Biodata of **Kristian Spilling** and **Jukka Seppälä**, authors of "***Photobiology and lipid metabolism in algae***."

Dr. Kristian Spilling is a senior scientist at the Marine Research Centre of the Finnish Environment Institute. He obtained his Ph.D. from the University of Helsinki in 2007. His scientific interest is in algal physiology, algae cultivation, and optimizing algal growth. He has for the past 4 years worked in various projects dealing with the potential of algae as a raw material for biofuel.

E-mail: **kristian.spilling@environment.fi**

Dr. Jukka Seppälä is a senior scientist at the Marine Research Centre of the Finnish Environment Institute. He has 20 years experience on phytoplankton ecology studies at the Baltic Sea and obtained his Ph.D. from the University of Helsinki in 2009. His scientific interests include biofuel production from algal biomass, physiology and especially photobiology of phytoplankton, and development of instruments, measuring platforms, and algorithms for marine optical studies.

E-mail: **jukka.seppala@environment.fi**

Kristian Spilling

Jukka Seppälä

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PHOTOBIOLOGY AND LIPID METABOLISM IN ALGAE

KRISTIAN SPILLING AND JUKKA SEPPÄLÄ
Marine Research Centre, Finnish Environment Institute,
P.O. Box 140, 00251 Helsinki, Finland

1. Introduction

On a global scale, roughly half of the annual carbon fixation takes place in the ocean, and in aquatic environments, microalgae is the dominating contributor to primary production. Although the carbon fixation is approximately the same, the standing stock of organic material is much lower in the ocean compared with terrestrial systems. The reason for this is that algae do not build structural components such as wood. This difference is also seen in the turnover time, which, in general, is much faster in the ocean compared with terrestrial systems, and the maximum growth rate of most single cell algae exceeds that of terrestrial plants by far.

The fastest growing algae can under favorable conditions go through several doublings per day. Some of the fast-growing algae also have the ability to build up high lipid reserves (Rai, 1995), which easily can be converted to biodiesel, and the potential of utilizing algae as raw material for biofuel has received a lot of attention dating back to the 1970s (Sheehan et al., 1998). Several reviews have been published recently on the topic of algal lipids (Guschina and Harwood, 2006; Guschina and Harwood, 2009; Harwood and Guschina, 2009), the potential of algal lipids as a raw material for biofuel (Chisti, 2007; Huntley and Redalje, 2007; Hu et al., 2008; Li et al., 2008; Wijffels and Barbosa, 2010), and addressed the question how this would be more sustainable than using traditional energy crop for biofuel production (Smith et al., 2010).

Lipids are a diverse group of compounds. By its simplest definition, lipids are fatty acids and their derivatives such as esters and amides. Lipids play several roles in the physiology of algae, and the two main classes of lipids are polar and neutral lipids (also referred to as nonpolar lipids). Generally, structural lipids found in membranes are polar lipids, whereas storage lipids are neutral lipids.

2. Photosynthesis

The conversion of energy from light to organic material is the key to understanding the metabolism of photosynthesizing organisms such as algae. The light energy fuels the photosynthetic machinery, which produces the chemical energy (ATP) and

reducing power (NADPH) required in the subsequent reactions of carbon fixation and other metabolic processes (Falkowski and Raven, 2007). ATP and NADPH can also be produced by respiration, but the organic material consumed in respiration has primarily been synthesized through photosynthesis. Consequently, all the energy needed for running the metabolism in algae is either directly or indirectly originating from light, driving the electron transport chain in the photosynthetic machinery of the cell (with some exceptions such as mixotrophic algae that can use organic carbon compounds from other sources).

Total solar irradiance in the top of the atmosphere is 1,373 $W m^{-2}$. As the light is transmitted through the earth's atmosphere, this irradiance is reduced by scattering and absorption by water vapor, oxygen, ozone, CO_2, dust, and clouds. This reduction is ranging from approximately 14% in a clean, dry atmosphere to ~90% during a thick cloud cover (Kirk, 1994). Furthermore, the sun elevation greatly affects the solar irradiance at sea level. For a hypothetical clear sky, the seasonal and latitudinal variations in photosynthetically available radiation (PAR) can be modeled accurately (e.g., Kirk, 1994; Williams and Laurens, 2010).

The first step in photosynthesis is light absorption, and photosynthetic pigments in algae and plants have evolved to harvest sunlight efficiently (Kiang et al., 2007). Various pigments of the light-harvesting antenna are complementary in harvesting different wavelengths and are characterized by different absorption spectra. However, they are not able to use the full spectrum of solar irradiation, that is, global irradiance, but only wavelength region from 400 (or 350) to 700 nm, which is termed PAR. The energy of PAR region is approximately 50% of the global irradiance. After absorption, the energy derived from light quanta is transferred rapidly toward the chlorophyll *a* (Chl *a*) molecules in the reaction centers of the two photosystems (Clegg, 2006). These are the sites where the primary photochemical reaction takes place. In the standard light reaction, excitation energy is transferred to photosystem II (PS II) reaction center, to photosystem I (PS I) reaction center, and ends up reducing NADP to NADPH. This linear system is called the *Z*-scheme (Fig. 1).

Absorbed light energy needs to reach the reaction centers in order to contribute to the photochemistry. However, there are loss processes both at the light absorption and the energy transfer steps that affect the energetic efficiency of photosynthesis. For example, some pigments have a photoprotective role acting as sunscreens, preventing damage caused by exposure to too high light energy levels. These pigments dissipate safely the excess energy as heat (Demmig-Adams and Adams, 2006). The amount of energy lost this way may vary from 0% to close to 100% of the absorbed energy, depending on the level and duration of irradiance and on the physiological state of the cells. The light absorbed by the photosynthetic antenna pigments is channeled toward the reaction centers, but the energy transfer is sometimes <100%. At times, the excitation energy cannot be utilized, for example, when all available reaction centers are closed, which may be caused for several reasons. Additionally, when the energy is transferred to the reaction centers, the distribution of excitation energy between PSI and PSII may

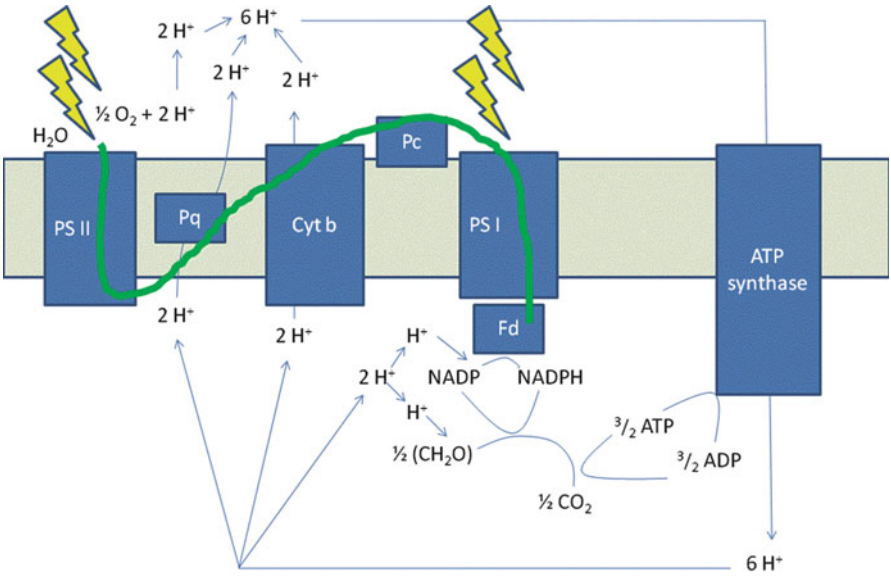

Figure 1. A simplified scheme showing the electron and proton transport across the thylakoid membrane in a classical *Z*-scheme, that is, the two photosystems (PSI and PSII) are connected sequentially. Protons are pumped into the thylakoid lumen and used for generating ATP through the ATP synthase complex. PSI faces the stroma side and provides the reducing power in the form of NADPH through reduced ferredoxin (*Fd*) (More details of the overall process can be found in, for example Falkowski and Raven, 2007).

be sub-optimal. Theoretical minimum quantum requirement for evolution of one O_2 molecule is 8. For the reasons described above, the actual measured requirements are much higher. The lowest quantum requirement obtained in low light is 9–10 mol quanta/mol O_2, and this may be considered the best obtainable efficiency in practice. Such a deviation from the minimum theoretical requirement yields at least 10% reduction in energy efficiency. In high light conditions, or during environmental stress, this value is much higher (e.g., Babin et al., 1996).

There is an additional energy loss because the primary photochemical reactions utilize red photons only. The energy of a light quantum is inversely proportional to its wavelength; blue photons have more energy than red ones. This loss fraction corresponds to the difference in energy between quanta absorbed and that of the lowest excited state of the Chl *a* in the reaction centers (680 nm for PSII and 700 nm for PSI). When calculated for natural sunlight at sea level, and assuming that all light is absorbed by photosynthetic pigments, this loss in energy is roughly 20%. Another loss process is respiration, some of the organic material produced through photosynthesis is used to run the cell metabolism, and subsequent respiration losses are typically 10–20%.

During photochemistry in the light reaction of photosynthesis, electrons originating from water are used for producing ATP and NADPH through the

Table 1. Loss factors affecting energy conversion from sunlight to organic matter by algae.

Loss factors	Reduction in energy (%)
Fraction of sunlight not utilized by algae; whole spectra → PAR[a]	50
Reduction of energy in electron transport chain; PAR → 680/700 nm	20
Reduction of energy due to inefficient light harvesting	10–100
Reduction of energy while converting energy of quanta to chemical energy, carbohydrates	66
Reduction of energy while converting energy of quanta to chemical energy, lipids	72
Respiration losses	10–50
Total, when carbohydrates are the end product[b]	89
Total, when lipids are the end product[b]	91

[a]Photosynthetic active radiation (PAR).
[b]Assuming minimal losses in all processes.

Z-scheme (Fig. 1). During this process, H^+ ions are pumped through the thylakoid membrane, and the ATP is generated as H^+ returns through the ATP synthase machinery. At maximum efficiency, $3H^+$ is pumped across the membrane per excited electron, and $4H^+$ is required per ATP. It is a flexible system, additional ATP can, for example, also be produced by PSI through cyclic electron flow. The NADPH and ATP generated in the light reaction are used in the Calvin cycle to fix carbon. In order to reduce and fix one CO_2 into its sugar equivalent, two NADPHs and three ATPs are consumed. The final product of the Calvin cycle is triose phosphate (3C atoms), which is subsequently combined to form different sugars: different hexoses (6C atoms) or sucrose (12C atoms). Sugars are affecting the osmotic potential of the cell organelle, and the cells need to store carbon in another form to avoid problems with osmoregulation. The most common storage products are lipids and starch, and the preferred storage product is species specific (Rai, 1995). Carbon in these forms can be stored in much higher concentrations than as sugars.

The maximum theoretical energetic yield of photosynthesis is approximately 34%, when calculated using energies of red light quanta, hexose as the end product, and applying maximal conversion efficiencies without any losses. When evident losses of using natural sunlight, losses in photochemical reactions, and requirements of basic cell metabolism are included, the attainable efficiency drops to ~11%, as calculated in Table 1 and also by several other studies (e.g., Melis, 2009; Williams and Laurens, 2010; Weyer et al., 2010; Zemke et al., 2010). This presents an upper limit for conversion of sunlight to biomass using photosynthesis. For the areal-based production of algal biomass, this approximates 70–100 g dry weight m^{-2} day^{-1} using highest available irradiance levels. The obtained values during algal cultivation are generally 5–20 times lower than this (e.g., Sheehan et al., 1998; Williams and Laurens, 2010; Zemke et al., 2010).

For many of the loss processes, little to nothing can be done to increase efficiency. The main loss process that can be reduced is the release of light

energy as heat at high light intensities. The highest photosynthetic efficiency is obtained in the relatively low light region where there is a linear relationship between irradiance and production. As irradiance increases, an increasing proportion of the light energy is dissipated as heat, and to some extent as fluorescence. Much of this loss is due to photoprotective pigments. At high irradiance, the only way to reduce the loss to heat and fluorescence is to have an effective light dilution, meaning that the light energy harvested by individual cells is reduced to a level where maximum efficiency is obtained. This may reduce the production per cell, but light can be distributed to more cells, increasing the total production. Several approaches have been taken for obtaining effective light dilution, from efforts to reducing the individual light-harvesting antennae to different designs of cultivation units (e.g., Sheehan et al., 1998; Zijffers et al., 2008). Developing a way to utilize full sunlight at maximum efficiency will be critical for developing algae as raw material for bulk chemicals and biofuel (Norsker et al., 2011).

3. From Light to Lipid: The Photon Cost of Lipid Synthesis

Algae, and plants in general, have a very limited ability to move to different locations when environmental conditions change. Instead, the metabolic pathways inside the cells have evolved to be very flexible. For example, a simple shift from light to dark requires the cell to be able to run required metabolic processes without photosynthetic products. When light returns, however, the photosynthetic machinery provides another engine to run metabolism through the production of chemical energy (ATP) and reducing power (NADPH). The ATP and NADPH originating from the light reaction are also used for other processes than to produce sugar, for example, to reducing nitrogen and sulfur, and in the synthesis of fatty acids.

As a result of the metabolic flexibility, there is often more than one pathway for synthesizing different compounds and often more than one enzyme that can do the job. This complicates things when trying to understand the specific pathways in a given process, for example, lipid synthesis. Fatty acid synthesis is additionally not a stand-alone process, but several processes need to run in parallel for the cell to function properly. Below we have made an assessment of the theoretical photon cost of lipid production without any loss processes.

CO_2 is one of the most oxidized forms of carbon found in nature, whereas a saturated fatty acid is a highly reduced form of carbon, and the transformation of C from CO_2 into fatty acids requires much energy and reducing power. In order to make one of the most common fatty acids, palmitic acid (16:0), 16C atoms are needed. However, as we will describe below, some carbon will be lost as CO_2 during this process, and in order to make one chain of palmitic acid, 24C atoms are needed in the form of sugar (two sucrose) at the start of the process. The minimum photon cost per C atom is as mentioned 8: 2 photons per NADPH

and 4/3 photons per ATP (Fig. 1). Thus, the total budget for producing the two sucrose molecules, needed for making one chain of palmitic acid, is a minimum of 192 photons (72 ATP and 48 NADPH).

Acetyl CoA is a central starting material in the lipid synthesis (it is central also in many other cellular processes, e.g., feeding into the citric acid cycle). The major pathways producing acetyl CoA involve glycolysis and fatty acid oxidation. There are some uncertainties as to where the acetyl CoA used to form fatty acids originates from (see, e.g., Rawsthorne 2002 for a review), but it is clear that the fatty acids are synthesized in the plastids. Considering lipid synthesis in algae, the likely source of acetyl CoA is through glycolysis via pyruvate. Glycolysis takes part in the cytosol, producing pyruvate that can cross the membrane into the chloroplast, where acetyl CoA is formed (acetyl CoA is most likely not able to cross membranes and has to be produced where there is a need).

In the overall process of glycolysis, sucrose is split up into four pyruvate, providing a net release of four ATP and four NADH, and then further, four NADH is produced when acetyl CoA is formed from pyruvate (Buchanan et al., 2000). In the process, 4C atoms are lost as CO_2 per sucrose molecule, a loss rate of 1/3C. There are alternative routes, for example, the Rubisco enzyme can take part, independent of the Calvin cycle, increasing the C transfer efficiency and reducing the loss to 1/5C (Schwender et al., 2004). Although NADH is also a reducing power, it does not have the same function as NADPH. Generally, NADPH is used to as a reducing power directly, whereas NADH is used to produce ATP; with some exceptions, for example, NADH can be used for nitrate reduction in algae (Syrett, 1982). We will, however, calculate NADH as ATP equivalents, and the exchange rate between NADH and ATP is depending on where the transfer takes place. In the cytosol, NAHD gives rise to 1.5 ATP, and in the mitochondrion, 2.5 ATP is produced per NADH. The ATP and NADH produced during glycolysis do not necessarily directly take part in the fatty acid synthesis, but it is producing chemical energy, which can be seen as sparing photons needed to run other processes. Using NADH = 1.5 ATP equivalents, two sucrose gives rise to 32 ATP in glycolysis, which is ~43 photons worth of ATP. At the start of fatty acid synthesis, with all carbon needed in the form of acetyl CoA, an absolute minimum of 149 photons are needed, when subtracting the 43 photons worth of ATP from the 192 photons needed for making two sucrose molecules. An overview of the process can be seen in Fig. 2.

Every acetyl CoA carries 2C atoms, and during fatty acid synthesis, the carbon needs further reduction in order to make the fatty acid chains. The process starts with the union of one acetyl CoA and one malonyl-ACP (derived from acetyl CoA) molecules. This is the first step in a cycle where 2C atoms are added for every cycle (Fig. 3). The process requires one ATP for transforming acetyl CoA to malonyl-ACP and two NADPH for every turn of the cycle. Each subsequent cycle adds one malonyl-ACP, and this pair-wise addition of C atoms is the reason fatty acids normally have an even number of C atoms. The chemical energy and reducing power needed to form one palmitic acid chain from acetyl

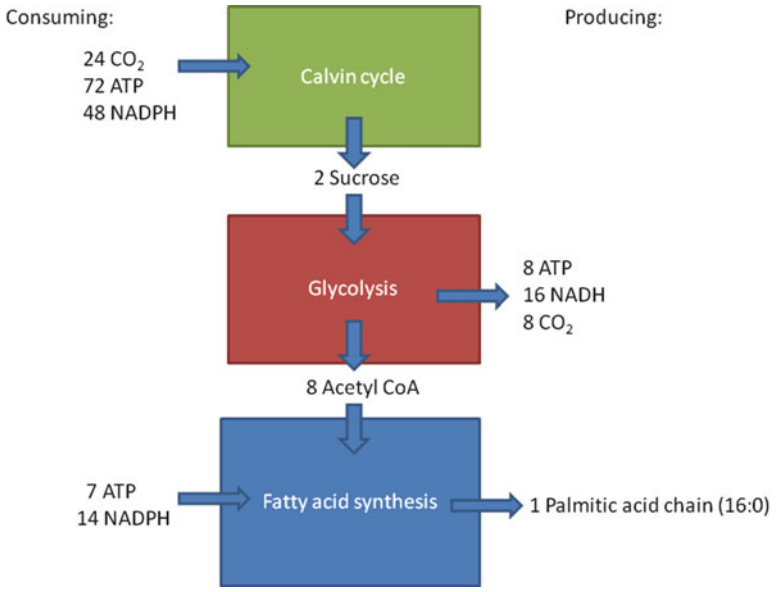

Figure 2. The theoretical stoichiometry of carbon, chemical energy (ATP) and reducing power (NADPH) used in the production of palmitic acid (16:0) when the acetyl CoA is generated through the glycolysis. There are other possible pathways, and this scheme does not take into account any loss processes or parallel processes needed to be run simultaneously (Further details can be found in Buchanan et al., 2000).

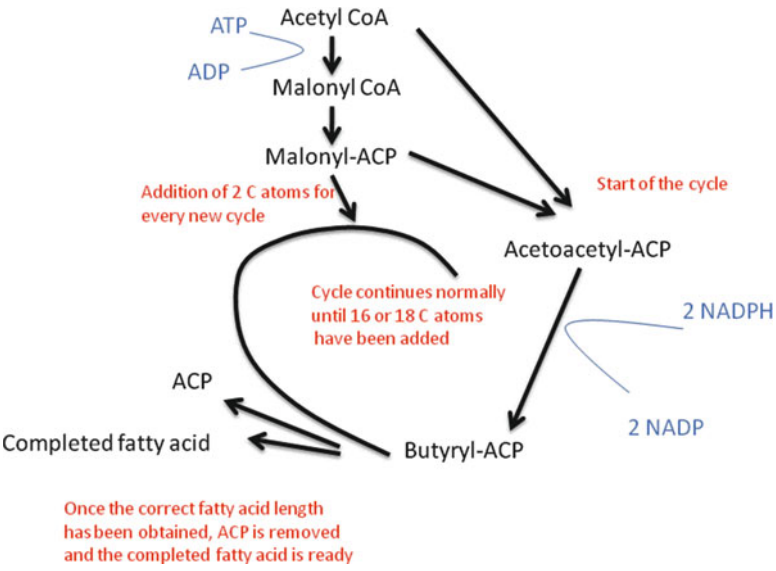

Figure 3. Cycle of fatty acid synthesis in the plastids of plants (Further details can be found in Buchanan et al., 2000).

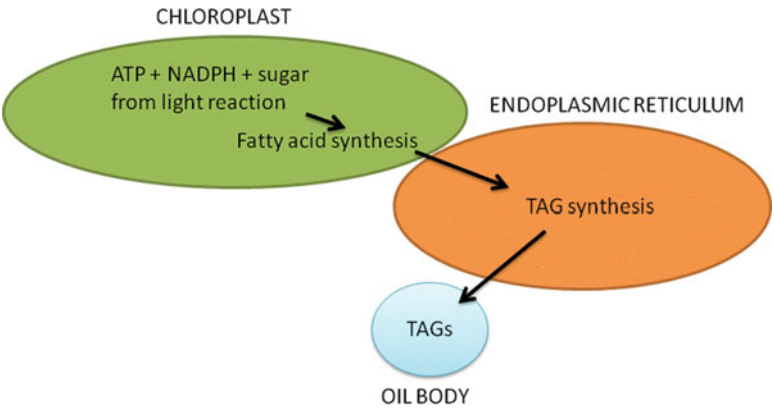

Figure 4. A general schematic of the synthesis of triacylglycerols (*TAGs*). The individual fatty acids are synthesized in the plastids, and the TAGs are combined in the endoplasmic reticulum and released as separate oil bodies into the cytosol.

CoA is consequently 7 ATP and 14 NADPH, which, using our conversion factors above, translates to ~37 photons. The total photon cost for one palmitic acid chain is consequently ~187.

The energy content of palmitic acid is 9.97 MJ mol^{-1}. Taking the requirement of 187 mol photons to produce 1 mol palmitic acid yields energy conversion of ~30% when using red photons or ~22% when using typical underwater light (with 0.24 MJ mol^{-1} photons) (Kirk, 1994). These values are somewhat lower than ones calculated for simple hydrocarbons (34 and 25%, respectively, for glucose), indicating an additional drop of ~12% in energy conversion to the values presented in previous chapter. In practice, however, the conversion factor from light to lipids is much lower. Taking into account the evident loss processes described in Table 1, the best possible energy conversion factor from sunlight to lipid is ~9%.

The fatty acids are synthesized in the plastids, and the process utilizes ATP and NADPH directly from the photosynthetic machinery when there is light. Further processing of the fatty acids takes place in the endoplasmic reticulum where, for example, the triacylglycerols (TAGs) are synthesized and the ready-made storage lipids are budded of in an oil body, which functions as an energy reserve (Fig. 4).

4. Effect of Light Quantity and Quality on Lipid Composition

The effect of light intensity, that is, photon flux density, on the lipid synthesis is not straightforward. There are large differences between different species, and it is clear that the physiological state of the cells is a major factor governing the lipid synthesis. During exponential growth, most of the energy/carbon is put into

growth. For this purpose, structural lipids for, for example, membranes are needed, while the production of storage lipids is at a minimum. During early stationary phase, vegetative growth slows down, and the excess organic carbon produced photosynthetically may be placed into storage lipids. However, not all species use lipids as the main storage product; starch is an alternative storage form used by some species.

In their study of light intensity effect on fatty acid composition under continuous light, Thompson et al. (1990) found large species-specific differences. Correlations between light and fatty acids were found for single species, but there were no consistent correlations over all eight species examined. However, for diatoms, there was a general trend of increasing concentration of palmitic acid (16:0) with increasing irradiance. Also for the diatom, *Thalassiosira pseudonana* did increasing the photon flux density lead to an increasing proportion of saturated fatty acids while decreasing the proportion of polyunsaturated fatty acids (PUFAs) (Brown et al., 1996). A decrease in PUFAs with increasing photon flux can be amplified with increasing temperature (Papina et al., 2007). High light intensities have been suggested to cause oxidative damage to PUFAs (Guschina and Harwood, 2009); however, higher concentration of saturated fatty acids might also reflect that these are the fatty acids stored as triacylglycerols (TAGs) (Khotimchenko and Yakovleva, 2004, 2005; Zhukova and Titlyanov, 2006).

Another aspect that will alter the ratio between saturated and unsaturated fatty acids is photoacclimation. The fatty acids associated with the photosynthetic machinery (e.g., glycolipids in the thylakoid membranes) are mostly polyunsaturated and under low light algae will increase the concentration of photosynthetic pigments and thereby increase the proportion of PUFAs (Walsh et al., 1997; Mock and Kroon, 2002; Zhukova and Titlyanov, 2006). Although there are large species-specific differences and differences due to the physiological state of the algae, the available literature suggests that the proportion of PUFAs increases at low light while the proportion of saturated fatty acids increases at high light intensities. The carbon allocation in different light environments reflects this difference; in low light or when cultures grow dense and cause self shading, low photon flux densities will increase the carbon allocation into light-harvesting pigments high in glycolipids (and PUFAs), but as nutrients are depleted, the fraction of carbon placed into neutral lipids starts to increase (Mock and Gradinger, 2000). A conceptual model of the effect of light on lipid concentration is presented in Fig. 5.

Spectral quality of light may affect composition of algal cell, for example, some pigments like astaxanthin are accumulated more in blue than in red light (Katsuda et al., 2004). However, overall the effect of spectral composition of light on the lipid metabolism has not been very much studied. In the few cases where the quality of light has been a factor, it has mainly been studies of the effect of UV light on cellular processes. Algal cells close to the surface will experience UV light, which has several negative effects on cellular processes. The lipid synthesis seems to be less affected by UV light than many other processes in the cells

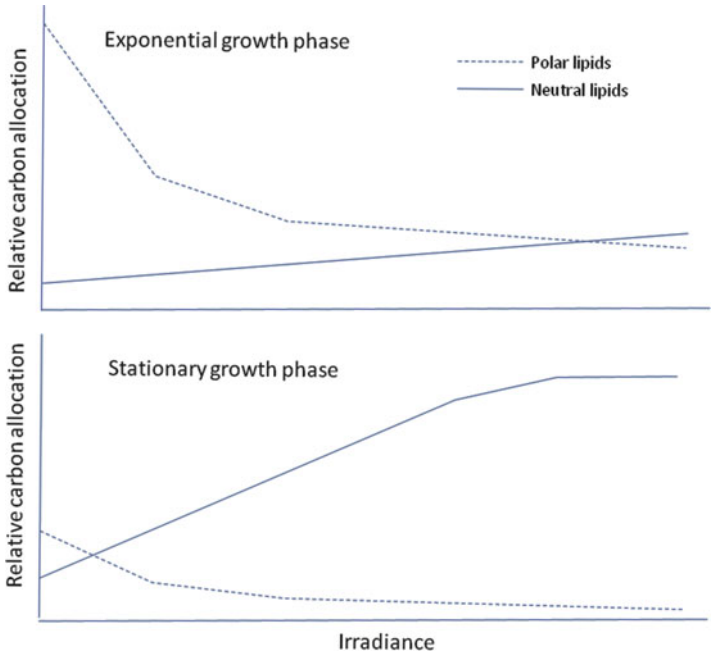

Figure 5. A conceptual, testable model of irradiance effect on the relative contribution of polar and neutral lipids during exponential and stationary growth phase for algal species that use lipids as their main storage product (Details are discussed in the text).

such as the protein synthesis (Smith et al., 1998), but the vulnerability to UV light and its effect on lipid synthesis is species dependent (Arts and Rai, 1997). For *Tetraselmis* sp., Goes et al. (1994) found that UV-B selectively suppressed PUFA synthesis.

5. Effect of Light Cycles on Lipid Composition

5.1. DIURNAL LIGHT-DARK CYCLES

It is clear that the diurnal light cycles directly affect a range of cellular processes such as primary productivity and cell division (Prézelin, 1992). Daily oscillations are commonly governed by biological clocks, and recent development has started to reveal the mechanism governing diurnal cycles down to the genetic level (Bell-Pedersen et al., 2005; Gardner et al., 2006; Monnier et al., 2010).

Generally, the internal C pool inside the cell builds up during the light period, reaching a peak by the end of the light period (Stramski and Reynolds, 1993; Jacquet et al., 2001; DuRand et al., 2002), which is not all that surprising

considering that this is when the photosynthetic production takes place. During the dark period, there is a loss of C due to respiration. For some species, parts of the cellular metabolism, such as protein synthesis, mainly take place during the dark period. Changing the photoperiod normally affects the primary production and thereby the growth rate, for example, increasing the photoperiod increases total production. However, some species of microalgae may need a dark period for running particular metabolic processes, and for these species, there will be an upper limit to how long a photoperiod is tolerated (Sicko-Goad and Andresen, 1991). For example, some species go through cell division mainly or only during the dark period, others, diatoms in particular, seem to go through cell division mainly during the light period (Nelson and Brand, 1979).

Although decreasing day length generally leads to decreased production and growth, microalgae can to some degree compensate for shorter days by increasing the concentration of Chl *a* and other photosynthetic pigments in the cell (Foy et al., 1976; Hobson et al., 1979; Reynolds, 2006). The lipids associated with the photosynthetic pigment would presumably follow the same pattern, and these are synthesized during the light period (Ragni and D'Alcala, 2007).

In one of the few studies on this topic, Brown et al. (1996) investigated the effect of different diurnal rhythms and irradiance on cellular constituents (carbohydrates, proteins, and lipids) of *Thalassiosira pseudonana*. Three treatments were used: 50 μmol photons m^{-2} s^{-1} in 24-h light, 100 μmol photons m^{-2} s^{-1} in 12-h light/12-h dark cycle, and 100 μmol photons m^{-2} s^{-1} in 24-h light. Their results suggested that longer photoperiod would increase growth compared with a shorter photoperiod with the equivalent light energy. The lipid content as percentage of dry weight did not seem to be affected by daily cycles during exponential growth phase, but was somewhat lower in the lowest irradiance during the stationary growth phase.

5.2. EFFECT OF LIGHT FLASHES

It is known from photobioreactors that short-term changes in light-dark cycling also affect primary production (Molina Grima et al., 1999). This effect is caused by turbulent eddies in a dense culture, moving the cells from high light to darkness and back again. This is experienced as light flashes by the microalgae, and the frequency of the light flashes is positively correlated with the productivity (Terry, 1986; Degen et al., 2001). In a classical study, Phillips Jr and Myers (1954) showed that light flashes of 0.001–0.1 s duration with tenfold longer dark periods boosted growth of the green algae *Chlorella pyrenoidosa*. The effect of light flashes can be modeled, and the mechanism is well understood (Rubio et al., 2003; Yoshimoto et al., 2005). The relaxation between light flashes decreases the loss rate, increasing efficiency of the photosynthetic machinery. The effect of distributing the light as light flashes has consequently some of the same effect as light dispersal. Distributing the light energy between cells lowers the production per cell, but increases the

overall production, as more cells receive light energy. The effect of light flashes on lipid metabolism has not been studied in great detail, but the effects could be similar to that of photon flux or diurnal light-dark cycles.

6. Conclusion

The metabolic pathways in algae are very flexible, and although many of the processes are known, it is difficult to precisely know what metabolic route is used when synthesizing lipids. Light is of paramount importance for growth and lipid accumulation in algae, and although a lot of work has been conducted to better understand photosynthesis and the effect of light on growth, there are very few studies on the effect of light on the lipid accumulation in algae. In particular, the effect of spectral quality of light on lipid composition is hardly studied at all.

In this chapter, we have evaluated the different loss processes when transforming light energy to chemical energy in lipids. For many of these loss processes, little can be done to minimize these effects, for example, reduction of irradiance in the atmosphere. The main loss process that can be reduced is the release of light energy as heat at high light intensities. Much of this loss is due to photoprotective pigments, and effectively utilizing high light levels at maximum efficiency is the challenge ahead for developing algae as a raw material for low cost commodities such as fuel.

7. References

Arts MT, Rai H (1997) Effects of enhanced ultraviolet-B radiation on the production of lipid, polysaccharide and protein in three freshwater algal species. Freshw Biol 38:597–610

Babin M, Morel A, Claustre H, Bricaud A, Kolber Z, Falkowski PG (1996) Nitrogen- and irradiance-dependent variations of the maximum quantum yield of carbon fixation in eutrophic, mesotrophic and oligotrophic marine systems. Deep Sea Res 43:1241–1272

Bell-Pedersen D, Cassone VM, Earnest DJ, Golden SS, Hardin PE, Thomas TL, Zoran MJ (2005) Circadian rhythms from multiple oscillators: lessons from diverse organisms. Nat Rev Genet 6:544–556

Brown MR, Dunstan GA, Norwood SJ, Miller KA (1996) Effects of harvest stage and light on the biochemical composition of the diatom *Thalassiosira pseudonana*. J Phycol 32:64–73

Buchanan BB, Gruissem W, Jones RL (2000) Biochemistry & molecular biology of plants. American Society of Plant Physiologists, Rockville

Chisti Y (2007) Biodiesel from microalgae. Biotechnol Adv 25:294–306

Clegg RM (2006) Nuts and bolts of excitation energy migration and energy transfer. In: Papageorgiou GC, Govindjee (eds) Chlorophyll a fluorescence. A signature of photosynthesis, vol 19, Advances in photosynthesis respiration., pp 83–105

Degen J, Ubele A, Retze A, Schmidt-Staigar U, Trosch W (2001) A novel airlift photobioreactor with baffles for improved light utilization through the flashing light effect. J Biotechnol 92:89–94

Demmig-Adams B, Adams WW III (2006) Photoprotection in an ecological context: the remarkable complexity of thermal energy dissipation. New Phytol 172:11–21

DuRand MD, Green RE, Sosik HM, Olson RJ (2002) Diel variation in optical properties of *Micromonas pusilla* (Prasinophyceae). J Phycol 38:1132–1142

Falkowski PG, Raven JA (2007) Aquatic photosynthesis, 2nd edn. Princeton University Press, Princeton

Foy RH, Gibson CE, Smith RV (1976) The influence of daylength, light intensity and temperature on the growth rates of planktonic blue-green algae. Br Phycol J 11:151–163

Gardner MJ, Hubbard KE, Hotta CT, Dodd AN, Webb AAR (2006) How plants tell the time. Biochem J 397:15–24

Goes JI, Handa N, Taguchi S, Hama T (1994) Effect of UV-B radiation on the fatty acid composition of the marine phytoplankter *Tetraselmis* sp.: relationship to cellular pigments. Mar Ecol Prog Ser 114:259–274

Guschina IA, Harwood JL (2006) Lipids and lipid metabolism in eukaryotic algae. Prog Lipid Res 45:160–186

Guschina IA, Harwood JL (2009) Algal lipids and effect of the environment on their biochemistry. In: Kainz M, Brett MT, Arts MT (eds) Lipids in aquatic ecosystems. Springer, New York, pp 1–24

Harwood JL, Guschina IA (2009) The versatility of algae and their lipid metabolism. Biochimie 91:679–684

Hobson LA, Hartley A, Ketcham DE (1979) Effects of variations in daylength and temperature on net rates of photosynthesis, dark respiration and excretion by *Isochrysis galbana* Parke. Plant Physiol 63:947–951

Hu Q, Sommerfeld M, Jarvis E, Ghirardi M, Posewitz M, Seibert M, Darzins A (2008) Microalgal triacylglycerols as feedstocks for biofuel production: perspectives and advances. Plant J 54:621–639

Huntley ME, Redalje DG (2007) CO_2 mitigation and renewable oil from photosynthetic microbes: a new appraisal. Mitig Adapt Strat Glob Chang 12:573–608

Jacquet S, Partensky F, Lennon J-F, Vaulot D (2001) Diel patterns in growth and division in marine picoplankton in culture. J Phycol 37:357–369

Katsuda T, Lababpour A, Shimahara K, Katoh S (2004) Astaxanthin production by *Haematococcus pluvialis* under illumination with LEDs. Enzyme Microb Technol 35:81–86

Khotimchenko SV, Yakovleva IM (2004) Effect of solar irradiance on lipids of the green alga *Ulva fenestrata* Postels et Ruprecht. Bot Mar 47:395–401

Khotimchenko SV, Yakovleva IM (2005) Lipid composition of the red alga *Tichocarpus crinitus* exposed to different levels of photon irradiance. Phytochemistry 66:73–79

Kiang NY, Siefert J, Govindjee, Blankenship RE (2007) Spectral signatures of photosynthesis. I. Review of earth organisms. Astrobiology 7:222–251

Kirk JTO (1994) Light and photosynthesis in aquatic ecosystems. Cambridge University Press, Cambridge

le B Williams PJ, Laurens LML (2010) Microalgae as biodiesel & biomass feedstocks: review & analysis of the biochemistry, energetics & economics. Energy Environ Sci 3:554–590

Li Q, Du W, Liu DH (2008) Perspectives of microbial oils for biodiesel production. Appl Microbiol Biotechnol 80:749–756

Melis A (2009) Solar energy conversion efficiencies in photosynthesis: minimizing the chlorophyll antennae to maximize efficiency. Plant Sci 177:272–280

Mock T, Gradinger R (2000) Changes in photosynthetic carbon allocation in algal assemblages of Arctic sea ice with decreasing nutrient concentrations and irradiance. Mar Ecol Prog Ser 202:1–11

Mock T, Kroon BMA (2002) Photosynthetic energy conversion under extreme conditions – II: the significance of lipids under light limited growth in Antarctic sea ice diatoms. Phytochemistry 61:53–60

Molina Grima E, Acien Fernandez FG, Garcıa Camacho F, Chisti Y (1999) Photobioreactors: light regime, mass transfer, and scaleup. J Biotechnol 70:231–247

Monnier A, Liverani S, Bouvet R, Jesson B, Smith JQ, Mosser J, Corellou F, Bouget FY (2010) Orchestrated transcription of biological processes in the marine picoeukaryote *Ostreococcus* exposed to light/dark cycles. BMC Genomics 11:1–13

Nelson DM, Brand LE (1979) Cell division periodicity in 13 species of marine phytoplankton on a light: dark cycle. J Phycol 15:67–75

Norsker N-H, Barbosa MJ, Vermuë MH, Wijffels RH (2011) Microalgal production – a close look at the economics. Biotechnol Adv 29:24–27

Papina M, Meziane T, van Woesik R (2007) Acclimation effect on fatty acids of the coral *Montipora digitata* and its symbiotic algae. Comp Biochem Physiol B Biochem Mol Biol 147:583–589

Phillips JN Jr, Myers J (1954) Growth rate of *Chlorella* in flashing light. Plant Physiol 29:152–161

Prézelin BB (1992) Diel periodicity in phytoplankton productivity. Hydrobiologia 238:1–35

Ragni M, D'Alcala MR (2007) Circadian variability in the photobiology of *Phaeodactylum tricornutum*: pigment content. J Plankton Res 29:141–156

Rai H (1995) The influence of photon flux density (PFD) on short term ^{14}C incorporation into proteins, carbohydrates and lipids in freshwater algae. Hydrobiologia 308:51–59

Rawsthorne S (2002) Carbon flux and fatty acid synthesis in plants. Prog Lipid Res 41:182–196

Reynolds CS (2006) Ecology of phytoplankton. Cambridge University Press, Cambridge

Rubio FC, Camacho FG, Sevilla JMF, Chisti Y, Grima EM (2003) A mechanistic model of photosynthesis in microalgae. Biotechnol Bioeng 81:459–473

Schwender J, Goffman F, Ohlrogge JB, Shachar-Hill Y (2004) Rubisco without the Calvin cycle improves the carbon efficiency of developing green seeds. Nature 432:779–782

Sheehan J, Dunahay T, Benemann J, Roessler P (1998) A look back at the U.S. Department of Energy's aquatic species program – biodiesel from algae. National Renewable Energy Laboratory. Report NREL/TP-580-24190

Sicko-Goad L, Andresen NA (1991) Effect of growth and light/dark cycles on diatom lipid content and composition. J Phycol 27:710–718

Smith REH, Furgal JA, Lean DRS (1998) The short-term effects of solar ultraviolet radiation on phytoplankton photosynthesis and photosynthate allocation under contrasting mixing regimes in Lake Ontario. J Gt Lakes Res 24:427–441

Smith VH, Sturm BSM, deNoyelles FJ, Billings SA (2010) The ecology of algal biodiesel production. Trends Ecol Evol 25:301–309

Stramski D, Reynolds RA (1993) Diel variations in the optical properties of a marine diatom. Limnol Oceanogr 38:1347–1364

Syrett PJ (1982) Nitrogen metabolism of microalgae. Can Bull Fish Aquat Sci 210:182–210

Terry KL (1986) Photosynthesis in modulated light: quantitative dependence of photosynthetic enhancement on flashing rate. Biotechnol Bioeng 28:988–995

Thompson PA, Harrison PJ, Whyte JNC (1990) Influence of irradiance on the fatty acid composition of phytoplankton. J Phycol 26:278–288

Walsh K, Jones GJ, Dunstan RH (1997) Effect of irradiance on fatty acid, carotenoid, total protein composition and growth of *Microcystis aeruginosa*. Phytochemistry 44:817–824

Weyer KM, Bush DR, Darzins A, Willson BD (2010) Theoretical maximum algal oil production. Bioenerg Res 3:204–213

Wijffels RH, Barbosa MJ (2010) An outlook on microalgal biofuels. Science 239:796–799

Yoshimoto N, Sato T, Kondo Y (2005) Dynamic discrete model of flashing light effect in photosynthesis of microalgae. J Appl Phycol 17:207–214

Zemke PE, Wood BD, Dye DJ (2010) Consideration for the maximum production rates of triacylglycerol from microalgae. Biomass Bioenergy 34:145–151

Zhukova NV, Titlyanov EA (2006) Effect of light intensity on the fatty acid composition of dinoflagellates symbiotic with hermatypic corals. Bot Mar 49:339–346

Zijffers J-WF, Janssen M, Tramper J, Wijffels RH (2008) Design process of an area-efficient photobioreactor. Mar Biotechnol 10:404–415