions that plants live in are characterized by the presence of various types of abiotic stresses. While plants are sessile organisms that have to coordinate their growth and development with their complex biosynthesis and metabolism processes to adapt to the changing environment. Lipids are one of the most crucial biomolecules in all plant tissues, and are the primary components of the biomembranes. Particularly, lipids are the matrix of photosynthetic membranes, where the photosynthesis happens. As the basis for the majority of the food and energy supply on Earth and the source of atmospheric oxygen necessary for most life forms, photosynthesis has dragged numerous attentions from biologists, physiologists and chemists for a long time. However, the studies on photosynthetic membrane lipids are greatly lagged, especially how those lipids response to various environmental stresses are still largely unclear.

In plants, compare with other cell membranes, the photosynthetic

membrane in chloroplast has a unique glycerolipid composition: they are characterized by a very high content in glycolipids, namely, monogalactosyldiacylglycerol (MGDG), digalactosyldiacylglycerol (DGDG) and sulfoquinovosyldiacylglycerol (SQDG), and one phospholipid, phosphatidylglycerol (PG) (Joyard et al., 1998; Boudière et al., 2014). Recently, increasing evidences have shown that alteration in photosynthetic membrane lipids biosynthesis could produce different effects on thylakoid assembly and development, and thus affect plant growth and development (Fujii et al., 2014; Kobayashi, 2016). In addition, it has been reported that galactolipids reduction could weaken the resistance of plants to various abiotic stresses. On the other hands, remodeling of photosynthetic membrane lipid has become an important role in plant accommodation to various detrimental environment (Moellering et al., 2010; Lippold et al., 2012; Gasulla et al., 2013; Higashi et al., 2015; Chen et al., 2018). Those detrimental environment conditions including drought (Dakhma et al., 1995; Gigon et al., 2004; Torres-Franklin et al., 2007; Chen et al., 2018; Zhang et al., 2018), salt

Abbreviations: MGDG, monogalactosyldiacylglycerol; DGDG, digalactosyldiacylglycerol; SQDG, sulfoquinovosyldiacylglycerol; PG, phosphatidylglycerol; 16:0, palmitic acid; 16:1, hexadecylenic acid; 16:2, hexadecadienoic acid; 16:3, hexadecatrienoic acid; 18:0, stearic acid; 18:1, oleic acid; 18:2, linoleic acid; 18:3, linolenic acid; Pi, phosphate

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(Wang et al., 2014; Bejaoui et al., 2016; Omoto et al., 2016), low temperature (Barnes et al., 2016; Zheng et al., 2016; Gu et al., 2017; Peppino Margutti et al., 2018), high temperature (Larkindale and Huang, 2004; Narayanan et al., 2016), nutrient deficiency (Härtel et al., 2000; Gaude et al., 2007; Narasimhan et al., 2013; Angkawijaya et al., 2017), aluminum stress (Huynh et al., 2012; Zhang et al., 2016), and heavy metal stresses (Jemal et al., 2000; Chaffai et al., 2007).

Photosynthetic membrane lipids have been well advocated to significantly contribute to plant abiotic stresses responses mainly through maintaining the chloroplast structure, such as keep the stack of grana lamellar structure, stabilize the chloroplast membranes (Shimojima and Ohta, 2011), and facilitate the dense packing of proteins of the membrane (Garab et al., 2000; Gaude et al., 2007; Wang et al., 2014), and by regulating the membrane fluidity through adjusting the degree of fatty acid desaturation (Dakhma et al., 1995; Zhang et al., 2005; Sui et al., 2010; Wang et al., 2010; Barnes et al., 2016). In addition, plants sense these abiotic stresses and transmit the signal into the downstream generally through the plasma membrane, thus, the signaling roles of lipids or the intermediates of lipid biosynthesis and metabolism play a crucial role in plant environmental stress response (Hou et al., 2016). Notably, the roles of glycerolipids in plants growth and development have been well documented in several excellent reviews (Dörmann and Benning, 2002; Boudière et al., 2014; Kobayashi, 2016). However, our current understanding of the photosynthetic membrane lipids remodeling under different abiotic stresses is still limited. This review dissects the changes of membrane lipids in response to widely occurred abiotic stresses based on meta-analysis, illustrating the possible underlying mechanisms of membrane lipid remodeling in mediating plant abiotic stress tolerance, and also the role of lipids or its' intermediates as signaling molecules under those stresses.

2. Structure of the photosynthetic membrane lipids

Photosynthesis takes place in chloroplast thylakoid membranes, where protein complexes containing pigments and many photosynthetic cofactors are embedded into photosynthetic membranes (Nakamura and Li-Beisson, 2016). In photosynthetic membranes, the most abundant uncharged galactolipids are MGDG and DGDG, which represent up to 80% of the total lipids (Block et al., 1983; Awai et al., 2001). They contain either one (for MGDG) or two (for DGDG) galactose molecules attached to the *sn*-3 position of the glycerol backbone. Those galactolipids are highly rich in polyunsaturated fatty acids, which endow them unusual biophysical features and the ability to maintain the appropriate fluidity and flexibility of the membrane (Webb and Green, 1991). Based on the polyunsaturated fatty acid (trienoic acid) composition in photosynthetic membranes, two kinds of plants can be distinguished. Some plant species, such as pea (*Pisum sativum*) and rice (*Oryza sativa*), which have almost exclusively 18:3 in MGDG (both at *sn*-1 and *sn*-2 position) are called “18:3 plants”; while other plants, such as Arabidopsis (*Arabidopsis thaliana*), tobacco (*Nicotiana tabacum*) and spinach (*Spinacia oleracea*), which contain large amounts of 16:3 fatty acid at the *sn*-2 position in MGDG are called “16:3 plants” (Heinz and Roughan, 1983; Joyard et al., 1998). In 16:3 plants, both prokaryotic and eukaryotic pathways are used to generate plastid glycolipids, while 18:3 plants exclusively use the eukaryotic pathways (Negi et al., 2018).

As the most abundant polar lipid on the earth, MGDG contains mostly 16- and 18-carbon ω -3 trienoic acids (i.e. 16:3 and 18:3 fatty acids), and DGDG is mainly contains 18:3 fatty acids. In case when a 16-carbon fatty acid is presented in DGDG, it contains mostly saturated form (i.e. 16:0) at its *sn*-1 position of the glycerol backbone (Boudière et al., 2014). Moreover, due to the smaller head group and high contents of polyunsaturated fatty acids, MGDG harbors conical shape of non-bilayer lipid molecules, causing the lipid mixture a high tendency to form non-lamellar or non-bilayer lipid phases, with the polar head groups facing towards the centre of micellar or tube-like structure in

mixtures with water at room temperature (Webb and Green, 1991; Eband, 1998). Thus, MGDG generally forms an inverted hexagonal (H_{II}) phase in aqueous media. On the contrary, DGDG has a large headgroup than in MGDG and possesses cylindrical lipid molecules, which enable it spontaneously to form lamellar phases in mixtures with water (Webb and Green, 1991).

In addition to galactolipids, SQDG and PG are anionic lipids. SQDG is the most important sulfolipid found in higher plants, and the sulfonic residue at C6 of deoxyglucose carries a strong negative charge at physiological pH (Joyard et al., 1998). It has been demonstrated that a significant proportion of SQDG in higher plants has a dipalmitoyl backbone, and the presence and absence of this dipalmitoyl SQDG depend on different plant species (Murata and Hoshi, 1984; Joyard et al., 1998). PG is the major phospholipid in chloroplast, and it is characterized by the presence of a unique fatty acid molecular species, *trans*-3-hexadecenoic acid (C16:1*t*), located exclusively at position *sn*-2 of the glycerol backbone (Boudière et al., 2014). It has been shown that SQDG could compensate the deficiency of PG under phosphate (Pi) deficiency to maintain the amount of total anionic lipids in chloroplasts, but PG also has specific roles in photosynthesis that could not be compensated by SQDG and galactolipids (Nakamura and Li-Beisson, 2016). Therefore, PG is a vital lipid with its role as a cofactor of photosystems, while SQDG somehow appears as a sort of stand-in actor (Boudière et al., 2014). In addition, given the fact that galactolipids MGDG and DGDG are the most abundant lipids in photosynthetic membranes, we will focus on the function of MGDG and DGDG and their response to different abiotic stresses in the following sections.

3. The role of galactolipids biosynthesis in thylakoid assembly and development

The increasing evidences have shown that alteration in galactolipids biosynthesis plays an important role on thylakoid assembly and development. In Arabidopsis mutant *mgd1*, 42% reduction in the content of MGDG caused the severely underdeveloped chloroplast, and the chloroplasts of this mutant were found to be smaller in size than those in the wild type, had more spherical shapes, and contained fewer internal thylakoid membranes (Jarvis et al., 2000). More severe suppression was found in Arabidopsis mutant of *mgd1-2*, which has an approximately of 98% reduction of MGDG, the mutant leaves did not contain mature chloroplasts, the membrane structure was greatly disrupted, and the proper alignment or stacking of internal chloroplast membrane were scarcely detected, indicating that MGDG is indispensable for proper thylakoid membrane biosynthesis (Kobayashi et al., 2007). Similarly, transgenic tobacco with a 53% reduction in MGDG level caused a decrease of the abundance of thylakoid membranes, and a retarded growth and chlorotic phenotype (Wu et al., 2013). Additionally, the MGDG content was decreased in a rice UDP-glucose epimerase mutant (*phd1*), which exhibited diminished chlorophyll content, reduced photosynthesis, and damaged chloroplast ultrastructure (Li et al., 2011). In addition, loss of galactolipids often lead to the reduction of chlorophyll, thus caused pale green phenotype (Botte et al., 2011; Fujii et al., 2014; Sun et al., 2016). In contrast, heterologous overexpression of a rice *MGD* gene in tobacco increased the MGDG content, which resulted in tight stacking of thylakoid membrane and fewer thylakoid-free areas under salt stress (Wang et al., 2014). Crystallographic studies have shown that MGDG is the most abundant integral lipid in the photosystem II (PSII) complex (Guskov et al., 2009; Umena et al., 2011), and also plays important roles in maintain both the linear electron transport process and the photostability of PSII (Wu et al., 2013).

Similarly, another Arabidopsis mutant *dgd1*, which has a more than 90% reduction in DGDG levels compared with the wild type, also exhibits an altered chloroplast morphology and a large thylakoid-free stromal area (Härtel, 1997; Holzl et al., 2009; Lin et al., 2016). This mutant contains less chlorophyll and its thylakoid organization is

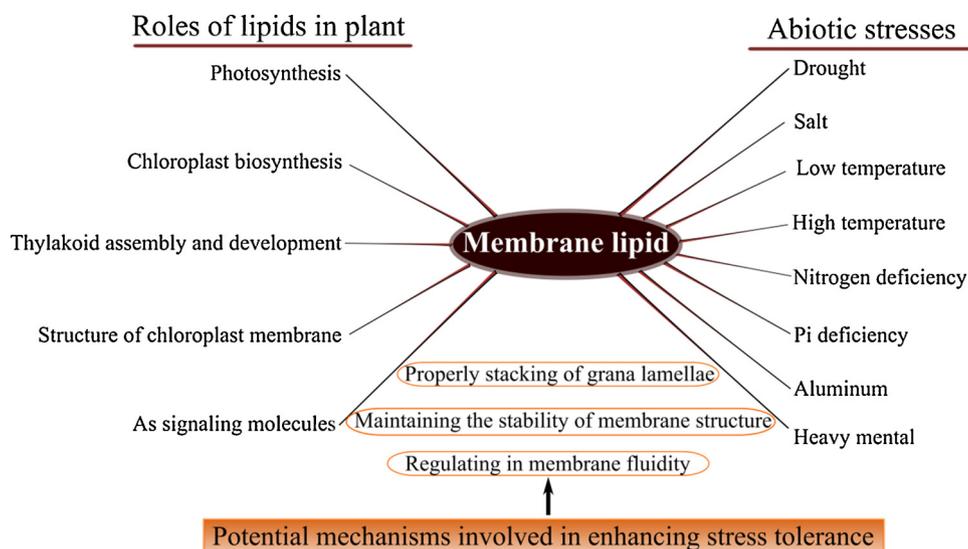


Fig. 1. Roles of lipids in plant and the potential mechanisms involved in enhancing plant stress tolerance.

changed (Dörmann et al., 1995). Besides, different components of the photosynthetic electron transport chain and the regulation of distribution of excitation energy between the photosystems are affected in *dgd1* mutant (Dörmann and Benning, 2002). Such as the defective in the structure of the water-oxidizing complex; the amounts of photosynthetic complex, including photosystem I (PSI), PSII, chlorophyll *b*₅₅₉, D1 and the ratio of PSII to PSI; the xanthophyll-cycle activity and sensitiveness to photoinhibition; and the increased capacity for PSI cyclic electron transfer (Härtel, 1997; Reifarh et al., 1997; Härtel et al., 1998; Ivanov et al., 2006; Essemine et al., 2012). Obviously, galactolipids play an important role in photosynthesis, thylakoid assembly and chloroplast biosynthesis and development in plants (Fig. 1).

4. Roles of photosynthetic membrane lipid remodeling in response to abiotic stresses

Plants have been evolved various biochemical and physiological strategies to respond and acclimatize to the ever-changing environmental conditions. It has been reported that crop production is severely reduced because of different type of abiotic stresses viz drought, salinity, chilling, nutrient deficiency and heavy metal stresses. Abiotic stresses are known to lead to membrane lipid peroxidation and inhibit plant growth and development (Zhang et al., 2016). Recently, photosynthetic membrane lipid has been aroused high attention and the remodeling and turnover of photosynthetic membrane lipid has been considered as one of the effective adapting strategies to accommodate and acquire tolerance to the detrimental environment (Moellering et al., 2010; Lippold et al., 2012; Gasulla et al., 2013; Higashi et al., 2015). In the following sections, we will summarize the relationship between lipid remodeling and abiotic stresses response based on meta-analysis using response ratio of abiotic stress compared with that of the control (Table 1). The detailed analysis procedures can be found in supplementary data.

4.1. Changes in membrane lipids and fatty acid compositions under different abiotic stresses

First, we analyzed the alteration of membrane lipid in response to various abiotic stresses. The results showed that the content of MGDG, DGDG, PG and the total lipid were all decreased when plants were suffered stresses, meanwhile, the fatty acid composition of total lipid altered variously under different stress conditions (Fig. 2). Previous studies showed that the abundance of membrane lipid was diminished

under many diverse adversities, including salt, low temperature and drought stresses (Bejaoui et al., 2016; Omoto et al., 2016; Zheng et al., 2016; Chen et al., 2018). Here, the meta-analysis further showed that the decrease of membrane lipids in response to different abiotic stresses were mainly due the greatly decrease in MGDG amount, compared with the reduction in DGDG and PG (Fig. 2A). In more detail, these abiotic stresses significantly reduce the levels of 16:1, 16:3 and 18:3 fatty acids, while the levels of 16:0 and 18:2 fatty acids were increased (Fig. 2B), suggesting that the plant membrane unsaturation was reduced upon suffering stresses. Moreover, 16:3 and 18:3 are the major acyl chain in MGDG and DGDG, the reduction in these trienoic acid levels further indicates the important roles of MGDG and DGDG in plant stress response.

Then, since MGDG and DGDG are the major components of photosynthetic membrane, we analyzed their responses to each individual abiotic stress specially. Not surprisingly, the content of MGDG was greatly decreased after exposed to stresses, especially under drought, low temperature, nitrogen deficiency and aluminum stress (Fig. 3). The reduction in MGDG content has been considered as a common adaptation strategy for plants when cope with drought, salinity, low temperature and aluminum stresses (Gigon et al., 2004; Wang et al., 2014; Barnes et al., 2016; Zhang et al., 2016; Chen et al., 2018). On the contrary, the decrease in DGDG in response to different abiotic stresses was less than that of MGDG, with only showed a significant decreased under drought and a slightly decrease under salt, low temperature, high temperature, nitrogen deficiency and heavy metal stresses. However, a significant increase in DGDG level was found under Pi deficiency, which is consistent with the results in Arabidopsis under Pi deficient condition (Yu et al., 2002; Kobayashi et al., 2006, 2009; 2015), suggesting that DGDG may play a special role in plants coping with Pi deficiency. In addition, both MGDG and DGDG contents were nearly unchanged under high temperature stress among all the plant species that tested in this study, indicating that other membrane lipids (other than MGDG and DGDG) may play an important role in plant adaptation to high temperature. It is known that MGDG and DGDG are rich in polyunsaturated acids, and heat stress usually causes an increase in membrane lipid saturation level over time (Boudière et al., 2014; Higashi et al., 2015; Spicher et al., 2016). Thus, another possible explanation may be that the alteration in the level of MGDG or DGDG under high temperature may vary a lot among different plant species and different treatment periods in different studies.

Moreover, modulation of DGDG/MGDG ratio occurs in response to several abiotic stresses in different plant species (Gigon et al., 2004;

Table 1

A list of the collected literature in the present study.

Plants/Crop species	16:3 or 18:3 plants	Abiotic stresses	Reference
Rape (<i>Brassica napus</i>)	16:3	Drought	Dakhma et al. (1995)
<i>Lotus corniculatus</i> L. <i>Cerastium fontanum</i>	/	Drought	Olsson et al. (1996)
<i>Ctenanthe setosa</i> (Marantaceae)	/	Drought	Ayaz et al. (2001)
Rape (<i>Brassica napus</i> L.)	16:3	Drought	Benhassaine-Kesri et al. (2002)
Moss (<i>Atrichum androgynum</i>)	/	Drought	Guschina et al. (2002)
<i>Arabidopsis thaliana</i>	16:3	Drought	Gigon et al. (2004)
Wheat (<i>Triticum aestivum</i> L.)	18:3	Drought	Kaoua et al. (2006)
Cowpea (<i>Vigna unguiculata</i> L.)	18:3	Drought	Torres-Franklin et al. (2007)
Bean (<i>Phaseolus vulgaris</i> L.)	18:3	Drought	Martins Junior et al. (2008)
Rice (<i>Oryza sativa</i> L.)	18:3	Drought	Liu et al. (2011)
Tobacco (<i>Nicotiana tabacum</i>)	16:3	Drought	Zhai et al. (2012)
<i>Parkinsonia aculeata</i>	/	Drought	Benadjaoud et al. (2013)
Tobacco (<i>Nicotiana tabacum</i>)	16:3	Drought	Zhai et al. (2013)
Maize (<i>Zea mays</i> L.)	18:3	Drought	Chen et al. (2018)
Tall fescue (<i>Festuca arundinacea</i>)	/	Drought	Zhang et al. (2018)
<i>Catharanthus roseus</i>	/	Salt	Elkahoui et al. (2004)
<i>Crihnum maritimum</i>	/	Salt	Hamed et al. (2005)
<i>Suaeda salsa</i> L.	/	Salt	Sui et al. (2010)
Tobacco (<i>Nicotiana tabacum</i>)	16:3	Salt	Wang et al. (2014)
<i>Sulla carnosa/coronaria</i>	/	Salt	Bejaoui et al. (2016)
Maize (<i>Zea mays</i> L.)	18:3	Salt	Omoto et al. (2016)
<i>Arabidopsis thaliana</i>	16:3	Salt	Huang et al. (2017)
<i>Arabidopsis thaliana</i>	16:3	Low temperature	Hugly and Somerville (1992)
<i>Arabidopsis thaliana</i>	16:3	Low temperature	Falcone et al. (2004)
Tobacco (<i>Nicotiana tabacum</i>)	16:3	Low temperature	Khodakovskaya et al. (2006)
<i>Arabidopsis thaliana</i>	16:3	Low temperature	Chen and Thelen (2013)
<i>Arabidopsis thaliana</i>	16:3	Low temperature	Barnes et al. (2016)
<i>Arabidopsis thaliana</i>	16:3	Low temperature	Zheng et al. (2016)
Rice (<i>Oryza sativa</i> L. indica)	18:3	Low temperature	Zheng et al. (2016)
Maize (<i>Zea mays</i> L.)	18:3	Low temperature	Gu et al. (2017)
Barley (<i>Hordeum vulgare</i>)	18:3	Low temperature	Peppino Margutti et al. (2018)
<i>Arabidopsis thaliana</i>	16:3	High temperature	Falcone et al. (2004)
Creeping bentgrass (<i>Agrostis stolonifera</i>)	/	High temperature	Larkindale and Huang (2004)
<i>Arabidopsis thaliana</i>	16:3	High temperature	Chen et al. (2006)
<i>Arabidopsis thaliana</i>	16:3	High temperature	Routaboul et al. (2012)
Wheat (<i>Triticum aestivum</i> L.)	18:3	High temperature	Narayanan et al. (2016)
Tall fescue (<i>Festuca arundinacea</i>)	/	High temperature	Zhang et al. (2018)
<i>Arabidopsis thaliana</i>	16:3	Nitrogen deficiency	Gaude et al. (2007)
Soybean (<i>Glycine max</i>)	18:3	Nitrogen deficiency	Narasimhan et al. (2013)
Wheat (<i>Triticum aestivum</i>)	18:3	Nitrogen deficiency	Qi et al. (2017)
Wheat (<i>Triticum aestivum</i>)	18:3	Nitrogen deficiency	Li et al. (2018)
<i>Arabidopsis thaliana</i>	16:3	Pi deficiency	Härtel et al. (2000)
<i>Arabidopsis thaliana</i>	16:3	Pi deficiency	Yu et al. (2002)
<i>Arabidopsis thaliana</i>	16:3	Pi deficiency	Kobayashi et al. (2006)
<i>Arabidopsis thaliana</i>	16:3	Pi deficiency	Kobayashi et al. (2009)
<i>Arabidopsis thaliana</i>	16:3	Pi deficiency	Kobayashi et al. (2015)
<i>Arabidopsis thaliana</i>	16:3	Pi deficiency	Angkawijaya et al. (2017)
Rice (<i>Oryza sativa</i> L.)	18:3	Aluminum	Huynh et al. (2012)
Rice (<i>Oryza sativa</i> L.)	18:3	Aluminum	Wang et al. (2016)
Tobacco (<i>Nicotiana tabacum</i>)	16:3	Aluminum	Zhang et al. (2016)
Pepper (<i>Capsicum annuum</i>)	/	Cadmium	Jemal et al. (2000)
Maize (<i>Zea mays</i> L.)	18:3	Copper	Chaffai et al. (2007)
Tomato (<i>Lycopersicon esculentum</i>)	16:3	Cadmium	Ammar et al. (2008)

Torres-Franklin et al., 2007). It has been reported that the DGDG/MGDG ratio is correlated with the resistance to salinity both in salt-tolerant or salt-sensitive plants, and it may play an important role in protecting plants from the damage of salt stress (Hirayama and Mihara, 1987). Based on the meta-analysis, it is showed that the DGDG/MGDG ratio was increased in response to different abiotic stresses, both in 16:3 and 18:3 plants (Figs. 2A and 5). Here, the DGDG/MGDG in 16:3 plants exhibited a relatively big error bar, this may due to the limited studies available on lipid analysis under stress conditions in 16:3 plants (Fig. 5A). Similar results were observed in snow alga *Chlamydomonas nivalis* under high salt stress condition that the DGDG/MGDG ratio was significantly increased (Lu et al., 2012). It has been reported that during plant acclimation to abiotic stress conditions, including nitrogen deprivation, salt stress and osmotic stress, plants are likely to adjust their DGDG/MGDG ratio to consolidate the reorganization of membranes (Du et al., 2018). Besides, adjustment of the composition of lipids to

balance the ratio of bilayer-forming to non-bilayer-forming membrane also plays a crucial role in plants under low temperature, which could result in increased DGDG/MGDG ratio (Moellering et al., 2010).

Additionally, stress acclimated plants can also regulate their membrane fluidity through releasing trienoic fatty acids from membrane lipids when they were exposed to stresses (Upchurch, 2008). When plants were exposed to drought stress, the degree of fatty acid desaturation was decreased (Depaula et al., 1993; Dakhma et al., 1995). The decline in fatty acid desaturation under abiotic stress conditions is destructive to the stability of the thylakoid membrane, which could diminish the fluidity of the chloroplast membrane (Zhang et al., 2005; Sui et al., 2010). Decreased level of 18:3 fatty acid was found in non-salt-tolerant plants, suggesting that the decline in 18:3 fatty acid has negative effects on salt tolerance and could be one of the reasons for salt-induced membrane damage in plants (Upchurch, 2008). On the contrary, increasing of fatty acid desaturation by overexpression of ω -3

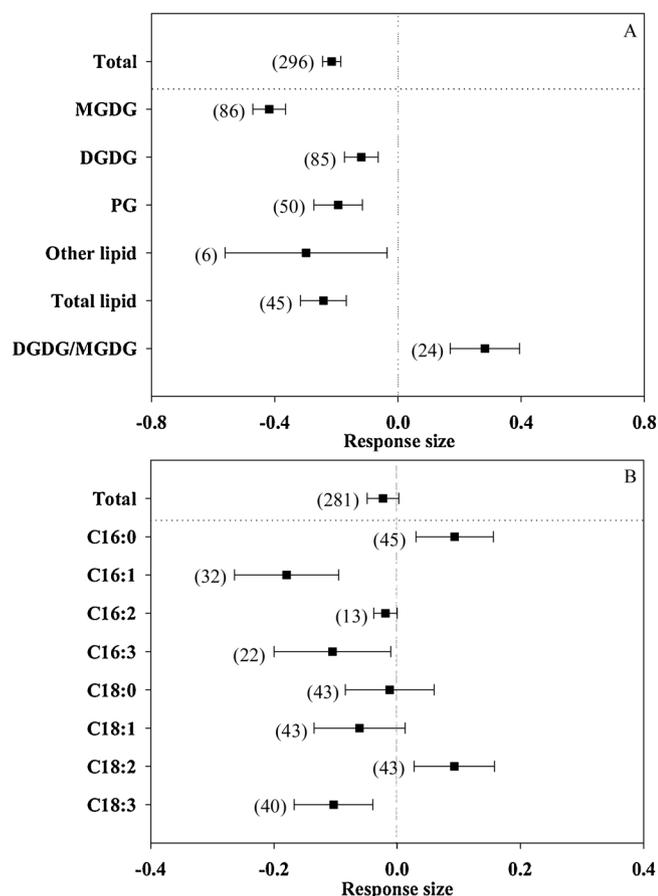


Fig. 2. Response size of membrane lipids (A) (including MGDG, DGDG, PG, other lipid and total lipid), DGDG/MGDG ratio and fatty acids compositions (B) (including 16:0, 16:1, 16:2, 16:3, 18:0, 18:1, 18:2 and 18:3) in leaves in response to various abiotic stresses (drought stress, salt stress, low temperature stress, high temperature stress, nitrogen deficiency stress, Pi deficiency stress, aluminum stress and heavy metal stress) based on the meta-analysis of 577 observations from 50 published studies. The “other lipid” in (A) refers to the sum of lipids in leaves except MGDG, DGDG and PG, but including SQDG, phosphatidylcholine (PC), phosphatidylethanolamine (PE), phosphatidylinositol (PI), phosphatidic acid (PA), and neutral lipids (NL); and the “total lipid” includes all lipid molecular species in leaves. The numbers in brackets specify the number of data points. The black square block with the error bar indicates the mean response size with a 95% confidence intervals.

desaturases in tobacco lead to enhanced ability to salt and drought tolerance (Zhang et al., 2005). Maintenance of polyunsaturated fatty acid levels in membrane lipids has been proved to contribute to low temperature survival and the formation of chloroplast membranes under chilling stress (Routaboul et al., 2000; Iba, 2002). Based on our meta-analysis, it was found that the response sizes of 16:0 and 18:2 were increased, while the 16:1, 16:3 and 18:3 fatty acids was decreased under abiotic stresses (Fig. 2B), indicating that plant may adapt to various abiotic stresses through alteration in their membrane lipid fatty acid compositions. In addition, among all investigated abiotic stresses in the current study, only heavy metal stress caused a significant decreased in levels of fatty acid components (Fig. 4), suggesting a severe decrease in all fatty acids in plants in response to heavy metal stress. While under other stresses, including drought, salt, low and high temperatures and nitrogen deficiency, the alterations in the levels of different components of fatty acids varied a lot.

4.2. Changes in membrane lipids composition in 16:3 plant and 18:3 plant

Based on the meta-analysis, notable decreases in the contents of

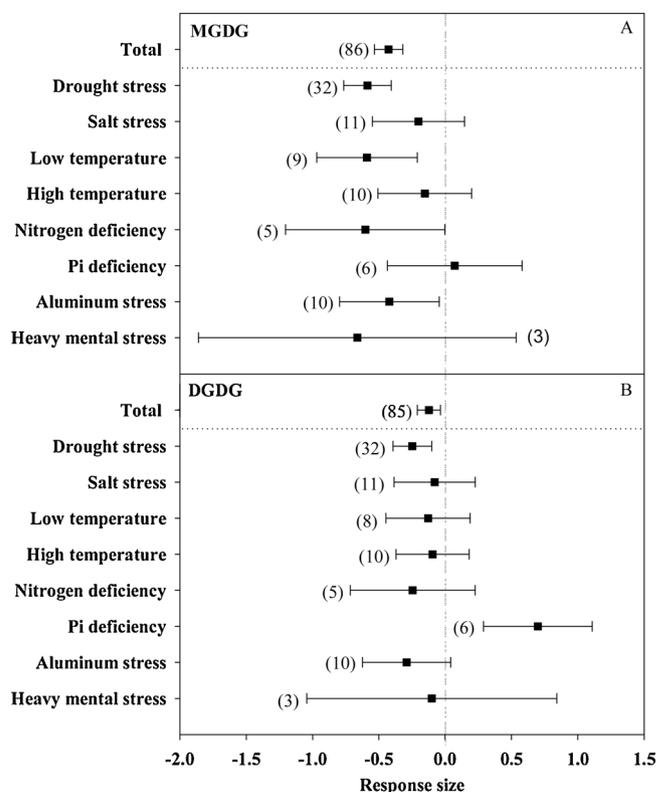


Fig. 3. Response size of the MGDG (A) and DGDG (B) contents in leaves in response to different abiotic stresses (including drought stress, salt stress, low temperature stress, high temperature stress, nitrogen deficiency stress, Pi deficiency stress, aluminum stress and heavy metal stress) based on the meta-analysis of 577 observations from 50 published studies. The numbers in brackets specify the number of data points. The black square block with the error bar indicates the mean response size with a 95% confidence intervals.

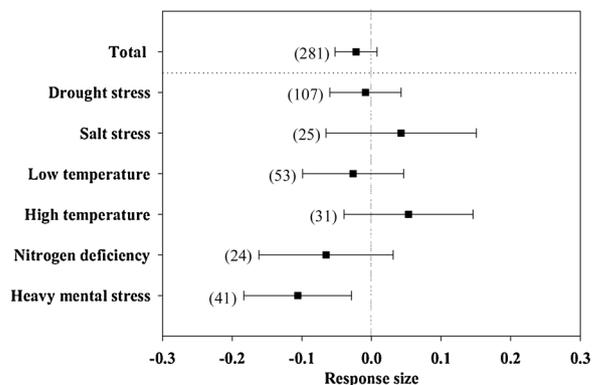


Fig. 4. Response size of different abiotic stresses (including drought stress, salt stress, low temperature stress, high temperature stress, nitrogen deficiency stress and heavy metal stress) on levels of fatty acids compositions in leaves (including 16:0, 16:1, 16:2, 16:3, 18:0, 18:1, 18:2 and 18:3) based on the meta-analysis of 577 observations from 50 published studies. The numbers in brackets specify the number of data points. The black square block with the error bar indicates the mean response size with a 95% confidence intervals.

MGDG, PG and total lipid in response to abiotic stresses were found in both 16:3 and 18:3 plants (Fig. 5). Although there was no markedly change in DGDG and DGDG/MGDG ratio in 16:3 plants, 18:3 plants exhibited a significantly decrease in DGDG and increase in DGDG/MGDG ratio in response to abiotic stresses. These results indicate that abiotic stresses may have different effects on lipid remodeling in 16:3 plants and 18:3 plants. In 16:3 plants, two pathways (prokaryotic and eukaryotic pathways) were existed to conduct the biosynthesis of

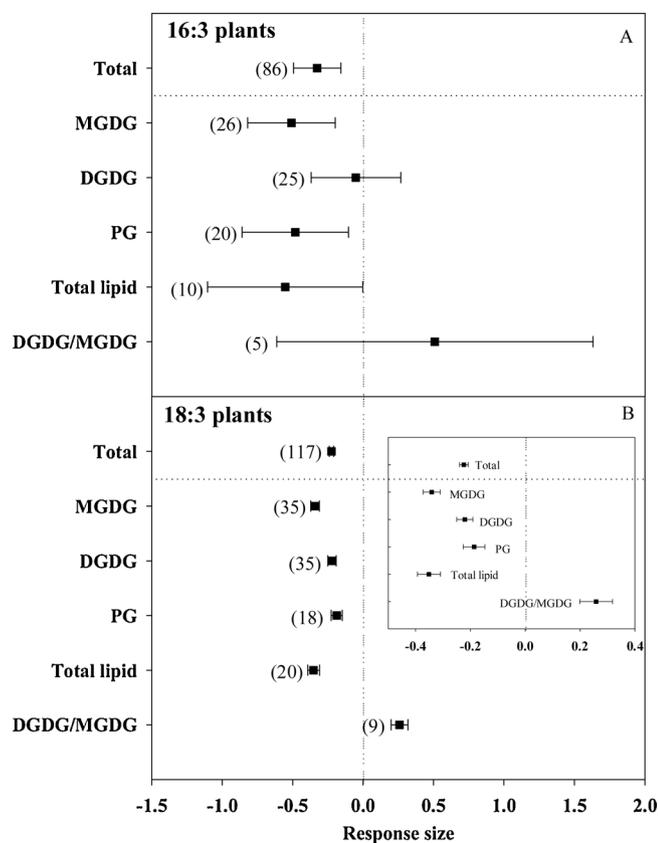


Fig. 5. Response size of the membrane lipid (including MGDG, DGDG, PG and total lipid) and DGDG/MGDG ratio in leaves in response to abiotic stresses (including drought stress, salt stress, low temperature stress, high temperature stress, nitrogen deficiency stress, Pi deficiency stress, aluminum stress and heavy metal stress) in 16:3 plants (A) and 18:3 plants (B) which are differ in glycerolipid assembly pathway based on the meta-analysis of 577 observations from 50 published studies. The “Total lipid” includes all lipid molecular species in leaves. The numbers in brackets specify the number of data points. The black square block with the error bar indicates the mean response size with a 95% confidence intervals.

MGDG (also a precursor for DGDG biosynthesis), but 18:3 plants possess only one. Thus, the less change of DGDG in 16:3 plants under stresses indicates that the two lipid biosynthesis pathways may have different responses under different stresses, and 16:3 plants may use this feature to adjust their lipid biosynthesis to adapt to different stresses. In addition, the distinctive mode of transition of lipid biosynthesis pathway in response to different stresses has been showed in three plant species. In typical 16:3 plant *Arabidopsis*, an increase in prokaryotic pathway under low temperature, and an enhanced in eukaryotic pathway under high temperature was found. In 18:3 plant wheat, low temperature induced a decreased contribution from the endoplasmic reticulum pathway (eukaryotic pathway) to chloroplast lipid biosynthesis (prokaryotic pathway). Whereas, in *Atriplex lentiformis*, a switched lipid profile from 16:3 to 18:3 was found when suffered from high temperature stress (Li et al., 2015). These results suggest that the adjustment of different glycerolipid biosynthesis pathways is helpful for plants to regulate their membrane property, and thus endows them an adjustment ability to different temperature stresses. In addition, it has been showed that compare with the 16:3 *Arabidopsis thaliana*, the 18:3 rice is a kind of chilling-sensitive plant (Zheng et al., 2016). However, *Solanum nodiflorum* and *Spinacia oleracea* are both 16:3 plants, but they are cold-sensitive, whereas *Saussurea medusa* is an 18:3 plant, but it is considered as a low temperature-tolerant species in alpine screes (Zheng et al., 2011). Those different responses between 16:3 and 18:3 plants may be also ascribed to the degree and the

duration of low temperature that plants exposed. Therefore, at this timepoint, we can not conclude that the differences in glycerolipid biosynthesis pathways between 16:3 and 18:3 plants contribute directly to the differences in plant responses to abiotic stresses, at least in the case of temperature stresses.

5. Potential mechanisms of membrane lipid remodeling in enhancing plant abiotic stress tolerance

5.1. Properly stacking of the thylakoid membrane

Photosynthetic membranes are dynamic structure, which require both lipid biosynthesis and turnover during diurnal variation and life cycles. In oxygen-evolving photosynthetic organisms, MGDG and DGDG are the predominant thylakoid lipids in plants, and their abundance plays a crucial role in photosynthesis (Shimojima and Ohta, 2011; Boudière et al., 2014; Kobayashi, 2016). As the only non-bilayer-forming lipid in plastids, MGDG is considered to be critical for the formation of grana stacks (Webb and Green, 1991; Lee, 2000). In the mutant of tobacco, it was shown that MGDG is indispensable for maintaining chloroplast structure, especially the grana stack, the changes in abundance of photosynthetic membrane lipid under adverse conditions are most likely related to the hyperstacking of grana (Wu et al., 2013; Wang et al., 2014). Similar result has been found in *Chlamydomonas*, a mutant deficient in the MGDG-specific lipase PGD1 (PLASTID GALACTOGLYCEROLIPID DEGRADATION1), that the change in MGDG abundance lead to a hyperstacking phenotype of the thylakoid grana (Du et al., 2018). Besides, it has been shown that lipid-to-chlorophyll ratio is a well criterion to estimate the damage that plants are suffered from, and the lipid-to-chlorophyll ratio is negative to the protein-packing density (Kirchhoff et al., 2013). It was found that under nitrogen deficiency, the lipid-to-chlorophyll ratio is significantly increased, indicating that the protein-packing density in thylakoids tends to be diminished under nitrogen-deficient stress (Gaude et al., 2007). Moreover, overexpressing of *OsMGD* tobaccos have lower lipid-to-chlorophyll ratio (high protein-packing density) than wild type under salinity (Wang et al., 2014). Therefore, alteration in membrane lipid abundance, especially the MGDG content, may facilitate proper stacking and well development of the thylakoid membranes and proteins, and thus maintaining the intact chloroplast structure under abiotic stresses.

5.2. Maintaining membrane stability through regulation of DGDG/MGDG ratio

Given the natural properties of cone-shape MGDG and cylinder-shape DGDG molecules, 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 exhibited 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). Likewise, in *Arabidopsis*, the DGDG/MGDG ratio was increased under drought stress (Gigon et al., 2004). 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 and Li-Beisson, 2016). In addition, increase in DGDG/MGDG ratio is also believed to enhance the stability of the thylakoid membrane at high temperature, which endowing the *Arabidopsis* a high thermotolerance (Chen et al., 2006). 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 ratio may not be a determinant of plant stress tolerance, but plant could

molecules but are found to play roles in pollen development, stomatal opening, and responses to freezing and salt stress (Meijer et al., 2001; Welti et al., 2002; Arisz and Munnik, 2011; Wang et al., 2019). Phospholipase As (PLA₁ and PLA₂) are key enzymes for the generation of lysophospholipids, therefore, analysis of PLA function and regulation mode will contribute to understand the lysophospholipid signaling cascades. In plants, it has been shown that G-proteins are involved in regulation of PLA₂ activities (Heinze et al., 2013). In addition, the expressions of PLA₂ were upregulated upon salt, osmotic and cold stresses, while downregulated under heat and drought stresses, according to an analysis of web-based software tool (Genevestigator) (Hruz et al., 2008). However, compare with the widely studies signaling molecule of PA, the signaling role and regulatory mechanism of lysophospholipids is still less know.

Another product of PLAs is free fatty acids, which is the precursor for oxylipins synthesis. The phytohormone jasmonic acid (JA) and its intermediate 12-oxo-phytodienoic (OPDA) are the best-known oxylipins involved in the activation of various defense responses in plants (Browse, 2009; Okazaki and Saito, 2014). First, the 18:3 and 16:3 fatty acids are oxidized by lipoxygenase (LOX) to generate OPDA and dinor-OPDA, which then exported from the plastids conducting JA biosynthesis in peroxisome (Wasternack and Feussner, 2018). Both OPDA and dinor-OPDA could be induced by abiotic stresses. It has been reported that OPDA and dn-OPDA containing lipids are formed rapidly after disruption of cellular integrity in leaf tissue, and after 5 min freeze-thawing, 60–70% of the trienoic acids esterified to chloroplast galactolipids are converted to OPDA and dinor-OPDA (Nilsson et al., 2012). Moreover, there is a strong link between galactolipids generation and JA accumulation. Digalactosyldiacylglycerol synthase1 (DGD1) is a key enzyme in the synthesis of DGDG from MGDG in the outer chloroplast membrane (Moellering and Benning, 2011). The Arabidopsis *dgd1* mutants that deficient in DGDG lead to accumulation of higher levels of JA, JA-isoleucine, OPDA, and Arabidopsides (Lin et al., 2016). Similarly, Arabidopsis mutant deletion of *thylakoid formation1* (THF1), having higher levels of basal α -linolenic acid (α -LeA), and methyl jasmonate (JA)-induced α -LeA and OPDA compared with wild type (Gan et al., 2014). A recently study on a chloroplast PLA₁ (named as PLASTID LIPASE, PLIP) showed that Arabidopsis plants with overexpression of PLIP2 and PLIP3 accumulated the bioactive form of jasmonate and related oxylipins, and the expression of these two genes was strongly induced by ABA, thus, it is supposed that PLIP2/3 provide a link between ABA-mediated abiotic stress responses and oxylipin signaling (Wang et al., 2018). Moreover, PLIP2 prefers MGDG as substrate and PLIP3 prefers PG, in vivo, providing further evidence that chloroplast lipids play an important role in facilitating plant adaptation to abiotic stresses.

In fact, lipid-mediated signaling is omnipresent in cellular processes in plants. In addition to play an important role in response to abiotic stresses, it also participates in plants' complex physiological processes (Okazaki and Saito, 2014; Hou et al., 2016; Wang et al., 2019). Thus, monitoring the changes in signaling lipids could provide valuable information for improving plant stress tolerance and regulating plant growth and development.

7. Conclusion and perspectives

In summary, as photosynthetic organisms, plants could adjust their photosynthetic membrane lipid compositions in response to various environmental challenges (Fig. 6). This membrane lipid remodeling has a great effect on the stacking of thylakoid grana, the stability of chloroplast membrane, abundance of fatty acid desaturation and the membrane fluidity. These changes are beneficial to the integrity of the chloroplast membrane, which contribute to the maintenance of plant growth and development and the enhanced tolerance to different stresses. Moreover, plant responses to abiotic stress are regulated by various complex signals. There are strong links between lipids signals

and the regulation of plant responses to various environmental stress conditions. The remodeling of membrane lipids and changes in membrane lipid signals could both protect the plant from severe damages caused by abiotic stresses. Our current study provided a relative comprehensive relationship between photosynthetic membrane lipid remodeling and abiotic stress responses as well as the role of membrane lipid signals, which could contribute to a better understanding of plant stress response and provide a useful strategy for improving plant stress tolerance. In addition, more studies should be carried out to characterize the changes in whole lipid profiles in response to various stresses, including both abiotic and biotic stresses.

Author contributions

Xiaoxiao Liu and Lina Yin designed the concept and wrote the manuscript, Dengke Ma, Zhiyong Zhang and Shiwen Wang contribute substantially in data analysis and interpretation of the data, Sheng Du and Xiping Deng critically reviewed the manuscript. All authors read and approved the final manuscript.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.envexpbot.2019.06.005>.

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