



Growth and neutral lipid synthesis in green microalgae: A mathematical model

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ARTICLE INFO

Article history:

Received 1 April 2010

Received in revised form 28 May 2010

Accepted 7 June 2010

Available online 8 July 2010

Keywords:

Mathematical model

Green algae

Neutral lipids

Photosynthesis

Biofuel

ABSTRACT

Many green microalgae significantly increased their cellular neutral lipid content when cultured in nitrogen limited or high light conditions. Due to their lipid production potential, these algae have been suggested as promising feedstocks for biofuel production. However, no models for algal lipid synthesis with respect to nutrient and light have been developed to predict lipid production and to help improve the production process. A mathematical model is derived describing the growth dynamics and neutral lipid production of green microalgae grown in batch cultures. The model assumed that as the nitrogen was depleted, photosynthesis became uncoupled from growth, resulting in the synthesis and accumulation of neutral lipids. Simulation results were compared with experimental data for the green microalgae *Pseudochlorococcum* sp. For growth media with low nitrogen concentration, the model agreed closely with the data; however, with high nitrogen concentration the model overestimated the biomass. It is likely that additional limiting factors besides nitrogen could be responsible for this discrepancy.

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1. Introduction

The realization of industrial-scale production of algal-derived biofuel faces many hurdles, and its success may require progress and development in many different scientific and engineering disciplines. An active research problem is to better understand why and how, under certain environmental conditions, some species of algae up-regulate neutral lipids (NL), which can be readily converted to biodiesel and other biofuels (Scott et al., 2010; Hu et al., 2008). This article deals specifically with those species of green microalgae such as *Pseudochlorococcum* sp. that have been observed to accumulate extremely high levels of NLs. In the following, unless specified otherwise, “algae” will refer to such species.

Cultures suspended in growth media with low nitrogen (low-N) concentration yield biomass with significantly higher lipid content than those suspended in high-N media. On the other hand, cultures suspended under high-light tend to yield greater lipid content than those suspended under low-light (Hu et al., 2008; Rodolfi et al., 2009). The neutral lipid content can increase from zero to well over fifty percent of dry weight. This trend has been confirmed repeatedly by laboratory experiments (Hu et al., 2008; Scott et al., 2010; Scragg et al., 2002; Rodolfi et al., 2009).

Photosynthesis is a highly complex process that is life-sustaining; however, excess light energy can be potentially harmful. Algae absorb light energy in order to oxidize water, providing electrons that can face a number of different fates. This process must be safely regulated, for there is an inherent danger to continuously exchanging electrons between and within proximity of molecules such as singlet oxygen or triplet chlorophyll *a*, for harmful reactive oxygen species (ROS) can form. When ROS accumulate and cause more damage than can be reconciled, algae experience photoinhibition and oxidative stress. Hence, with increased light there is an increased susceptibility to photo-oxidative stress (Niyogi, 2000). It has been proposed that increased NL synthesis is perhaps the “default pathway” to defend against photo-oxidative stress that can occur as a result of too much reducing energy (Hu et al., 2008). Moreover, N-limitation reduces cell growth, a high energy-consuming process. A lack of electron sinks downstream of photosystem I (e.g. carbon fixation) can result in a buildup of electrons in the electron transport chain and subsequently an increased risk of photoinhibition and ROS production (Niyogi, 2000).

Metabolic pathways downstream of the electron transport chain may serve as important defenses against ROS production during nutrient limitation. During N-stress, cell growth is halted, but carbon fixation may continue at rates exceeding the needs of the cell. It may be that the “uncoupling of photosynthesis and biomass production” as reviewed in Berman-Frank and Dubinsky (1999) is the mechanism that allows adequate electron sinks to function when cell growth is hindered as a result of nutrient

Abbreviations: NL, neutral lipid; N, nitrogen; C, carbon; Chl, chlorophyll; Dw, dry weight; ROS, reactive oxygen species; PS I/II, photosystem I/II.

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limitation. Some species up-regulate nitrogen-free pigments or simply excrete excess photosynthate during stressful growth conditions—the many mechanisms with which phytoplankton handle excess carbon reduction is an important research area (Dubinsky and Berman-Frank, 2001; Hessen and Anderson, 2008).

Up-regulation of NL synthesis may be a means by which energy can be spent during stressed conditions, helping to maintain a safe turnover rate of the ATP and reductant pools sustained by the light reactions. Fatty acid production is expensive in terms of ATP and reductant requirements (Xiong et al., 2010). NLs store significantly more energy than carbohydrates do: 37 kJ/g versus 17 kJ/g, respectively; and, on a per-mass basis, NL synthesis requires twice the reducing energy (NADPH) than that of carbohydrate or protein synthesis (Hu et al., 2008). NL synthesis is an effective energy sink. It may be that certain species maintain a relatively high rate of photosynthesis during N-stress, but compensate by synthesizing NLs. It has been suggested that newly fixed carbon is used for NL synthesis (Scott et al., 2010), particularly in instances when the NL dry weight of a suspension exceeds its initial dry weight (Rodolfi et al., 2009). Oleaginous species of algae use excess carbon and energy to synthesize storage lipids under N-stress, whereas non-oleaginous species synthesize carbohydrates or halt growth (Rodolfi et al., 2009).

Since N-limitation appears to be a key catalyst for excessive NL accumulation, an immediate question is whether or not ecological models of phytoplankton–nutrient interactions can be extended to this phenomenon. Ecological stoichiometry (Sterner and Elser, 2002) in particular provides a useful foundation for mathematical models by considering the relationship between the elemental compositions of organisms and their environment. Given that NLs serve as C storage in N-limited environments, the N:C ratio of an algal suspension may provide the means of modeling TAG accumulation using plausible ecological models. The N:C ratio decreases with decreasing N-availability and increasing irradiance, both of which have been observed to increase NL synthesis. Can NL synthesis be simplified ecologically and mathematically as the cause (or effect) of a low N:C? This question is important, as ecological stoichiometry may be applicable to other bioengineering processes, see e.g. (Mauzerall, 2008).

As of yet, there have been no published mathematical models of algal lipid production with respect to nutrient and light conditions. Such models are important not only for gaining insight into and testing theories of oleaginous NL synthesis, but also for optimizing biodiesel production. Devising a mathematical model of phytoplankton NL production poses several challenges. The mechanisms behind NL synthesis are not fully understood (Hu et al., 2008), and modeling NL production entails modeling non-NL dynamics such as photosynthesis and nutrient assimilation. While there are existing models of phytoplankton growth with respect to both light and nutrient limitation (Geider et al., 1998; Flynn, 2001; Loladze et al., 2000), it remains an important research area with need for more models (Klausmeier et al., 2008). The model to be formulated below, while comprehensive, is largely based on existing but uncoupled modeling efforts (Geider et al., 1998; Huisman, 1999; Loladze et al., 2000). Existing frameworks are combined in order to model both biomass and NL production subject to nutrient and light limitation.

2. Methods

2.1. Mathematical model

The model describes four state variables:

$A(t)$ = algal biomass concentration, excluding neutral lipids (g dw m^{-3}),

$L(t)$ = neutral lipid concentration ($\text{g NL} \cdot \text{m}^{-3}$),
 $H(t)$ = chl a content of A ($\text{g chl g}^{-1} \text{ dw}$),
 $N(t)$ = extracellular nitrogen concentration (g N m^{-3}),

The phytoplankton mass is divided into two compartments: non-NL biomass A and neutral lipids L . Therefore the total algae density is the sum of the two compartments, $A + L$. The model is derived based upon four major assumptions:

A1. The growth rate of A , defined as $\mu := \frac{1}{A} \frac{dA}{dt}$, is either N- or light limited. N-limited growth takes the form of the well-established (Droop) cell-quota model. An increase in A , the non-lipid dry weight, requires a fixed proportion c ($\text{g C g}^{-1} \text{ dw}$) of accumulated carbon.

A2. The net carbon fixation rate is governed by the standard single-hit Poisson model of photosynthesis, normalized to the chl a content of A .

A3. Following Geider et al. (1998), chlorophyll a synthesis is coupled with nitrogen uptake. The proportion of nitrogen devoted to chl a synthesis is regulated by the utilization to uptake ratio of carbon. N-uptake is regulated by Q .

A4. NL synthesis results from an excess of C-fixation relative to the C requirements for growth. Therefore, when $Q = q$, all increases in total biomass are due to de novo NL synthesis.

Based upon these assumptions, a system of four ODEs is proposed to describe algal growth, N-assimilation, and chlorophyll and NL synthesis of a batch culture:

$$\frac{dA(t)}{dt} = \underbrace{\mu(A, L, H, N)A(t)}_{\text{cell growth}}, \quad (1)$$

$$\frac{dL(t)}{dt} = \underbrace{[p(A, L, H, N) - c\mu(A, L, H, N)]A(t)}_{\text{NL synthesis}}, \quad (2)$$

$$\frac{dH(t)}{dt} = \underbrace{c \frac{\mu}{p}(A, L, H, N) \rho v(A, N)}_{\text{N uptake devoted to chl a synthesis}} - \underbrace{H(t)\mu}_{\text{growth dilution}}, \quad (3)$$

$$\frac{dN(t)}{dt} = \underbrace{-v(A, N)A}_{\text{N uptake}}, \quad (4)$$

where

$$Q(t) = \frac{A(0)Q_0 + N(0) - N(t)}{A(t)}, \quad (5)$$

$$\mu(A, L, H, N) = \min \left\{ \mu_m \left(1 - \frac{q}{Q(t)} \right), \frac{p(A, L, H, N)}{c} \right\}, \quad (6)$$

$$p(A, L, H, N) = H(t)p_m(A, L, N) \left(1 - \exp \left(\frac{-a\Phi I(A, H)}{p_m(A, L, N)} \right) \right), \quad (7)$$

$$p_m(A, L, N) = \frac{(AQ)^2(t)p_0}{(AQ)^2(t) + q^2(A(t) + L(t))^2}, \quad (8)$$

$$I(A, H) = \frac{I_0}{aH(t)A(t)z} (1 - \exp(-aH(t)A(t)z)), \quad (9)$$

$$v(A, N) = \frac{q_M - Q(t)}{q_M - q} \left(\frac{v_m N(t)}{N(t) + v_h} \right). \quad (10)$$

A full list of parameter descriptions is given in Table 1.

2.1.1. Formulation of (6), $\mu(A, L, H, N)$

There are two aspects of growth considered in the model. The first, referred to as simply “growth,” is exclusive to A , the non-NL biomass. The other aspect is NL synthesis. NLs are considered a form of biomass that exists transiently under stressed conditions. When growth of A ceases, excess carbon and energy is used to

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