



Review article

Trends and strategies to enhance triacylglycerols and high-value compounds in microalgae



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ABSTRACT

Microalgae are important sources of triacylglycerols (TAGs) and high-value compounds such as carotenoids and long-chain polyunsaturated fatty acids (LC-PUFAs). TAGs are feedstocks for biofuels or edible oils; carotenoids are used as pigments in the food and feed industries; and LC-PUFAs are beneficial for human health, being also key to the correct development of fish in aquaculture. Current trends in microalgal biotechnology propose the combined production of biofuels with high-value compounds to turn large-scale production of microalgal biomass into an economically feasible venture. As TAGs, carotenoids and LC-PUFAs are lipophilic biomolecules, they not only share biosynthetic precursors and storage sinks, but also their regulation often depends on common environmental stimuli. In general, stressful conditions favor carotenoid and TAGs biosynthesis, whereas the highest accumulation of LC-PUFAs is usually obtained under conditions promoting growth. However, there are known exceptions to these general rules, as a few species are able to accumulate LC-PUFAs under low light, low temperature or long-term stress conditions. Thus, future research on how microalgae sense, transduce and respond to environmental stress will be crucial to understand how the biosynthesis and storage of these lipophilic molecules are regulated. The use of high-throughput methods (e.g. fluorescent activated cell sorting) will provide an excellent opportunity to isolate *triple-producers*, i.e. microalgae able to accumulate high levels of LC-PUFAs, carotenoids and TAGs simultaneously. Comparative transcriptomics between wild type and triple-producers could then be used to identify key gene products involved in the regulation of these biomolecules even in microalgal species not amenable to reverse genetics. This combined approach could be a major step towards a better understanding of the microalgal metabolism under different stress conditions. Moreover, the generation of triple-producers would be essential to raise the biomass value in a biorefinery setting and contribute to meet the world's rising demand for food, feed and energy.

1. Commercial available species of microalgae and their evolutionary relationships

Phototrophic microalgae are of great interest as microscopic factories for the production of biomolecules for the energy and added-value compound markets. Compared with terrestrial plants, microalgae do not compete with crop plants for arable land. In addition, they have higher areal productivities, in some cases 20 times higher than those of terrestrial plants [1], thus being a good alternative feedstock for feed, food and fuel. Only about 20 species are currently commercialized, mainly belonging to the unranked Stramenopiles/Haptista lineages or to Archaeplastida [2]. Most prominent candidates of the Stramenopiles/Haptista lineages (Fig. 1) include the genera

Nannochloropsis and *Phaeodactylum* due to their high contents of the long-chain polyunsaturated fatty acids (LC-PUFAs) eicosapentaenoic (EPA) and docosahexaenoic (DHA) acids. These important microalgal-based ω -3 fatty acids find their applications in aquaculture, animal feed and nutraceutical industry and can replace those obtained from fish meal or oils. Furthermore, microalgae of the Archaeplastida lineage produced industrially are usually chlorophytes, such as *Dunaliella*, *Haematococcus* and *Chlorella*. These algae are rich in the carotenoids β -carotene, astaxanthin and canthaxanthin used as pigments in food and feed [3]. Microalgae are also source of other carotenoids such as lutein and fucoxanthin which are utilized as antioxidants. Although, there have been efforts to use microalgal triacylglycerols (TAGs) as feedstock for biofuels, there is a current trend in microalgal research to

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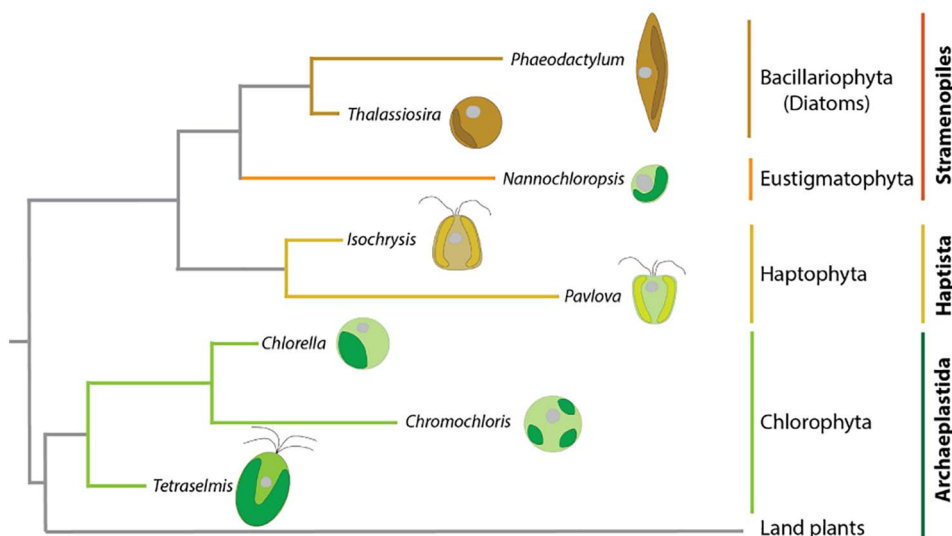


Fig. 1. Evolutionary relationships of target microalgal lineages for combined production of TAGs, LC-PUFAs and carotenoids. Branch length does not represent distance values. Adapted from Burki et al. [2].

combine the biosynthesis of LC-PUFA-rich TAGs with the accumulation of other high-valuable lipophilic compounds, such as carotenoids. In this sense, microalgal TAGs would be used as edible oil in food and feed applications as well as a vehicle for carotenoids.

The production of large amounts of TAGs, LC-PUFAs and carotenoids by microalgae depends on the species and growth conditions. Environmental stimuli such as nutrient availability, light intensity and temperature, among other factors, further increase the accumulation of TAGs and high-value compounds as a response to unfavorable growth conditions, thus leading to improved survival of the microalgal cell. Nevertheless, the biosynthesis, signaling pathways and mechanisms responsible for their accumulation are not yet fully understood [4].

This review focuses on the microalgal production of TAGs, LC-PUFAs and carotenoids as well as methodologies promoting their accumulation and pathways involved in the biosynthesis of these high-value biomolecules and lipids. Even though several reviews on each class of biochemicals have been published [5–11], to the best of our knowledge a discussion on how the combined production of all three could be achieved in the same microalga is lacking. As these three classes of compounds can be considered to be lipids or lipophilic molecules, they share biosynthetic precursors, common environmental stimuli and accumulate in lipophilic “sinks”, such as lipid droplets and bilayers. Results from various studies using environmental factors for the induction of the three compounds are summarized. For each biomolecule class, induction methodologies are compared and the most promising species to become *triple-producers* are indicated. We further provide an overview of current and future strategies to improve TAGs, LC-PUFAs and carotenoid production via the selection of promising target species and high-throughput isolation of naturally occurring mutants thereof. Knowledge gaps are discussed and future lines of research for the improvement of the biotechnological applications of microalgae are suggested.

2. General views of lipid metabolism of microalgae

Microalgal lipids can be classified as polar (e.g. phospho- and glycolipids) and neutral or non-polar (e.g. TAGs, sterols and waxes) [12]. The assembly of polar lipids and TAGs can occur in the chloroplast envelope or at the ER membrane, depending on the microalgal species (Fig. 2). Polar lipids usually accumulate in membranes, such as the plasma, ER and thylakoid membranes, as well as the inner and outer membranes of the chloroplast and mitochondria, whereas TAGs are often deposited in plastidial or cytosolic lipid

droplets. Both polar lipids and TAGs can be composed of LC-PUFAs that are synthesized at the ER by specific desaturases and elongases (Fig. 2). Nevertheless, TAGs usually have high levels of saturated and monounsaturated fatty acids to maximize molecule packing, whereas membrane lipids tend to contain higher contents of LC-PUFAs [13,14].

Even though the exact topology of the enzymes involved in carotenoid biosynthesis has not been fully elucidated, it is often surmised that carotenoids are synthesized in the lipid compartment (Fig. 2). Based on studies in land plants and microalgae, the biosynthesis of carotenoids can occur in several places in the chloroplast, namely the plastidial envelope, plastoglobuli and thylakoid membranes, which might also depend on the function of the synthesized carotenoids [15]. For example, in *Dunaliella salina* var. *bardawil*, it has been proposed that β -carotene can be synthesized in the plastidial envelope as well as in plastoglobuli [16]. Furthermore, carotenoids are a very diverse group of 40-carbon isoprenoid biomolecules with > 750 structures and different functions, whose biosynthetic pathways may occur in a given microalgal lineage and be partially absent in another [6]. The xanthophylls (i.e. oxygen-containing carotenoids) astaxanthin and lutein occur mainly in Archaeplastida, whereas fucoxanthin and vaucherixanthin are mainly present in Stramenopiles/Haptista microalgae; β -carotene can be found in all three major microalgal lineages [17].

3. Induction of biosynthesis and accumulation of TAGs, LC-PUFAs or carotenoids in microalgae

Under optimal growth conditions microalgae are able to display fast growth rates with doubling times as low as 10 h (e.g. *Chlamydomonas reinhardtii* [18]), producing biomass with low amounts of lipids. However, under sup-optimal growth conditions algae tend to accumulate neutral lipids, carbohydrates and/or carotenoids and are thus able to adapt to environmental extremes. The biosynthesis and accumulation of specific compounds depend, however, on the genetics of the microalgal species, growth phase, nutrient availability, salinity, temperature and irradiation. The research focusing on how TAGs, carotenoids and LC-PUFAs can be induced rests heavily on the evolutionary lineage of the microalga under study. Recent trends indicate that Stramenopiles microalgae (e.g. *Nannochloropsis*) are often researched for their TAGs and LC-PUFAs content, whereas chlorophytes (e.g. *Chlorella*) are the target of most reports on TAGs and carotenoids.

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