Cost Benefit Analysis in Phytoplankton Ecophysiology

Richard Geider

Oliver Ross*, Mark Moore

Metodi Metodiev(co-I), Boyd McKew**, Gergana Metodieva**

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** Resource utilization by phytoplankton: is nitrogen allocation amongst functional catalysts optimized in response to resource limitation?

Optimal foraging

- MacArthur, R. H. and Pianka, E. R. (1966). On the optimal use of a patchy environment. American Naturalist, 100: 603-609
- Animals forage in such a way as to maximize their energy intake per unit time.
- A cost-benefit analysis of the tradeoff between the time expended in finding, capturing and eating food versus the energy gained from the food.
  - adjust behaviour to maximize energy gain per unit time
  - depends on environment (uniform versus patchy)
- Partial explanation of foraging because it does not take into account confounding factors (e.g., avoiding becoming food for another animal).

Optimal foraging

- “The basic procedure for determining optimal utilization of time or energy budgets is very simple: **an activity should be enlarged as long as the resulting gain in time spent per unit food exceeds the loss.** When any further enlargement would entail a greater loss than gain, no such enlargement should take place. **The problem is to find which components of a time or energy budget increase and which decrease as certain activities are enlarged**.”

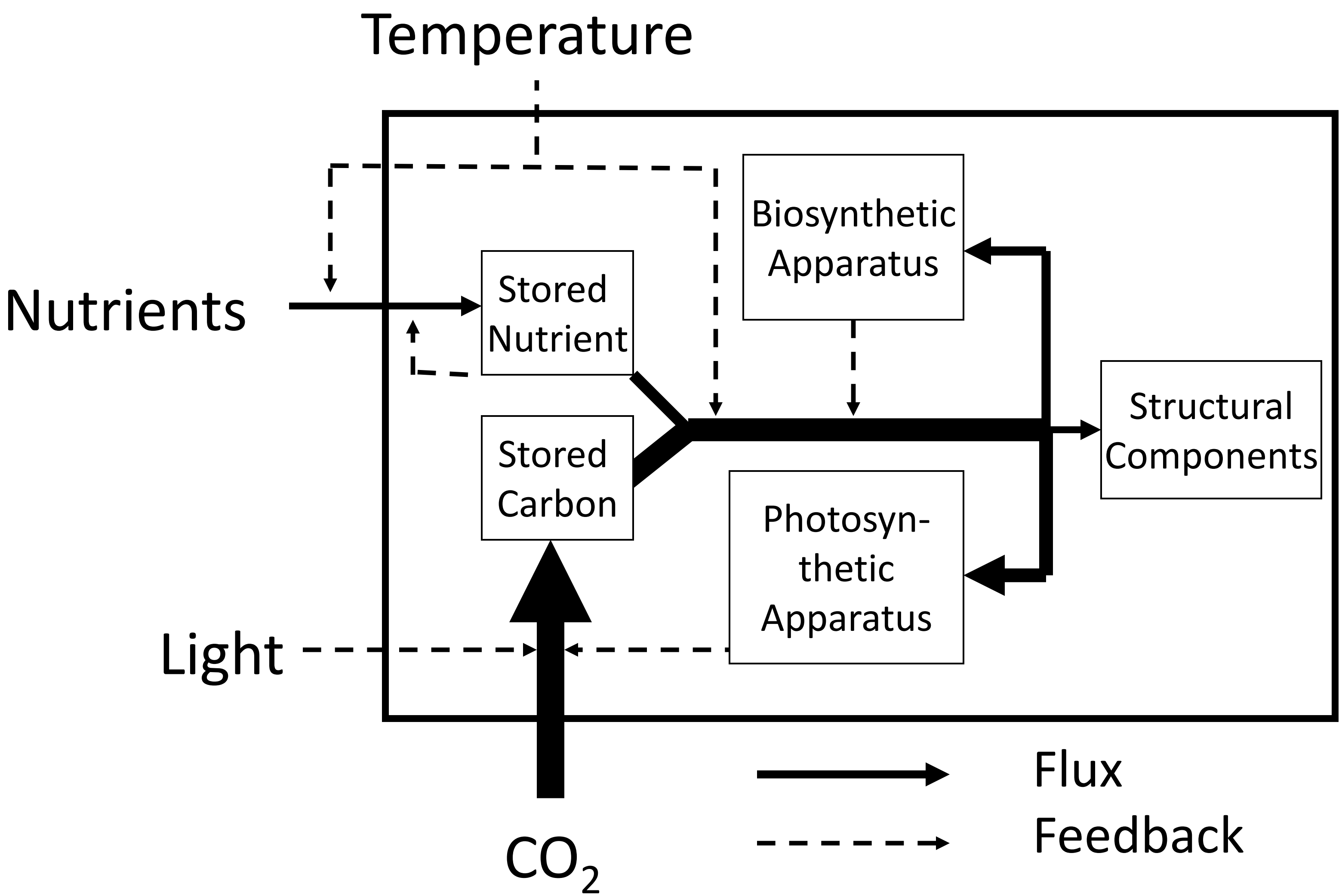
- MacArthur, R. H. and Pianka, E. R. (1966). On the optimal use of a patchy environment. American Naturalist, 100: 603-609

Optimal N (P, C) allocation in algae

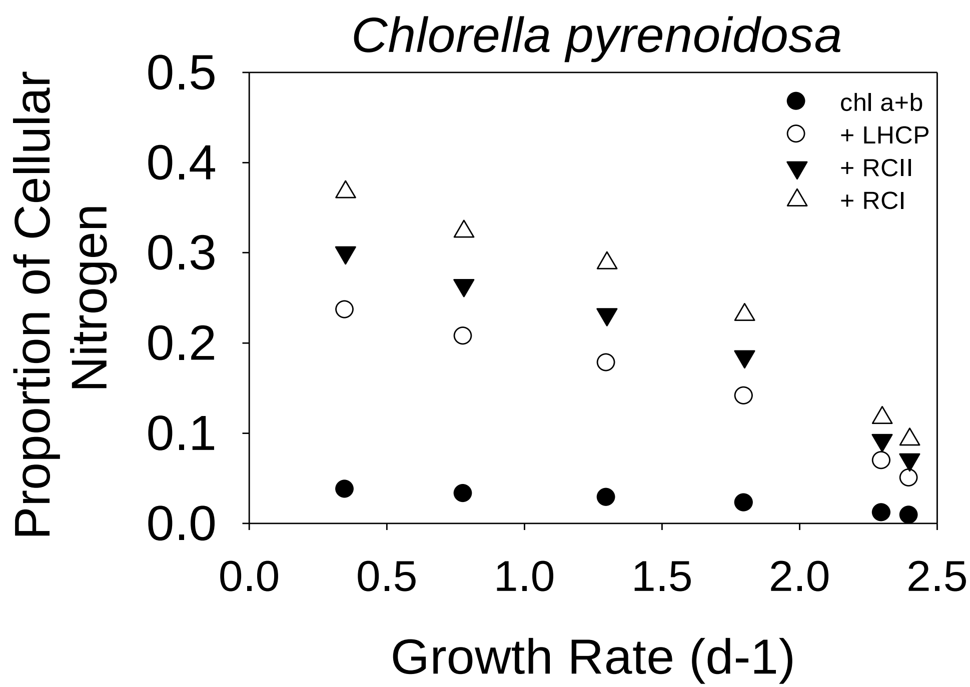
- Algae allocate N (P, C) in such a manner as to maximize net growth rate.
- Requires quantitative descriptions of costs and benefits of various traits so that optimal combination can be predicted.

- Armstrong RA. 2006. Optimality-based modelling of nitrogen allocation and photoacclimation in photosynthesis. Deep-Sea Research II 53:513–531
- Pahlow & Oschlies (2009) Chain model of phytoplankton P, N and light colimitation. Mar. Ecol. Prog. Ser. 376: 69-83

Shuter, B (1979) A model of physiological adaptation in unicellular algae. *J. Theor. Biol. 78: 519-5521*



Nitrogen Allocation to Light Harvesting under nutrient-replete growth



Low Light ---------- High LIght

Based on data of Myers J., Graham J-R. 1971. The photosynthetic unit in Chlorella measured by repetitive short flashes. Plant Physiology 48:282-286

Design Criteria for the Photosynthetic Apparatus (Raven 1980)

- **catalytic efficiency** defined as "the work output per unit of catalytic and structural material used,"
- **energetic efficiency** defined as "the intrinsic efficiency of the process, i.e. the ratio of useful work output to energy input," and
- **"safety"** because "otherwise advantageous mechanisms with local or global optimal balance of the first two design features might, in the long term, be too risky."

Optimizing light harvesting

$$\mu = \frac{1}{A}\frac{dA}{dt} = \frac{1}{B}\frac{dB}{dt} = \cdots = \frac{1}{X}\frac{dX}{dt}$$

- Simplest case is nutrient replete balanced growth in constant light
- Maximize μ (s^{-1}) through optimal allocation of N amongst the catalysts that determine the rates of (1) light harvesting, (2) CO_2 fixation (Calvin Cycle), (3) biosynthesis, (4) photodamage and (5) photoprotection.

Definitions

Λ_X = proportion of cellular N allocated to trait X (dimensionless):

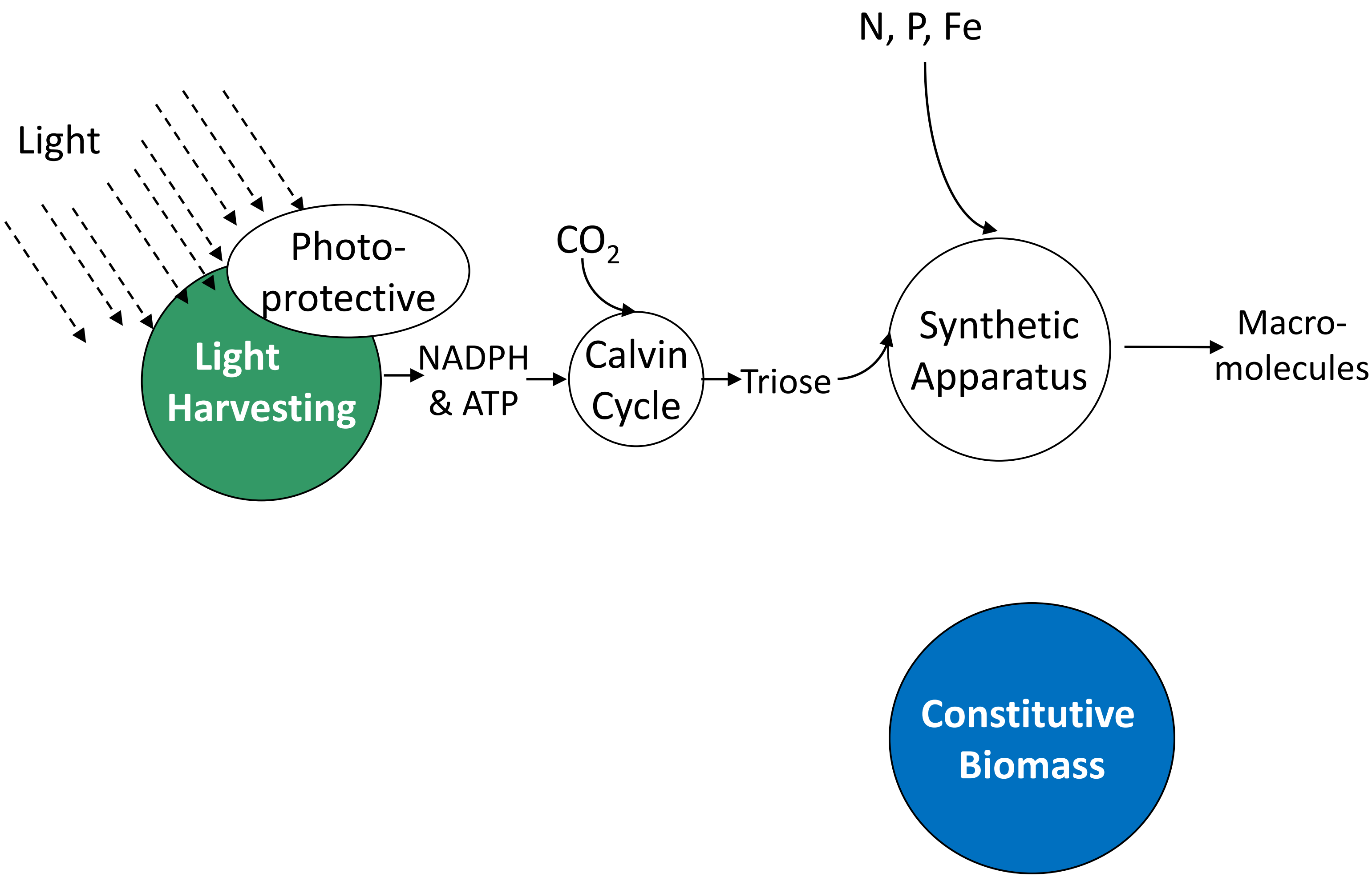
$$0 < \Lambda_X < 1.0$$

$$1.0 = \Sigma \Lambda_X$$

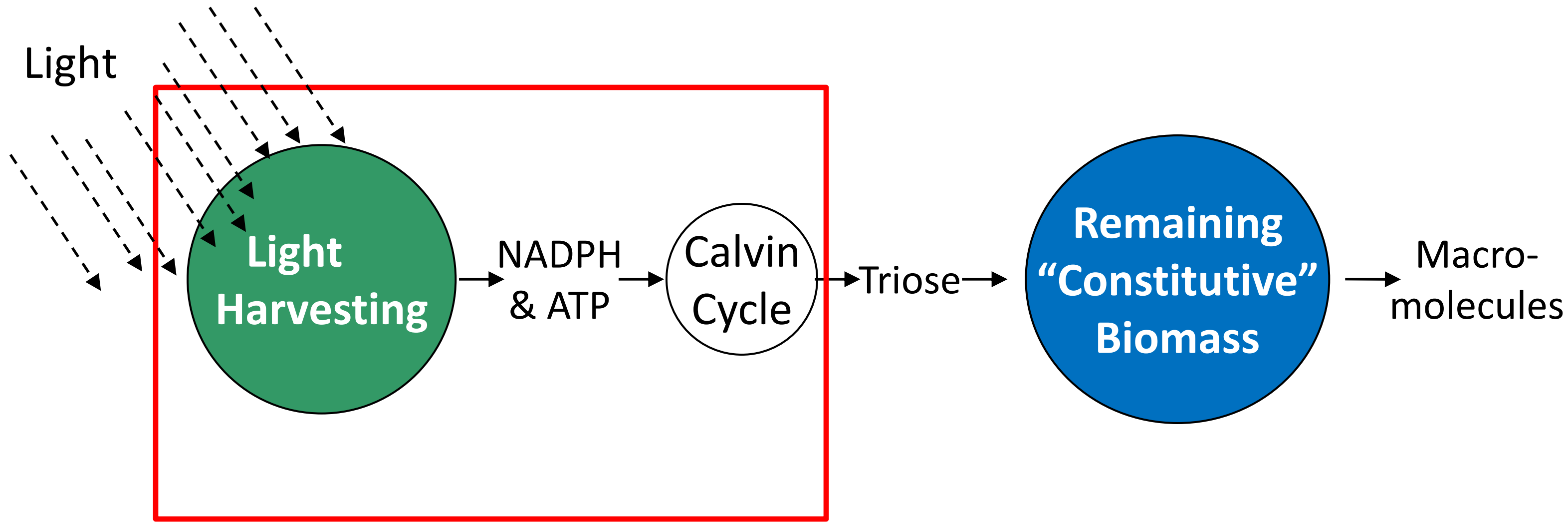
k_X = specific catalytic rate (s^{-1}) or effective cross-section (units of m^2 (μmol photons)$^{-1}$) of component X

Trait	Proportion of Cellular N	“Rate” Constant	Dimensions of k_X
Light Harvesting	Λ_{LH}	k_{LH}	m^2 (μmol photons)$^{-1}$
CO_2 fixation	Λ_{CC}	k_{CC}	s^{-1}
Biosynthesis	Λ_{SYN}	k_{SYN}	s^{-1}
Photodamage	Λ_{LH}	k_D	m^2 (μmol photons)$^{-1}$
Photoprotection	Λ_{PP}	k_{PP}	s^{-1}
“Constitutive”	Λ_{CON}		

Mass balance within and energy/mass flows through algal cells.

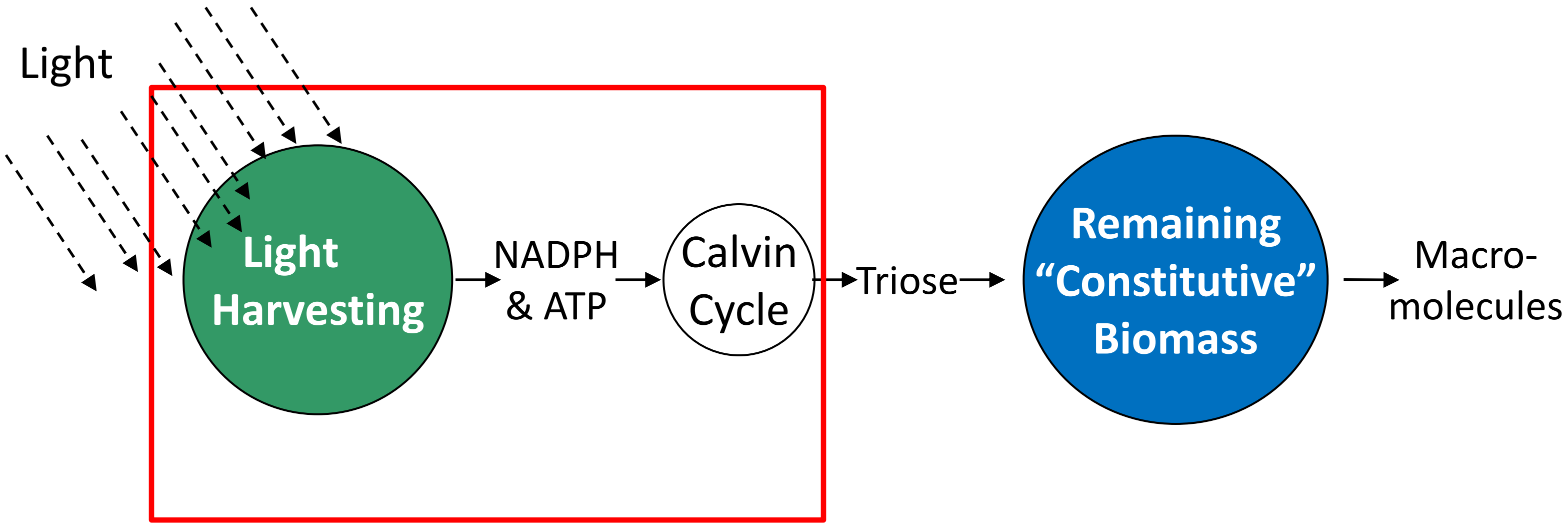


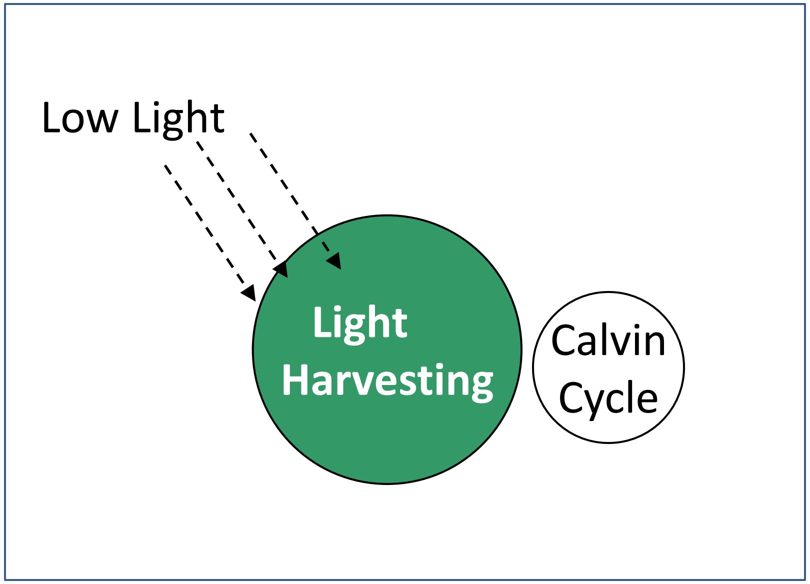
Trade off between Light Harvesting and CO_2 fixation

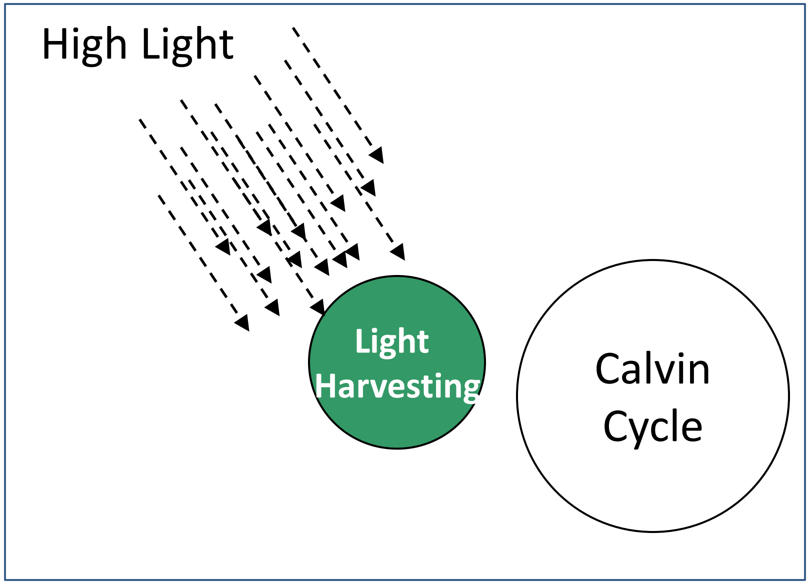


$$1.0 = \Lambda_{LH} + \Lambda_{CC} + \Lambda_{CON}$$

Trade off between Light Harvesting and CO_2 fixation







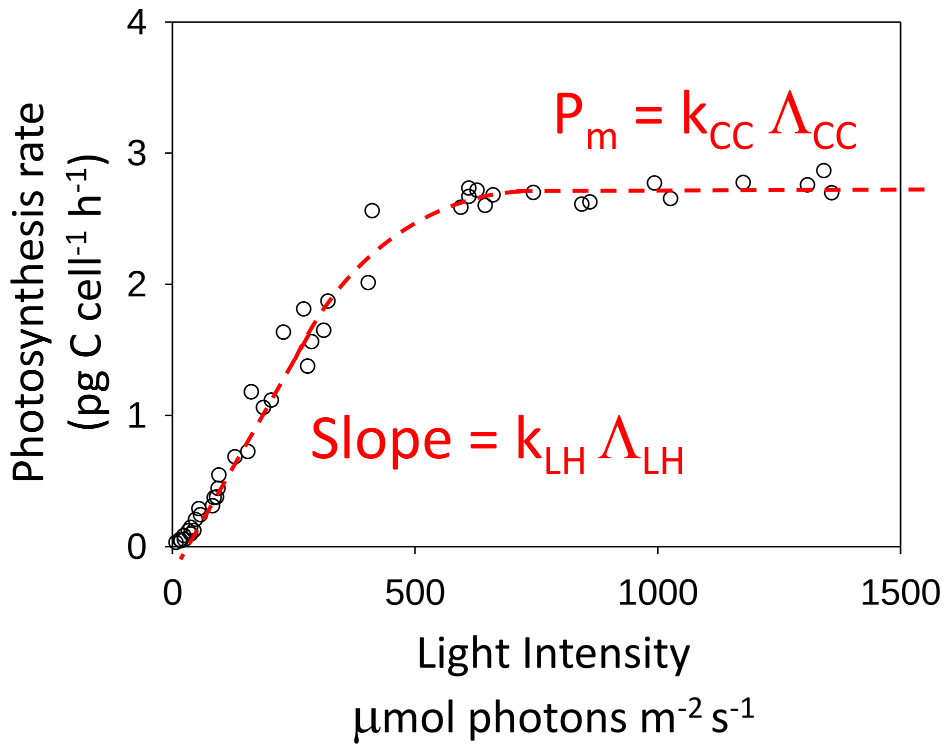
Trade off between Light Harvesting and CO_2 fixation

$$P = P_m \cdot \left(1 - \exp\left(\frac{-E}{E_K}\right)\right)$$

$$P_m = k_{CC} \cdot \Lambda_{CC}$$

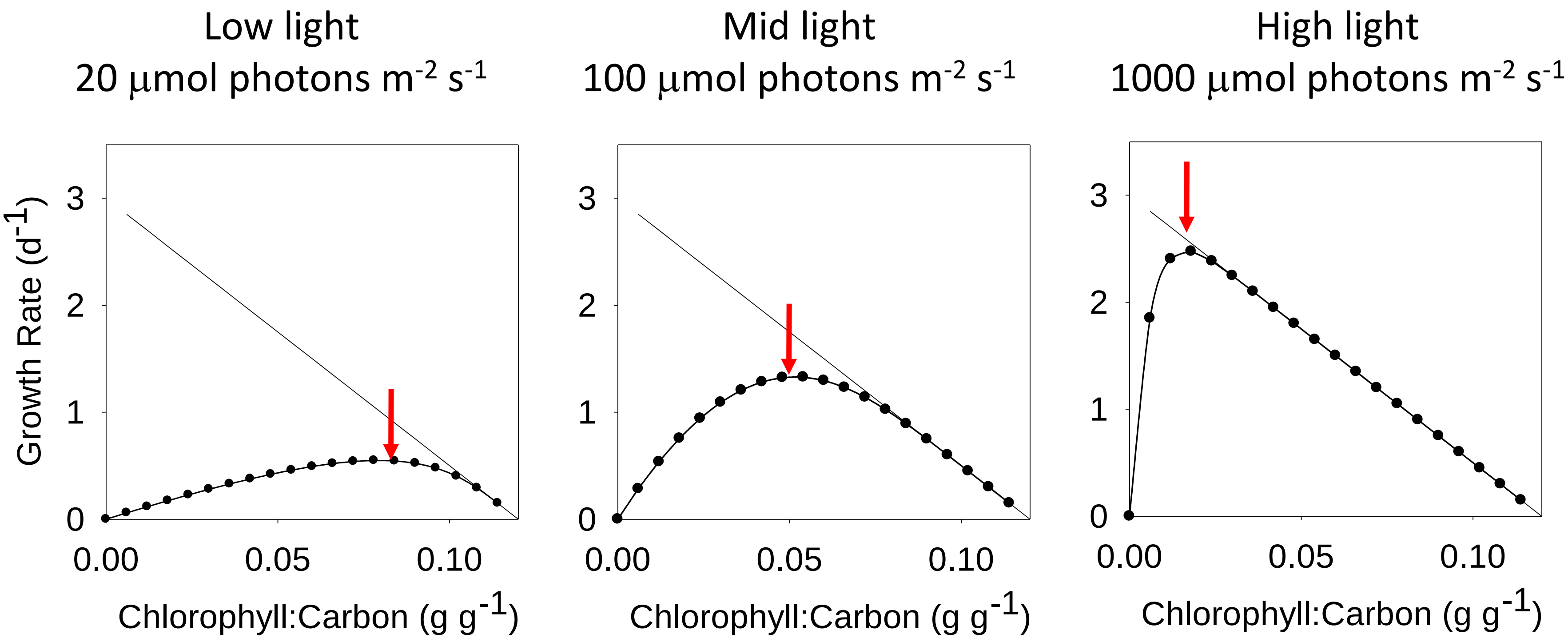
$$E_K = \frac{k_{CC} \cdot \Lambda_{CC}}{k_{LH} \cdot \Lambda_{LH}}$$

$$\mu = P - R$$



Data for high-light acclimated *Skeletonema costatum*. Anning et al. (2000) Limnology & Oceanography 45: 1807-1817

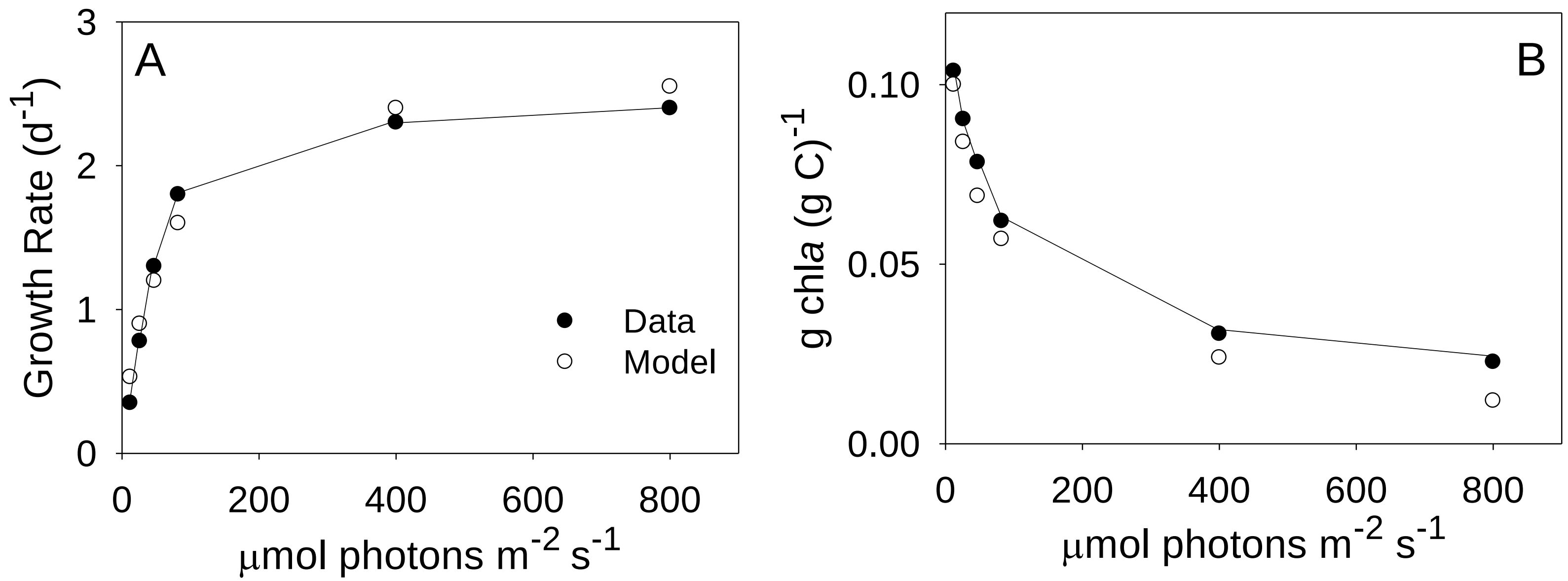
Trade off between Light Harvesting and CO_2 fixation



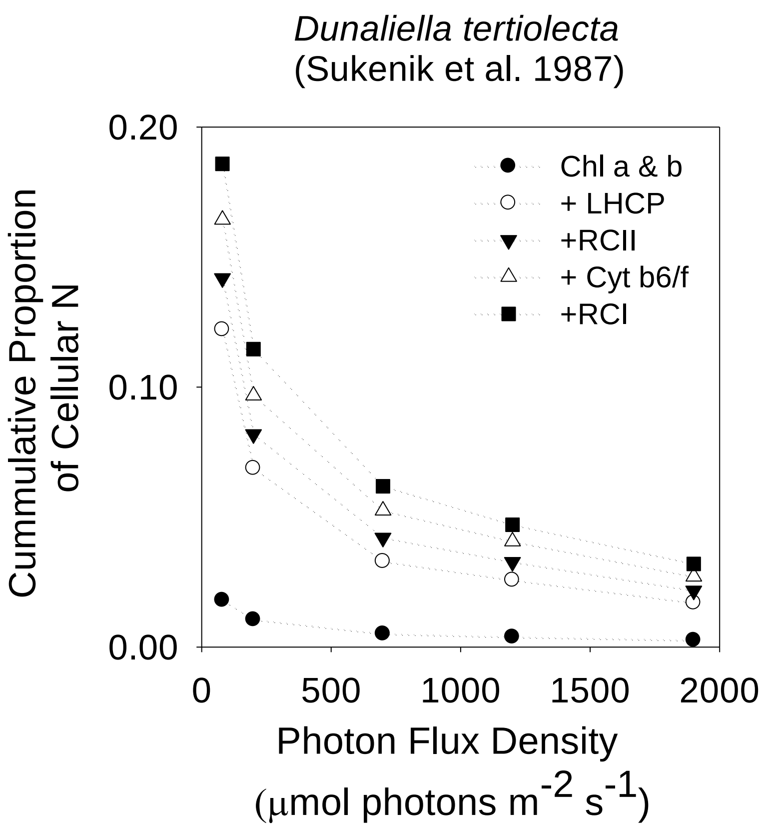
$$\Lambda_{LH} = \chi_{Chl}\,[Chl:C]$$

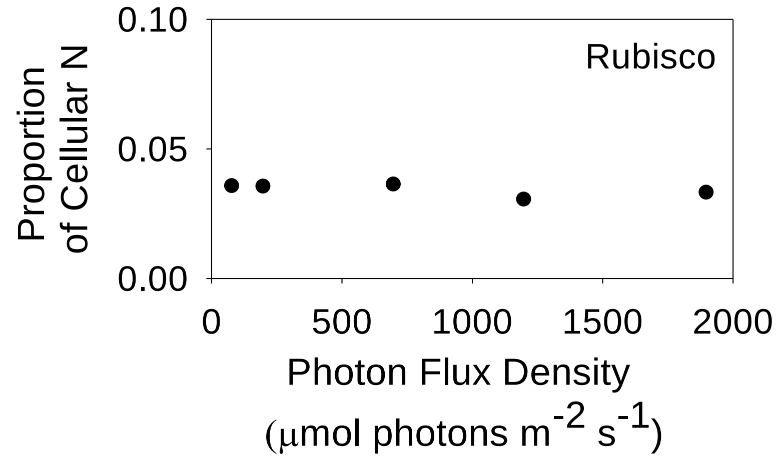
Geider R.J., Moore, C.M., Ross, O.N. (2009) "The role of cost-benefit analysis in models of phytoplankton growth and acclimation." Plant Ecology and Diversity 2: 165-178.

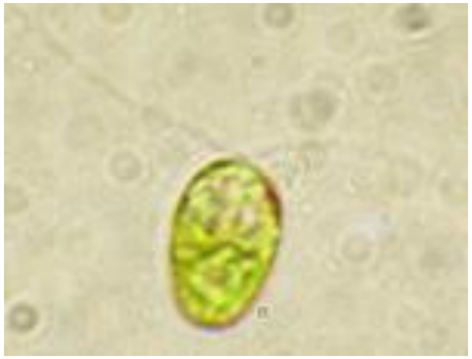
Trade off between Light Harvesting and CO_2 fixation



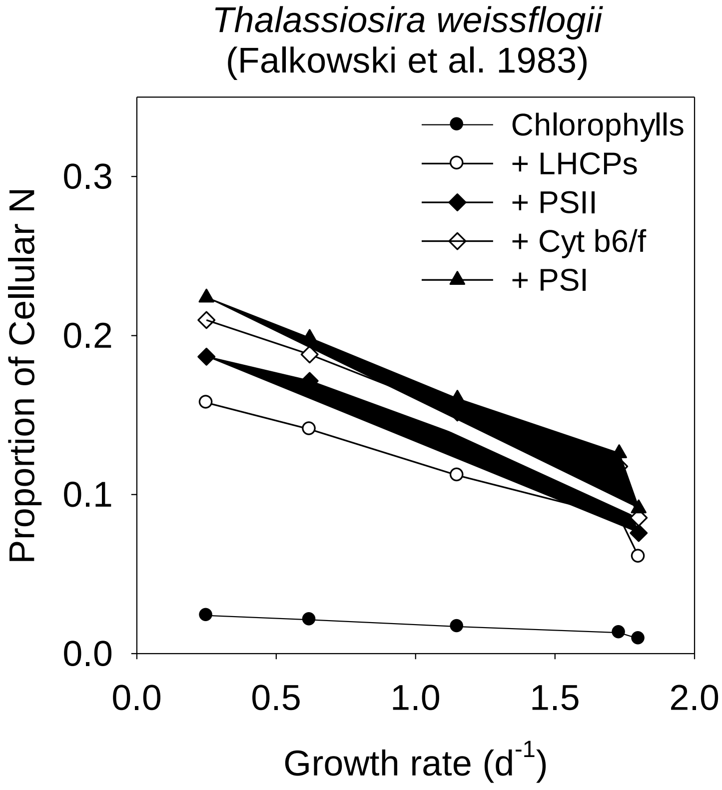
Trade off between Light Harvesting and CO_2 fixation?

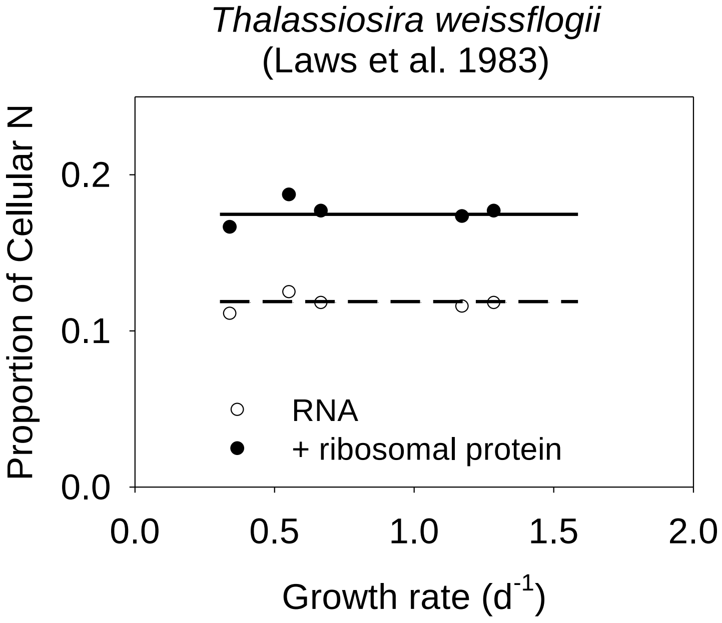




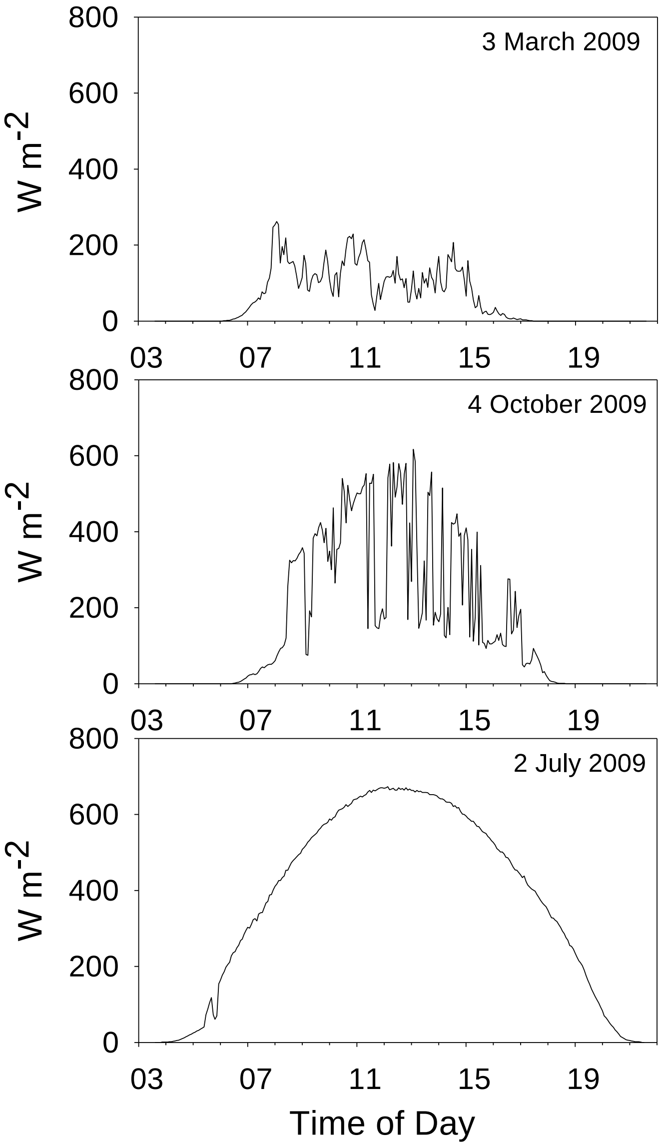


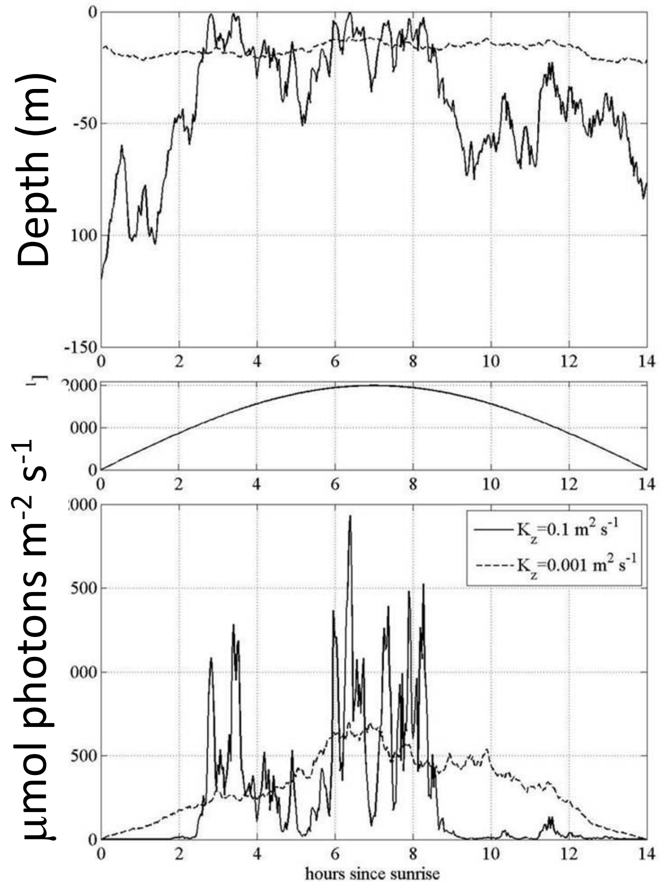
Trade off between Light Harvesting and Biosynthesis?





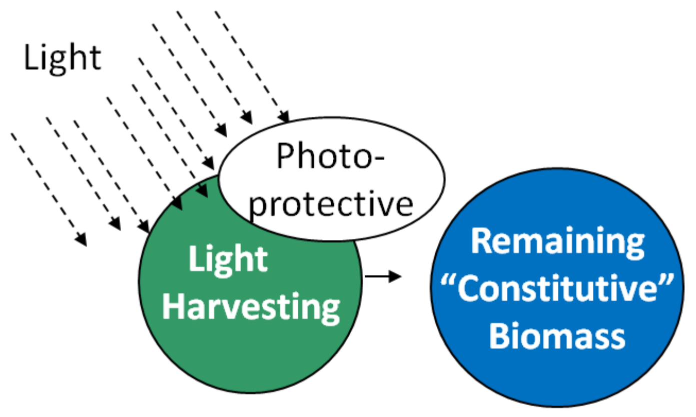
Between day and within day variability of solar radiation





Mixing through a light gradient

Trade off between Light Harvesting and Photoprotection



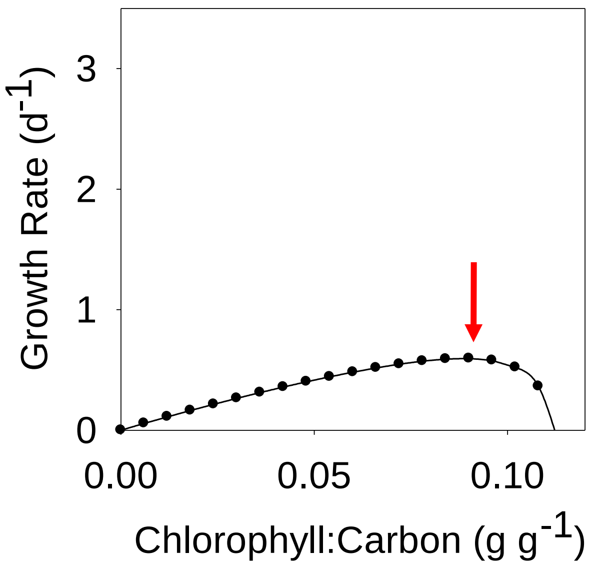
- Light harvesting has both benefits and costs.
- Increased photosynthesis at low light.
- Photo-oxidative damage at high light.

$$\mu = P_m^C \cdot \left(1 - \exp\left(\frac{-E}{E_K}\right)\right) - \frac{k_D \cdot \Lambda_{LH} \cdot E}{k_{PP} \cdot \Lambda_{PP}}$$

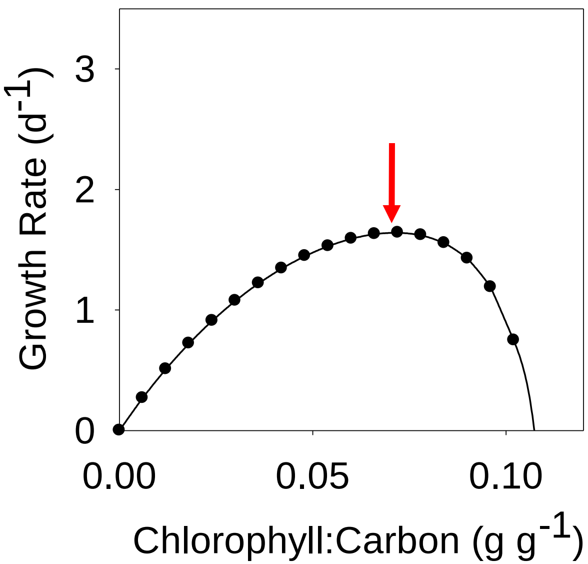
$$E_K = \frac{P_m}{f_{LH} \cdot k_{LH} \cdot \Lambda_{LH}}$$

Trade off between Light Harvesting and Photoprotection

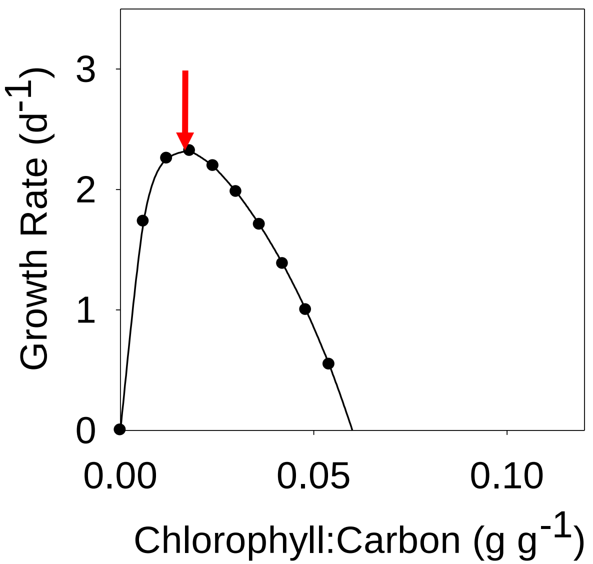
Low light
20 μmol photons m^{-2} s^{-1}



Mid light
100 μmol photons m^{-2} s^{-1}

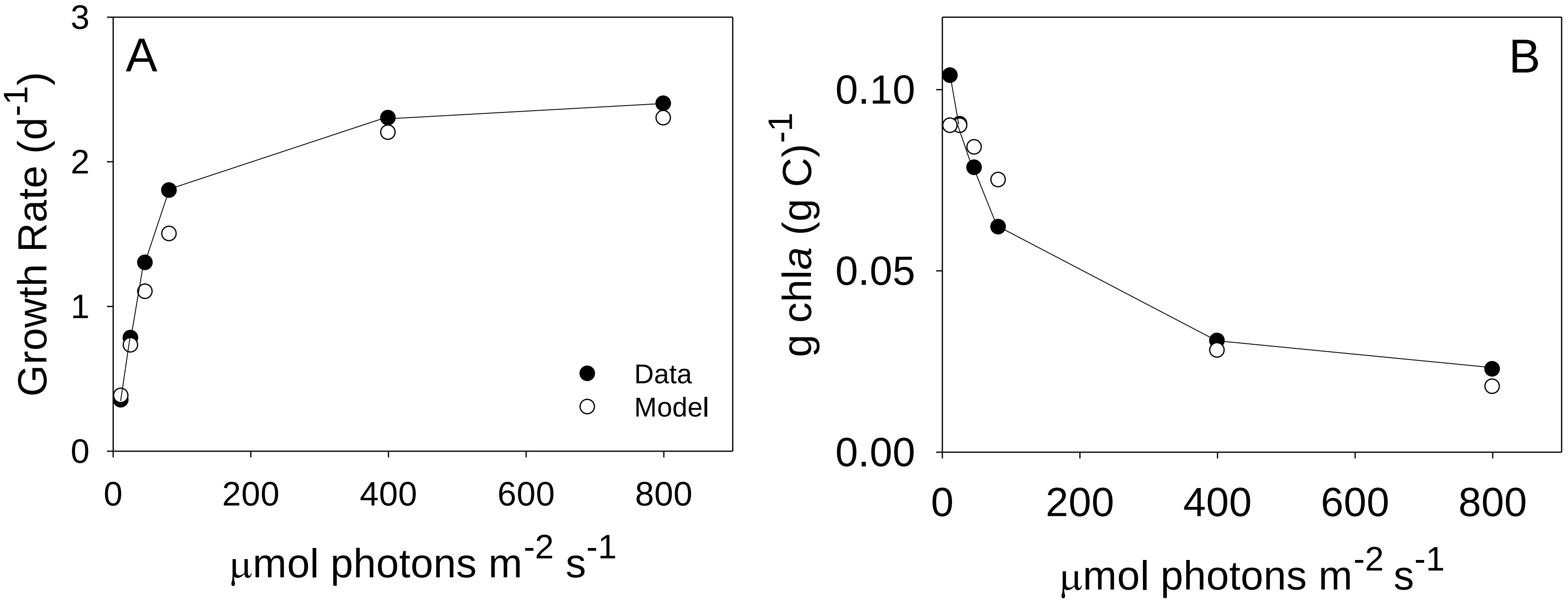


High light
1000 μmol photons m^{-2} s^{-1}

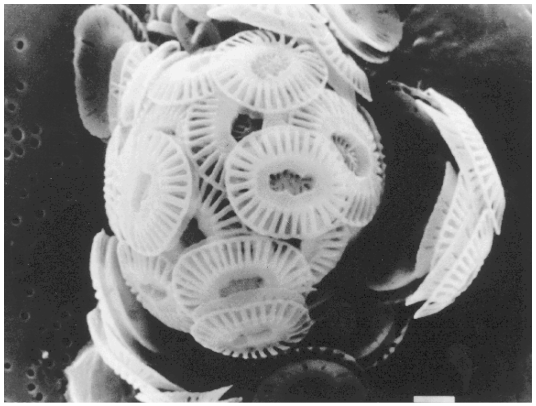


$$\Lambda_{LH} = \chi_{Chl}\ [Chl:C]$$

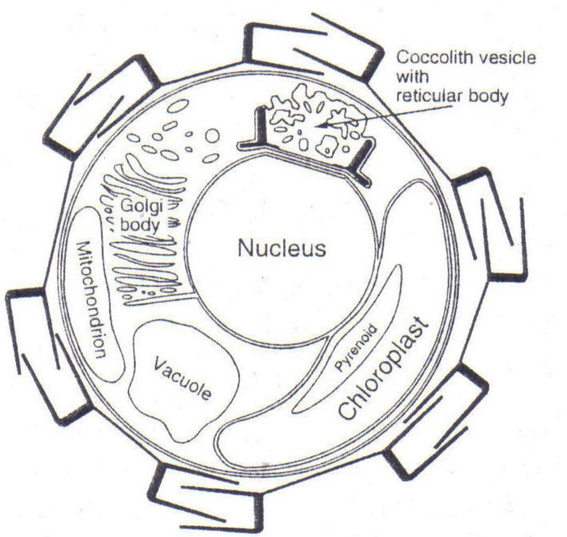
Trade off between Light Harvesting and Photoprotection

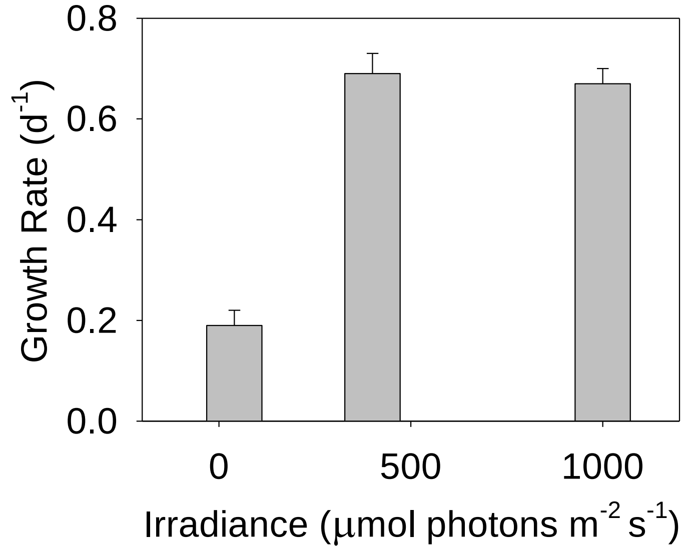


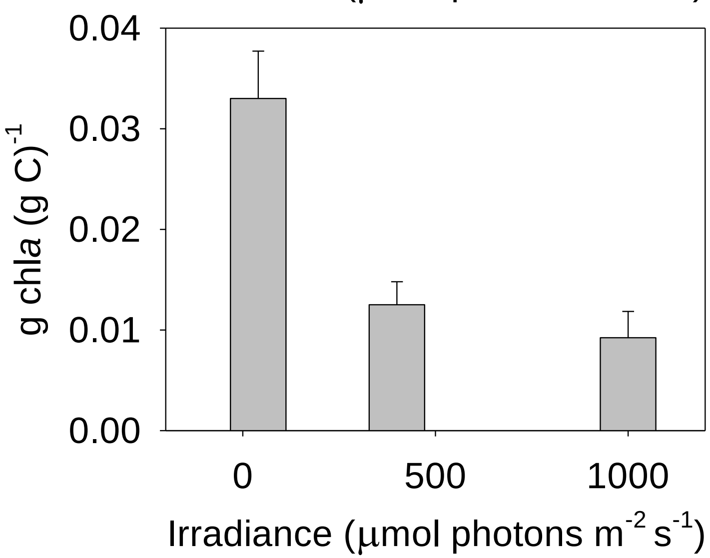
Acclimation of the proteome of *Emiliania huxleyi* 1516



(http://www.soes.soton.ac.uk/staff/tt/eh/cellpics.html)







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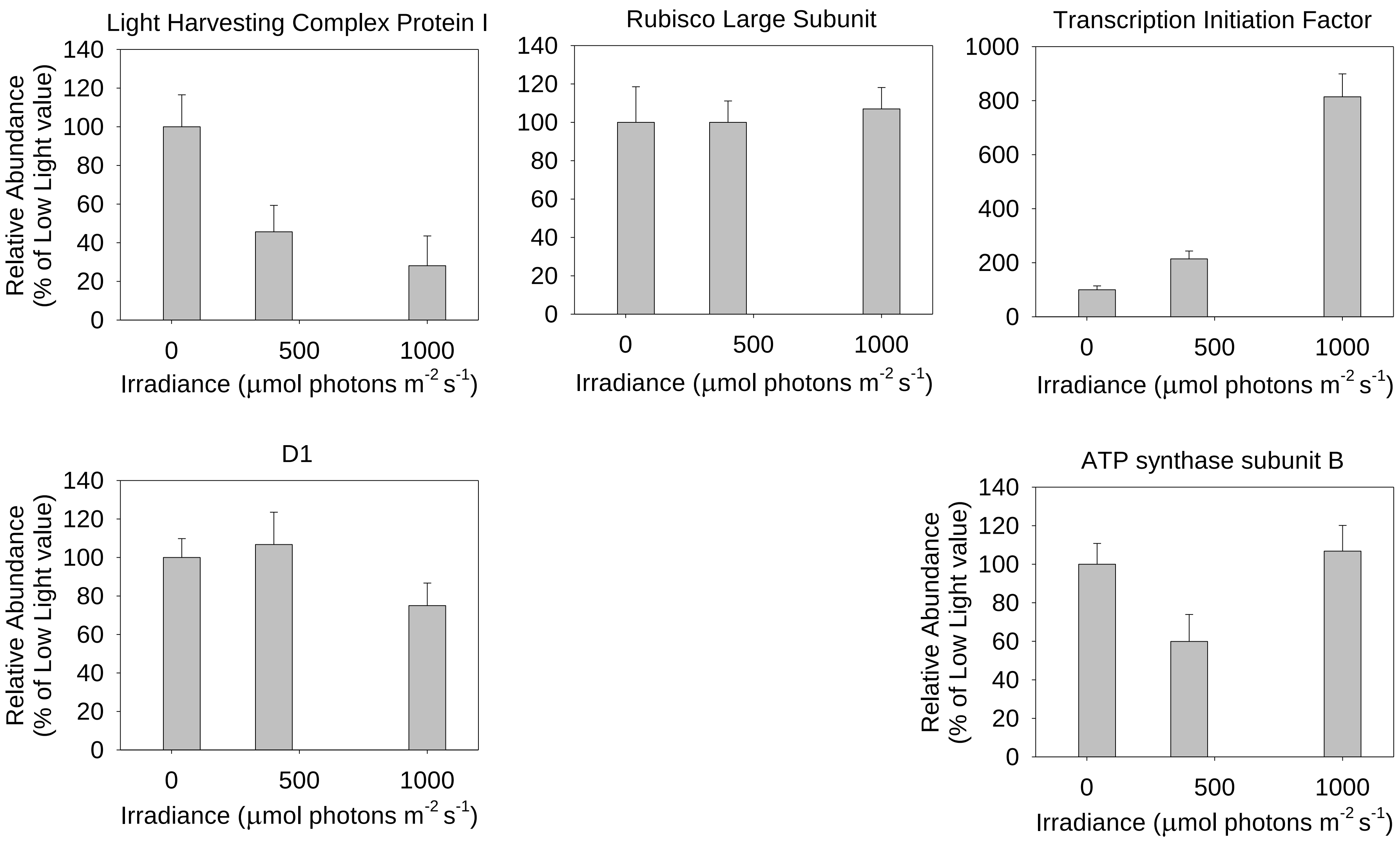


Where are we now?

We know there are known knowns:
there are things we know we know.

We also know there are known unknowns: that is to say we know there are things we know we don't know.

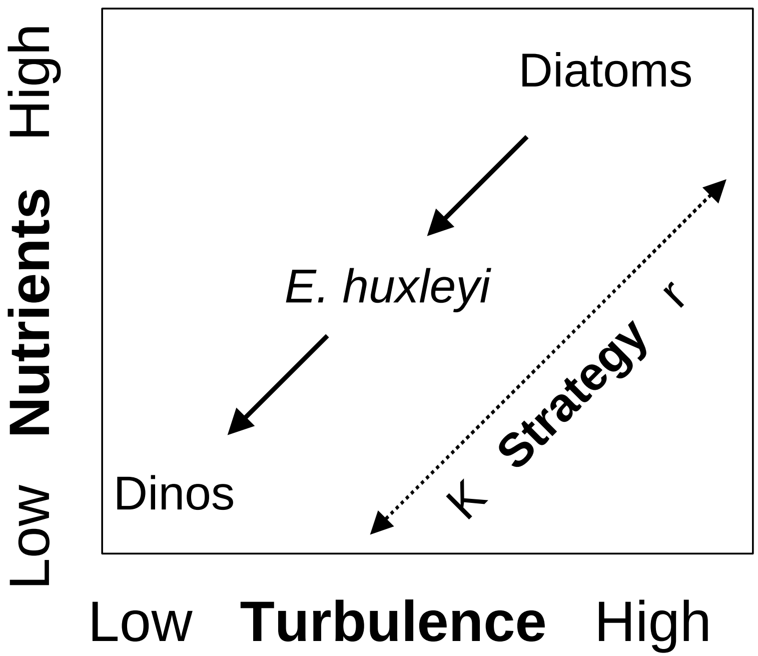
But there are also unknown unknowns - the ones we don't know we don't know."

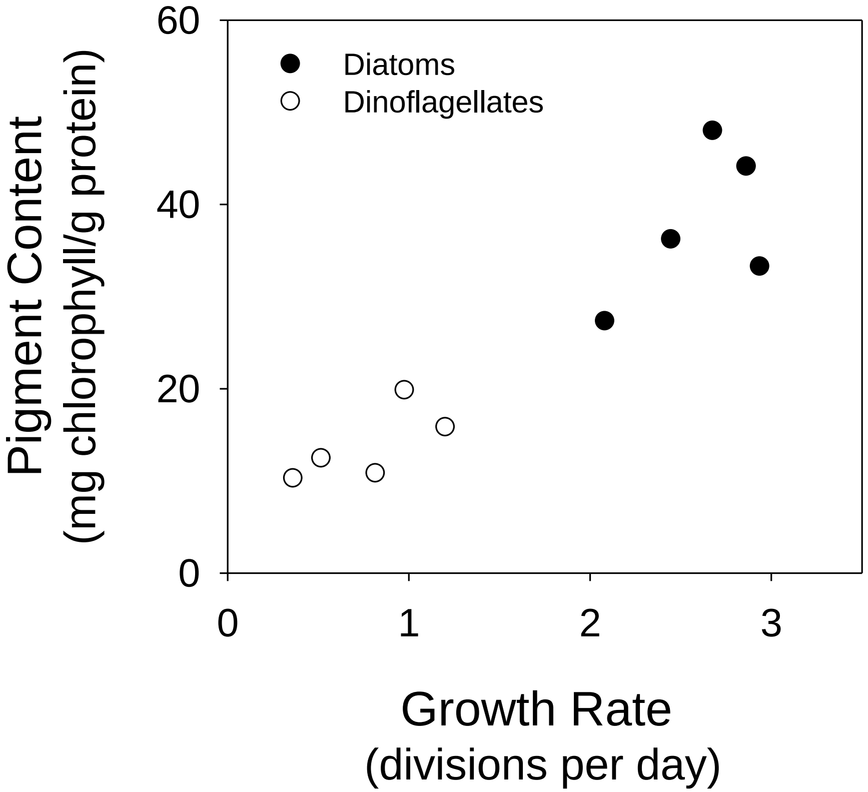
Donald Rumsfeld
U.S. Defense Secretary (1975-1977, 2001-2006)

Selection operates on evolutionary time scales

- Evolution favours organisms with the optimal combination of traits that maximizes evolutionary fitness.
- Evolutionary fitness = proportion an the individual's genes in all the genes of the next generation.
- Constraints imposed by evolution affect physiological trade-offs.

Evolutionary Constraint
(Adaptation)





Source: Chan (1978) Journal of Phycology 14: 396-402

Categories of costs

- **capital costs** of the structural and functional components of the cell,
- **running costs** of CO_2 fixation, nutrient acquisition, biosynthesis and repair,
- **opportunity costs** for exploiting variability in the environment,
- **taxes** imposed by losses associated with transport to unfavourable environments, grazers and parasites

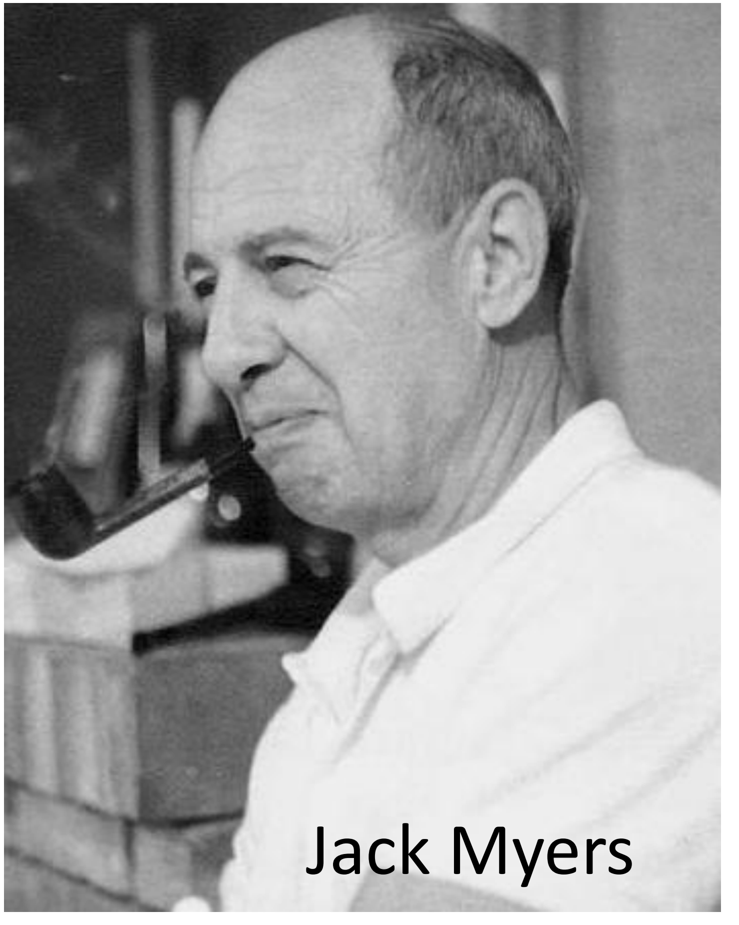
The essential principle & challenge of algal physiology.

"algae are microbes, powered by a photosynthetic metabolism …

they are mostly cell machinery, which goes about its business in synthesis of new cell machinery

they are highly adaptive …
response to an environmental factor depends on past history for that factor …
there is no fixed or static machinery

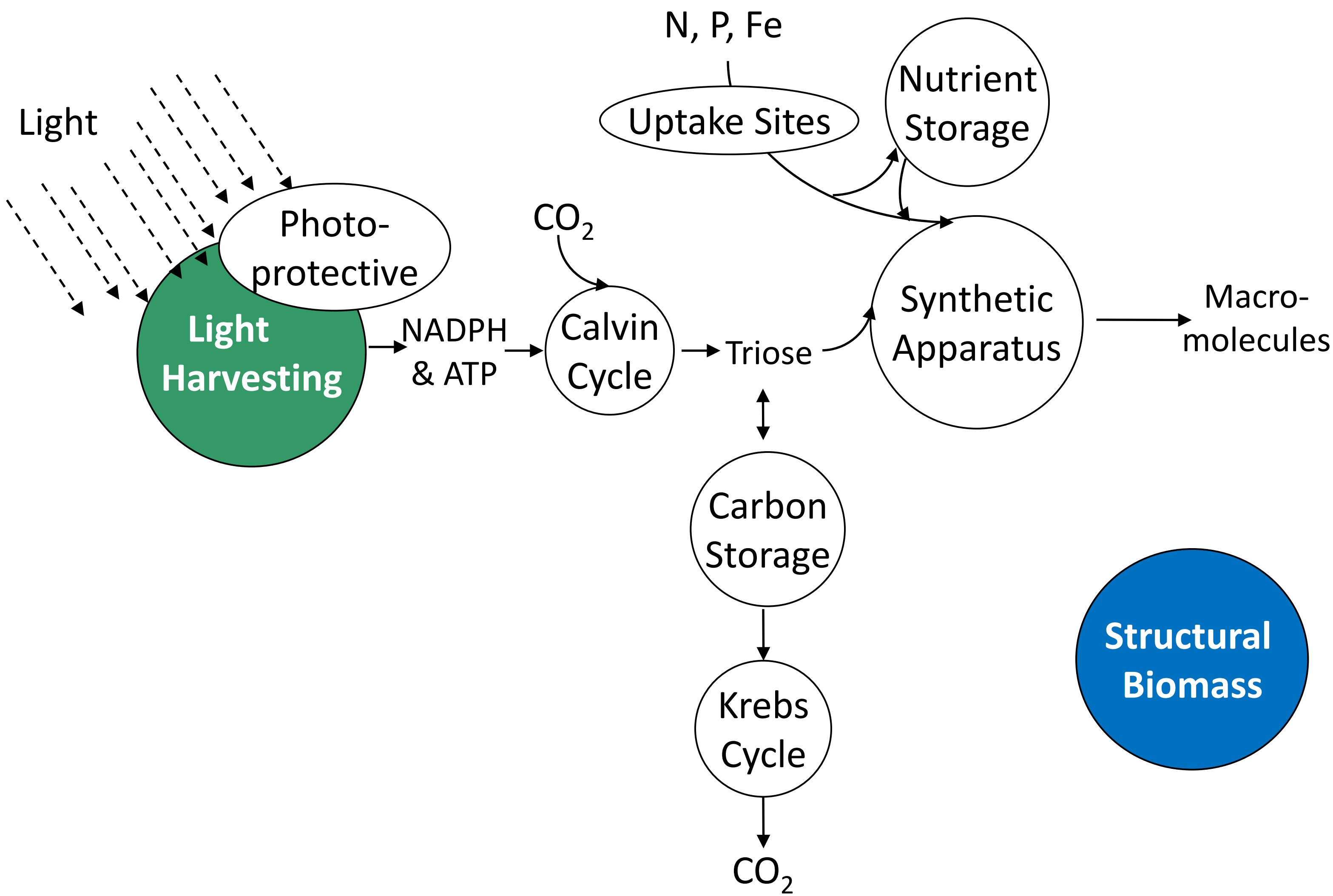
this is the particular challenge of algal physiology"



Jack Myers

(Myers 1980) page 4 in "Primary Productivity in the Sea." Plenum Press.

Generalize model to include nutrient uptake, and energy/nutrient “storage”



Functions

- Structure (maintain integrity and organization)
  - Cell wall, genome, cytoskeleton, membranes
- Metabolism & Growth
  - Light harvesting
  - CO_2 fixation
  - Nutrient assimilation
  - Biosynthesis
  - Cell division
- Homeostasis, Acclimation, Adaptation
  - “optimizing” resource utilization
  - coping with or reducing “stress”
  - coping with/exploiting environmental variability
  - insuring survival

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Mariella Ragni
Christine Raines
David Suggett

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