**Plant and Algal Lipids: In All Their States and On All Scales**

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**Main text:**
Lipids are essential for plant growth, signaling, development and environmental adaptation, and serve as important renewable sources of food, feed, biofuel, and industrial feedstocks. Plant and algal lipids are also at the core of our energy economy, as polar lipids form the photosynthetic membranes while neutral storage lipids (i.e. triacylglycerols, TAGs) represent an energy-dense reservoir of reduced carbon and fuel. These benefits, which are critical to human society, underscore the importance of understanding how lipids are produced and function within plants. Recent advances in lipidomics and lipid imaging, coupled with the development of high throughput, low-cost genome sequencing tools, and genome-editing techniques, now enable a deeper appreciation of the role of lipids at all scales and in all their state (membranes, storage, and signaling). This Special Issue of Plant and Cell Physiology provides a holistic view of plant and algal lipids in adaptation to environmental challenges. This issue includes 3 review papers and 11 research articles covering areas from regulation of lipid synthesis, enzyme structural determinants to roles of lipid in stress management and its relation to photosynthesis.

## Lipid biosynthesis and regulation

Acyl-lipid biosynthesis starts in the chloroplast where de novo fatty acids synthesis occur. The newly formed fatty acids are either used by chloroplast-located enzymes to synthesize chloroplast lipids, or exported to the endoplasmic reticulum (ER) where they are assembled by ER-resident enzymes to make extra-chloroplast lipids including TAGs. In higher plants and microalgae, TAG biosynthesis is catalyzed by two distinct acyltransferases families, i.e. the diacylglycerol:acyltransferase (DGAT) and phospholipid:diacylglycerol acyltransferase (PDAT) for the acyl-CoA-dependent and -independent pathway, respectively. Thanks to the specificities of these enzymes, variety of plant oils have been found in nature. Clews et al (Clews et al., 2023) discussed and compared the evolution of specialized oil metabolic pathways in diverse plant species including *Arabidopsis thaliana*, *Ricinus communis* (castor bean), *Linum usitatissimum L.* (flax), and *Elaeis guineensis* (oil palm). These analyses show that gene co-expressing networks, divergence in key enzymes/proteins, and the occurrence or not of protein interactom could all contribute to unique oil accumulation.

In addition to the role of TAG as a storage molecule, TAG metabolism plays critical roles in cellular energy balance, lipid homeostasis, cell growth and stress responses. PDAT by catalyzing the transferring of an acyl-chain from a membrane lipid (usually PC) to DAG to allow formation of a TAG molecule, therefore playing a critical role in lipid homeostasis and in connecting membrane lipid synthesis and growth with lipid storage. Sah et al (Sah et al., 2023) discuss the multifaceted roles of PDAT and TAG metabolism in cellular physiology. The divergence and similarities between PDAT from microalgae, plants and yeast are also compared.

Despite its importance, our knowledge on the regulation of lipid metabolism in plants and algae remain mostly limited to transcriptional regulations. In this issue, Flyckt et al (Flyckt et al., 2023) provide new data showing that three amino acid substitutions in the DGAT 1b protein can increase soybean oil content by 2.3% and this argumentation is maintained in a multiple location field. To fill the gap in our understanding of post-translational modifications (PTM) of plant lipid metabolism, Cannon and Horn (Cannon and Horn, 2023) has conducted a wide-ranging analysis of PTM proteomics PTM proteomics (comparing S-sulfenylation, persulfidation, S-nitrosylation, and S-acylation), genomics, and protein structures, with a specific focus on proteins involved in plant lipid metabolism. Cysteines are widely present, and these analyses also revealed discernible patterns in lipid biochemical pathways enriched with Cys PTMs, notably involving beta-oxidation, jasmonic acid biosynthesis, fatty acid biosynthesis, and wax biosynthesis. The significance of Cys-PTM in cellular physiology and metabolism remain to be investigated experimentally. This paper highlights the potential importance of Cys-PTMs on lipid metabolism and provides valuable insights for future investigations focusing on molecular mechanisms of Cys modifications.

**Role of lipids in chloroplast and photosynthesis**

The chloroplast is the main powerhouse of photosynthetic organisms where two major pathways occur i.e. photosynthesis and lipid biosynthesis. Thylakoid membranes are composed of mainly galactolipids and photosynthetic complexes. How cells coordinate the biosynthesis of these two major pathways is not known. It has been reported that suppression of galactolipid biosynthesis decreased the expression of photosynthetic polypeptides. In this issue, Fujii et al (Fujii et al., 2024) investigated this question by following gene expression patterns in a galactolipid-deficient Arabidopsis seedlings during the de-etiolation process. In combination with genetic analysis, the authors proposed a model that galactolipid synthesis determines the protein homeostasis in the chloroplast through the GENOMES UNCOUPLED1 (GUN1)-mediated plastid-to-nucleus signaling pathway. In addition to lipid amount, fatty acid composition and desaturation level play key role in ensuring membrane fluidity and protein function. The chloroplast houses multiple fatty acid modification enzymes, notably desaturases, which are essential to modulate fatty acid composition and therefore membrane fluidity and function. In this issue, Effendi et al (Effendi et al., 2023) report detailed characterization of two cyanobacteria desaturases DesC1 and DesC2. Further, the authors demonstrated DesC1 and DesC2 substrate specificities and divergent functions in the two Cyanobacteria species. Chloroplasts also import some unsaturated lipid species from the ER for lipid assembly. Matzner et al (Matzner et al., 2023) report here the importance of ER-derived desaturated lipid on thylakoid lipid composition and photosynthesis.

**Role of lipids in development and stress management**

Plants and algae face a multitude of environmental challenges, most of which require lipid adjustments for efficient tolerance or signaling. Understanding the lipid mechanisms that confer tolerance is needed to engineer their resilience. Seven papers from this special issue delve into the fascinating world of stress responses, offering insights from membranes and protective wax barriers.

Several papers explore the role of lipids in maintaining membrane integrity under abiotic stresses. Peng et al. (Peng et al., 2023) demonstrate changes in galactolipids (MGDG & DGDG) in rapeseed experiencing nitrogen deficiency. Their findings suggest that the MGDG to DGDG ratio may be important for adapting chloroplast membranes to nutrient stress. Minimal levels of MGDG were also implied to be essential for recovery from desiccation by Douchi et al. (Douchi et al., 2023), where they were retained by highly tolerant cyanobacteria *Chroococcidiopsis*. Interestingly, the same study showed sulfoquinovosyldiacylglycerol (SQDG) levels predominated during desiccation, suggesting a previously unrecognized function in tolerance. Similarly, the importance of maintaining membrane fluidity for stress acclimation is underscored by Ishikawa et al. (Ishikawa et al., 2024). They identify unusual Δ8-unsaturated sphingolipids with hexuronic acid headgroups in the microalga *Ostreococcus tauri*. Expression of the Δ8 desaturase was higher at cooler temperatures, and overexpression at normal temperatures was detrimental, likely due to its unknown effect on membrane function. In addition to temperature and water stresses, all eukaryotes can experience stress of the endoplasmic reticulum (ER). ER stress can be induced chemically, and Je et al. (Je et al., 2023) showed that when sterol biosynthesis was inhibited in *Chlamydomonas reinhardtii* by mutation of *erg5*, cells were more sensitive to chemically induced ER stress. This sensitivity was reversed if steps prior to *erg5* were inhibited, suggesting that specific sterols contribute to ER membrane health distinctly. van Hooren et al. (van Hooren et al., 2023) demonstrate that overexpression of Phospholipase C genes enhances drought tolerance in Arabidopsis, possibly through changes in shoot architecture, which points to a novel strategy for improving drought resistance via lipid modulation. Collectively, these investigations illustrate how plants strategically modify lipid synthesis and signaling pathways to fortify themselves against physical injury, water scarcity, and perturbations of protein homeostasis.

The issue also sheds light on the significance of lipids in forming protective barriers. Papers from Lewandowska et al. (Lewandowska et al., 2023) and Campoli et al. (Campoli et al., 2024) showcase how wax deposition is triggered by stress. Lewandowska et al. (Lewandowska et al., 2023) demonstrate wound-induced wax biosynthesis in Arabidopsis leaves. They show it depends not only on jasmonic acid, but also on abscisic acid. Campoli et al. (Campoli et al., 2024) explore the role of a specific lipase (HvGDSL1) in barley that controls wax deposition on various organs, including the grain. They highlight the importance of waxes for maintaining hull adhesion, thereby protecting the developing embryo.

In conclusion, this special issue offers a compelling exploration of plant and algal stress responses. By employing various approaches, the included papers illuminate the crucial role of membrane lipids, specific genes, and diverse adaptation strategies in ensuring plant and algal resilience in a constantly changing environment.

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