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Functions of triacylglycerols during plant development and stress

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Plant oil in the form of triacylglycerols (TAGs) is a major storage compound used as food, feed and sustainable feedstock for biofuel production. Recent findings suggest that TAGs are more than a carbon and energy reserve in seeds and other storage tissues. In vegetative tissues, TAG metabolism is involved in cell division and expansion, stomatal opening, and membrane lipid remodeling. Moreover, in reproductive tissues, TAGs are important for both organ formation and successful pollination. Here we provide a brief overview of the physiological function and contribution of TAGs during plant development under optimal and varying environmental conditions. These roles of TAGs need to be considered during engineering attempts to further improve TAG content in different tissues.

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Introduction

Plant oils in the form of triacylglycerols (TAGs) are composed of three fatty acids esterified to a glycerol backbone. Recent genetic, genomic and molecular studies of genes involved in TAG metabolism have provided revealing insights into the physiological functions of this lipid class. TAGs participate in many developmental events: first, cell building blocks such as sugars are synthesized from TAGs. Second, TAG degradation followed by β-oxidation of fatty acids (FAs) produces ATP, the cellular energy currency. Third, TAGs together with other lipids form the basis of lipid droplets, to reversibly sequester otherwise harmful free FAs. Lipid droplets containing TAGs may have additional functions serving as platforms for enzyme aggregates to facilitate metabolic channeling, allow the dynamic sequestration of proteins and protein transport, and may be the origin of cellular lipid signals. The biochemical pathways of TAG biosynthesis and its degradation have been covered in recent reviews [1,2]. Here, we focus on recent progress in understanding the physiological functions of TAGs and their FA constituents in plant development.

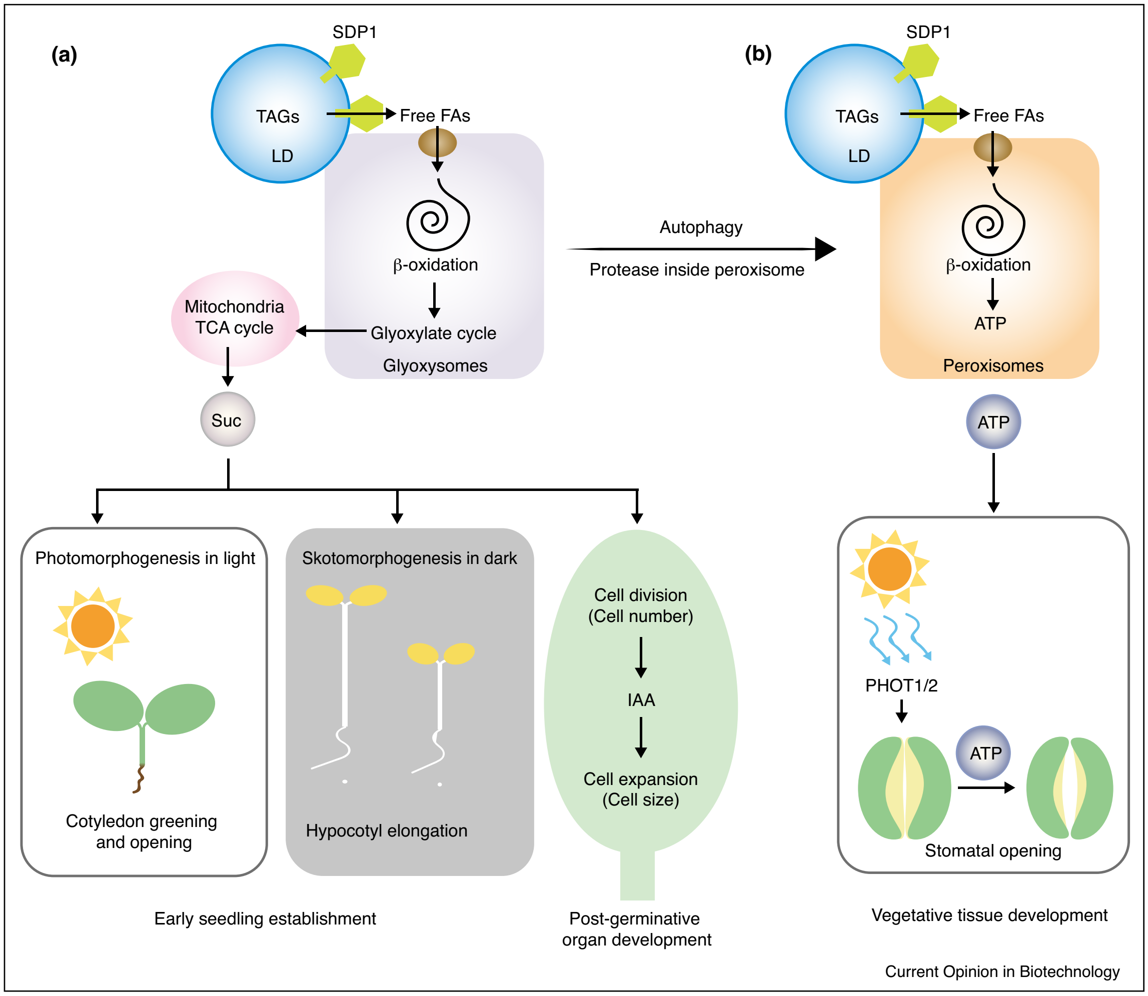
Germination and early seedling establishment

TAGs are the major carbon reserve in oilseeds and provide carbon skeletons and essential energy to fuel early growth until the seedling becomes photoautotrophic. Prior to germination, TAGs sequestered in lipid droplets are hydrolyzed by TAG lipases which release FAs [3•,4,5•]. The FAs are subsequently transported into glyoxysomes and then metabolized by β-oxidation to generate acetyl-CoA. This universal metabolite is converted in germinating oil seeds by the glyoxylate cycle to succinate, which in turn enters the tricarboxylic acid (TCA) cycle in the mitochondria and ultimately is converted by gluconeogenesis in the cytosol to hexoses used for post-germinative growth.

Seed germination and seedling establishment are independent processes. Germination does not require metabolic energy, while seedling establishment is largely driven by the energy derived from TAG degradation [6] (Figure 1a). Arabidopsis (*Arabidopsis thaliana*) mutants disrupted either in TAG accumulation [7] or β-oxidation [8] are compromised in germination and post-germinative growth when germinated on growth media without sucrose. However, in all these mutants, supply of sucrose rescues seedling development after the seeds have germinated [7,8], while germination itself is TAG-independent. In β-oxidation mutants, the accumulation of 2-oxo-phytodienoic acid (OPDA), rather than a block in storage TAG metabolism, represses germination [9]. The TAG-independence of germination is clearly apparent considering Arabidopsis mutants that are specifically disrupted in TAG degradation itself, such as the lipase mutants *sugar-dependent 1* (*sdp1*) and *sdp1 sdp1L*. These mutants are not compromised in seed germination, but require sucrose feeding for normal seedling establishment [10,11].

Seed TAGs accumulate in embryo and endosperm. Although the one cell layer endosperm of Arabidopsis only contains one-tenth of total seed TAGs, sucrose

Figure 1



Roles of TAGs during early seedling establishment and vegetative tissue development.
The TAG degradation/conversion process involves multiple interacting organelles. During early seedling establishment, glyoxysomes in the cotyledons directly interact with lipid droplets (LDs). This physical interaction is negatively regulated by sucrose derived from TAG conversion [3•]. In addition, TAG lipase SDP1 moves from the glyoxysome membrane to the lipid droplet surface [5•]. Seed TAGs are converted to sucrose to support early seedling development. In the light, seed TAGs are needed for seedling establishment, that is, cotyledon greening and opening. TAGs inside the endosperm are also involved in hypocotyl elongation in the dark. In addition, TAG-derived sucrose is also important for cell division and expansion during post-germinative organ development. After shifting from heterotrophic to autotrophic growth during the seedling establishment stage, glyoxysomes **(a)** undergo a light-dependent functional transition to peroxisomes **(b)**. Spent glyoxysomes are degraded by autophagy followed by the generation of new leaf peroxisomes. Meanwhile, the lipid catabolism enzymes inside the glyoxysomes are replaced with photorespiratory enzymes in peroxisomes. The interaction between glyoxysomes and lipid droplets ceases. Instead, the peroxisomes in photosynthetic tissues are closely associated with chloroplasts and mitochondria. The green seedlings start their autotrophic growth by photosynthesis. During the vegetative growth, TAG break down through β-oxidation is an important source of ATP during light-induced stomatal opening. This pathway is dependent on the blue light receptor PHOT1/2.

generated from endosperm TAGs plays an important role in skotomorphogenesis [12] (Figure 1a). Removing the endosperm from the Arabidopsis seeds blocked the carbon supply to the embryo and resulted in a reduction in hypocotyl elongation in the dark, which was completely reversed by provision of sucrose [12].

Cell division and expansion in cotyledons

Seedling development relies on cell division and post-mitotic expansion [13]. A decrease in leaf cell number often leads to compensation by cell enlargement [14•]. These complex interactions between cell division and expansion are affected by sucrose synthesis from storage TAGs (Figure 1a). Mutants lacking enzymes of the glyoxylate cycle or gluconeogenesis exhibit increased cell expansion of their cotyledon palisade cells, possibly in a auxin-dependent manner [14•]. Thus, the conversion of TAGs to sugars is not only crucial during early seedling establishment, but also for post-germinative organ development.