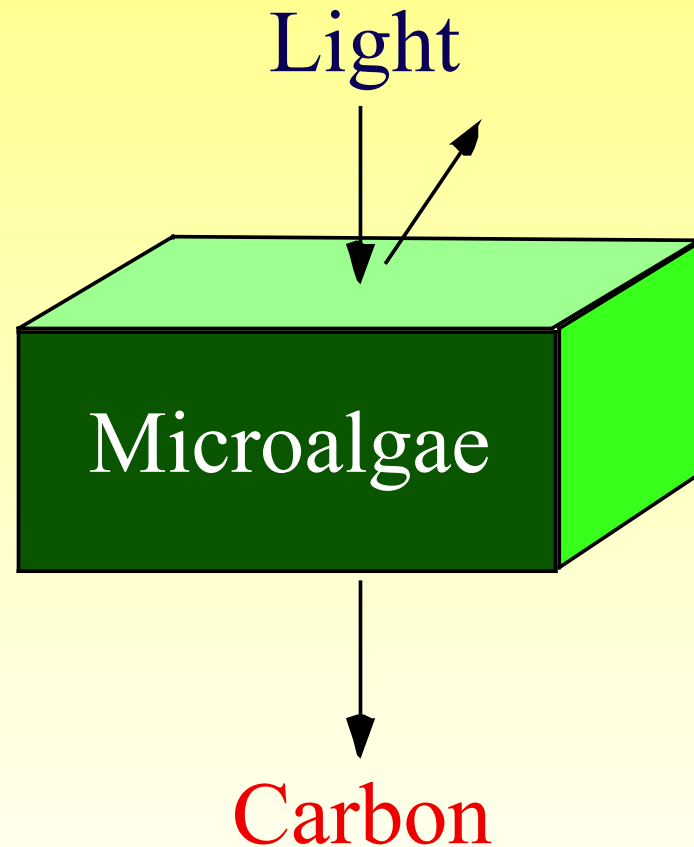


Proximate vs Ultimate Physiological Regulation of Photosynthetic Rates

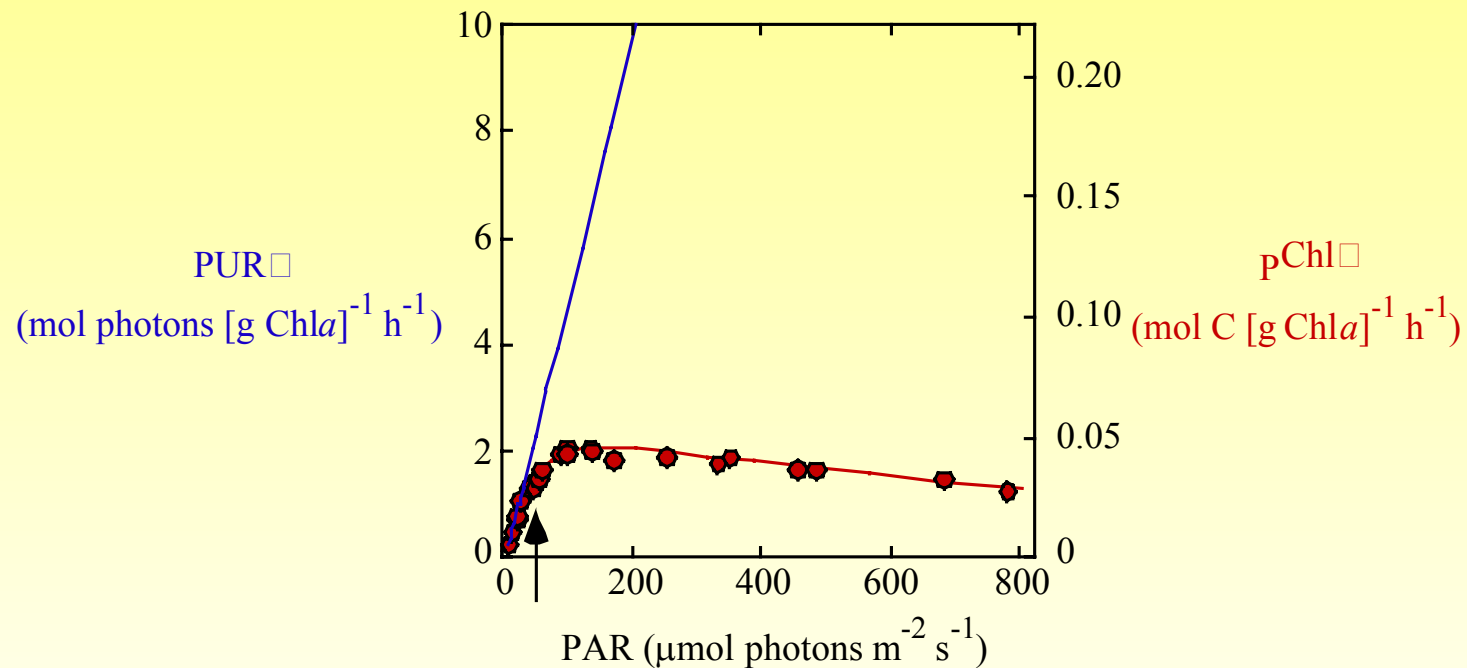


Hugh MacIntyre
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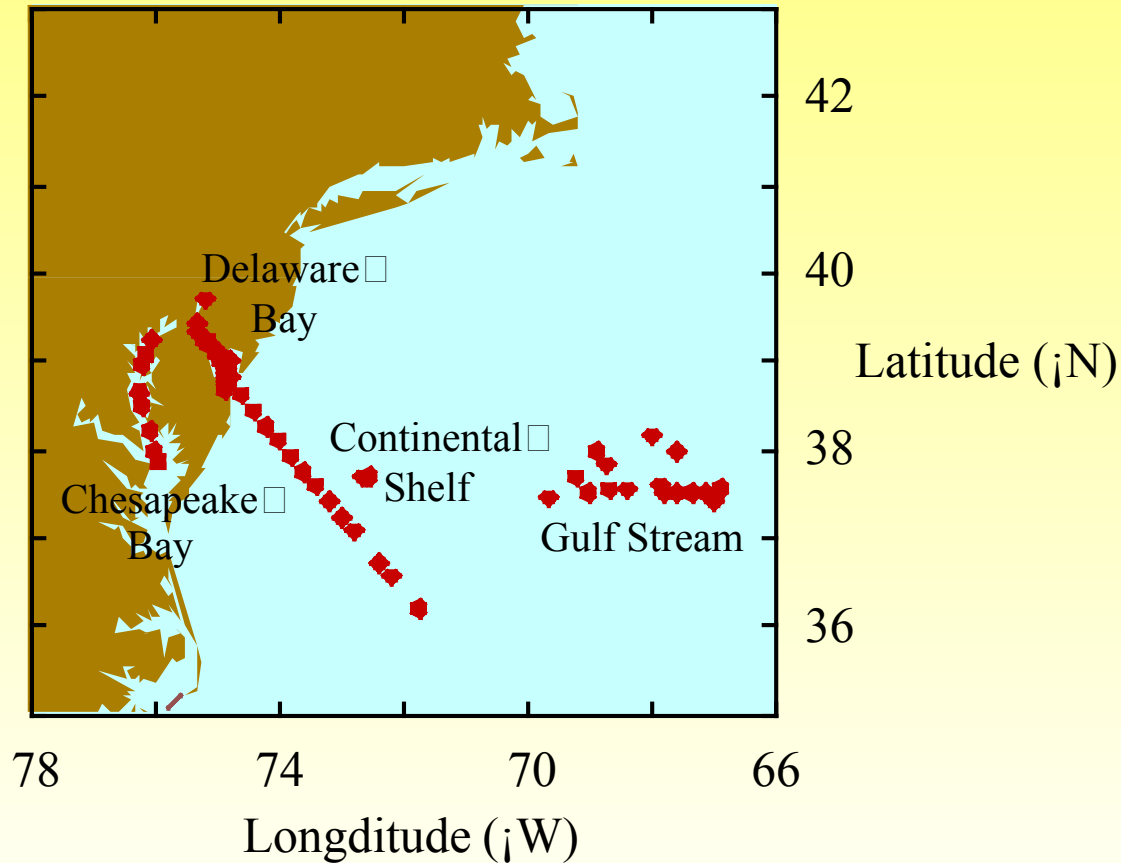
A box model of photosynthesis and light



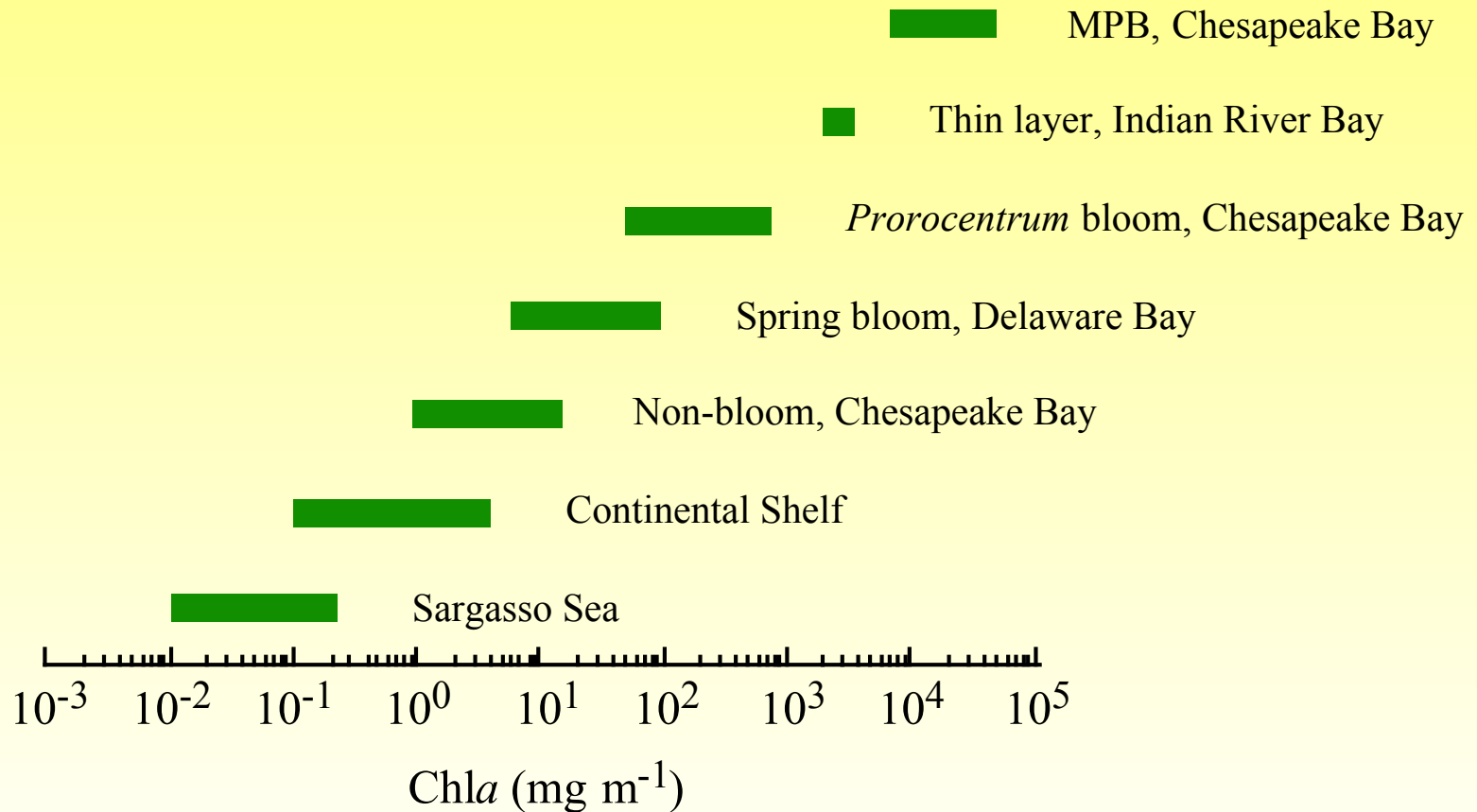
The Photosynthesis-Irradiance-Time response reflects the balance between light absorption and carbon fixation



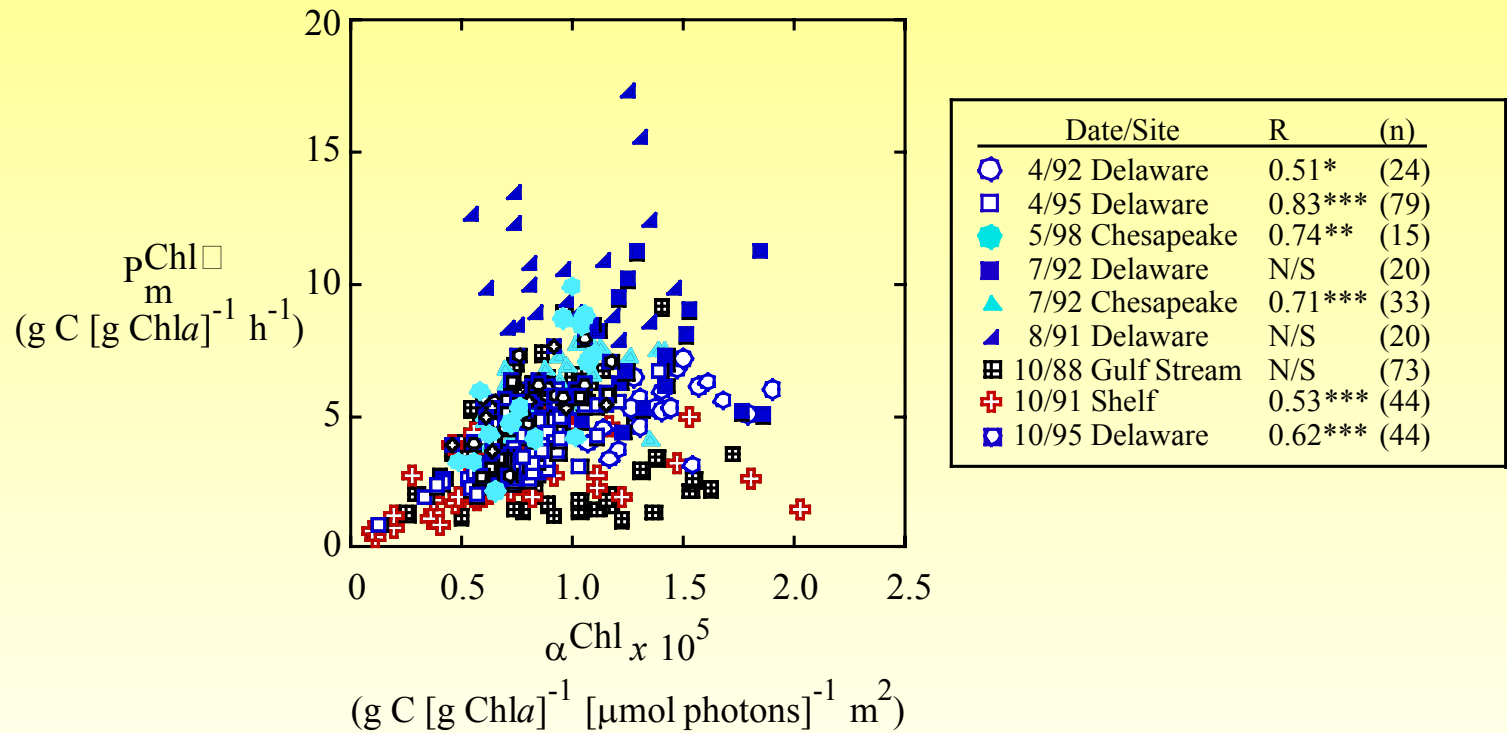
Microalgal biomass and productivity varies on small geographic scales



Biomass varies over wide ranges...

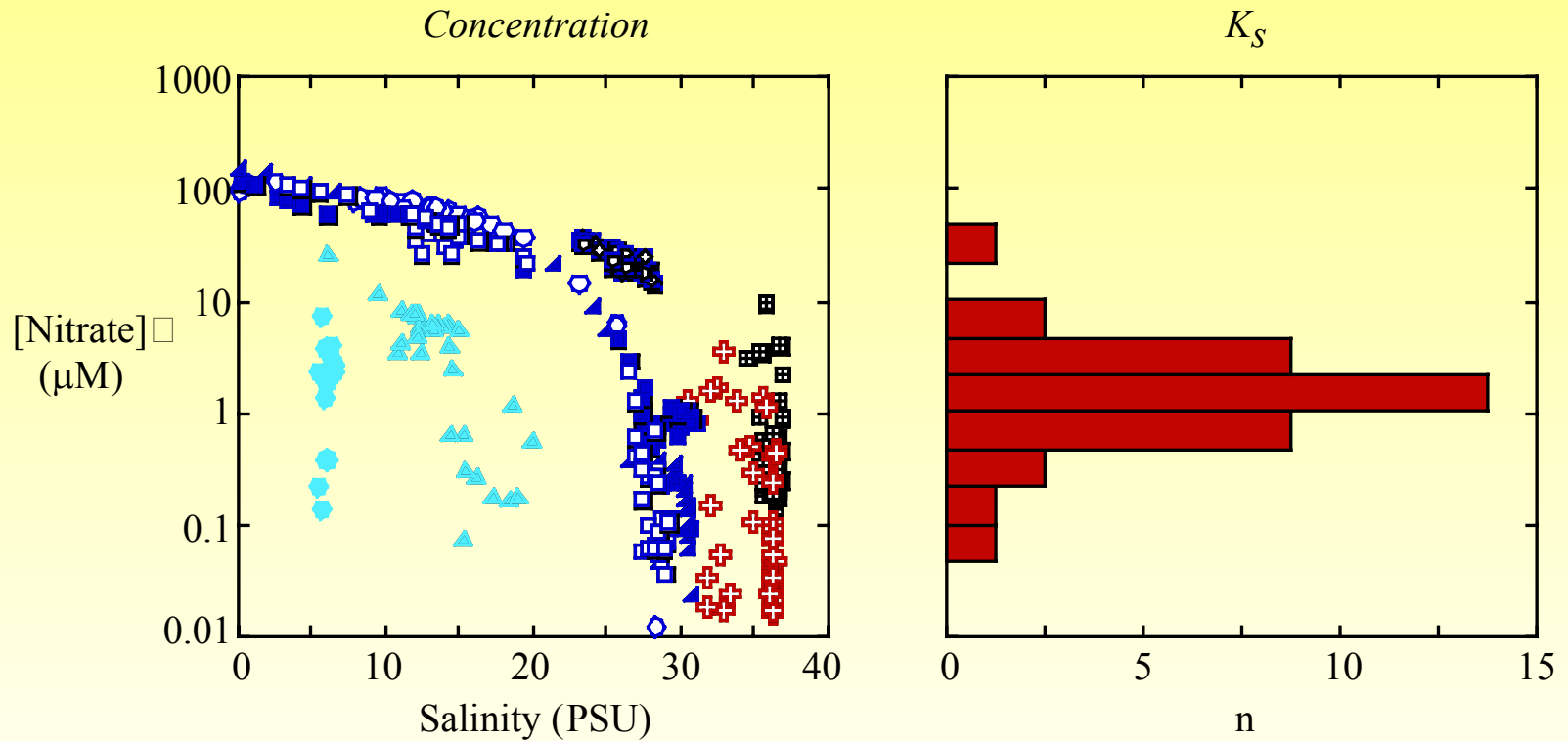


...as does P_{vsE} vs T



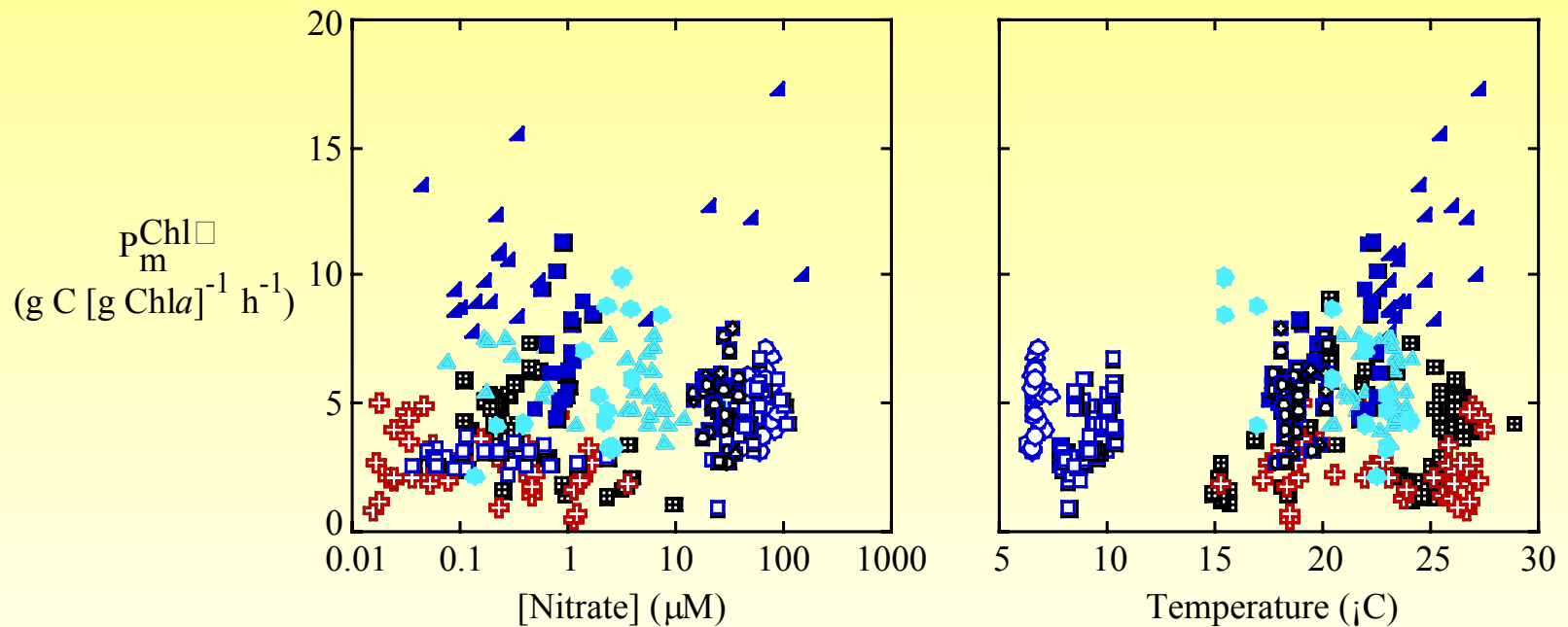
Data: MacIntyre, R.J. Geider, J.J. Cullen & J.E. Adolf (unpubl.)

...and nutrient availability



Data: MacIntyre, R.J. Geider, J.J. Cullen & J.E. Adolf (unpubl.) K_S : Smayda (1997)

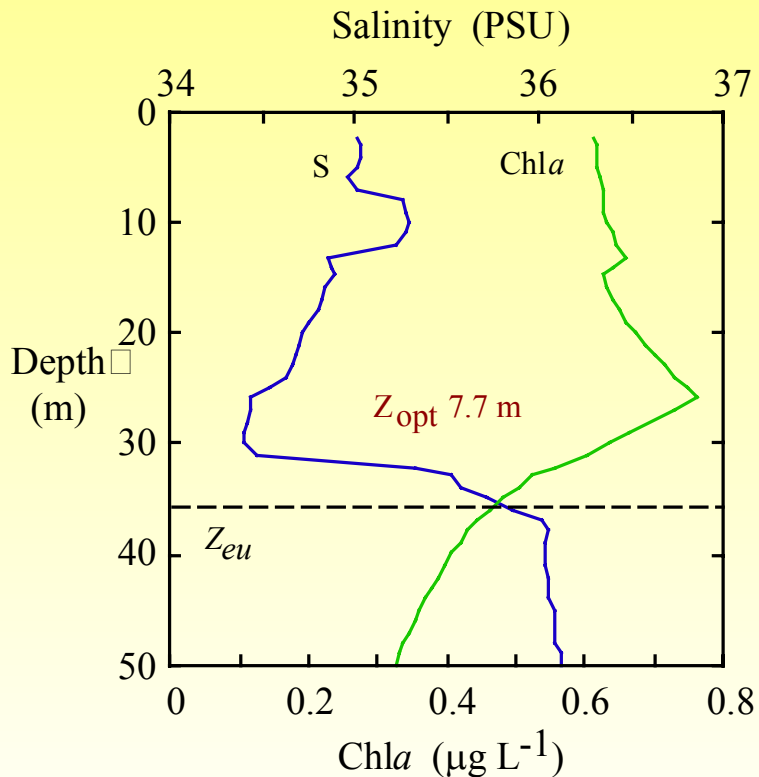
But the variability can rarely be explained by a single factor



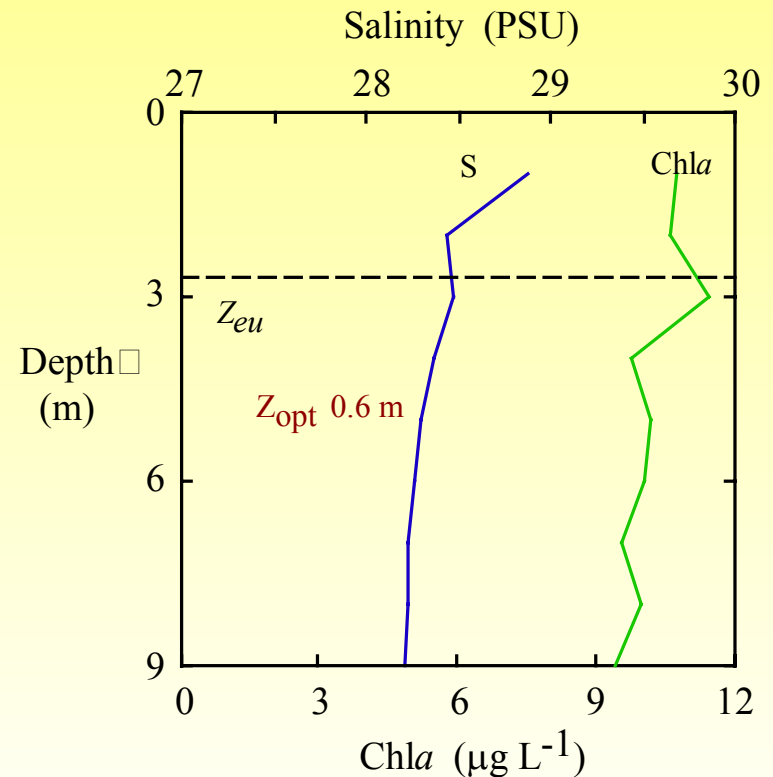
Data: MacIntyre, R.J. Geider, J.J. Cullen & J.E. Adolf (unpubl.)

Differences in clarity and stability in shelf vs estuarine water columns...

Integrated Chla: 22.5 mg m⁻²

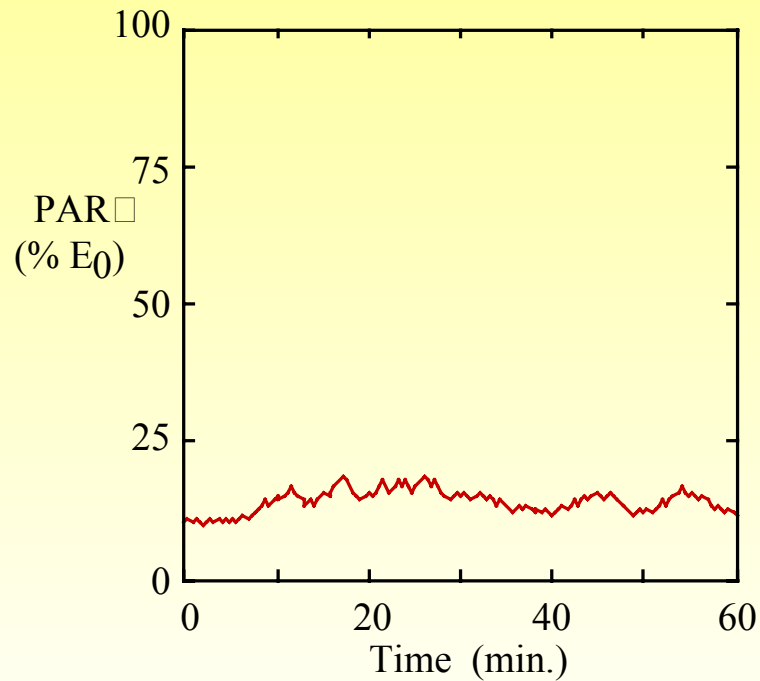


Integrated Chla: c. 29 mg m⁻²

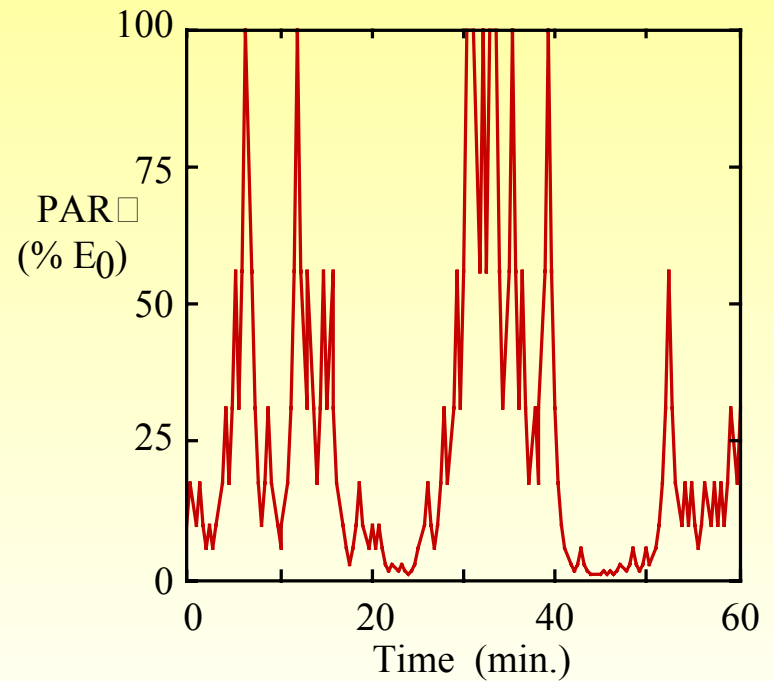


...lead to very different rates of change of irradiance

Continental Shelf

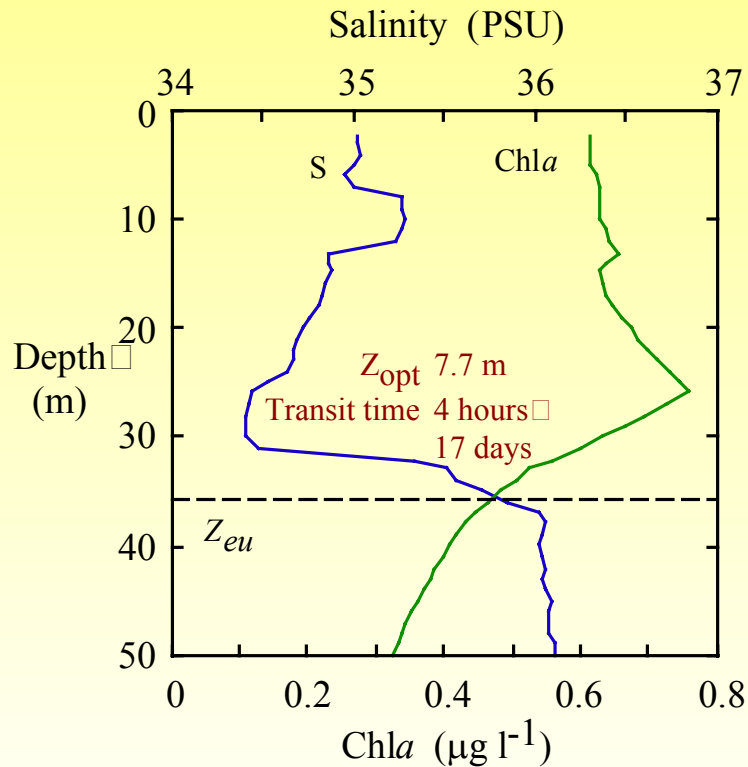


Estuary

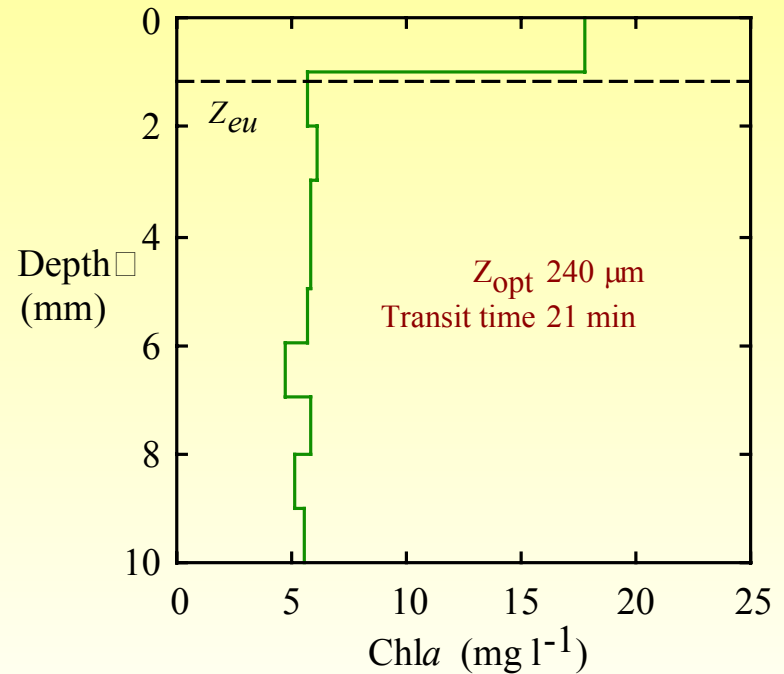


Migration in benthic communities also leads to rapid changes

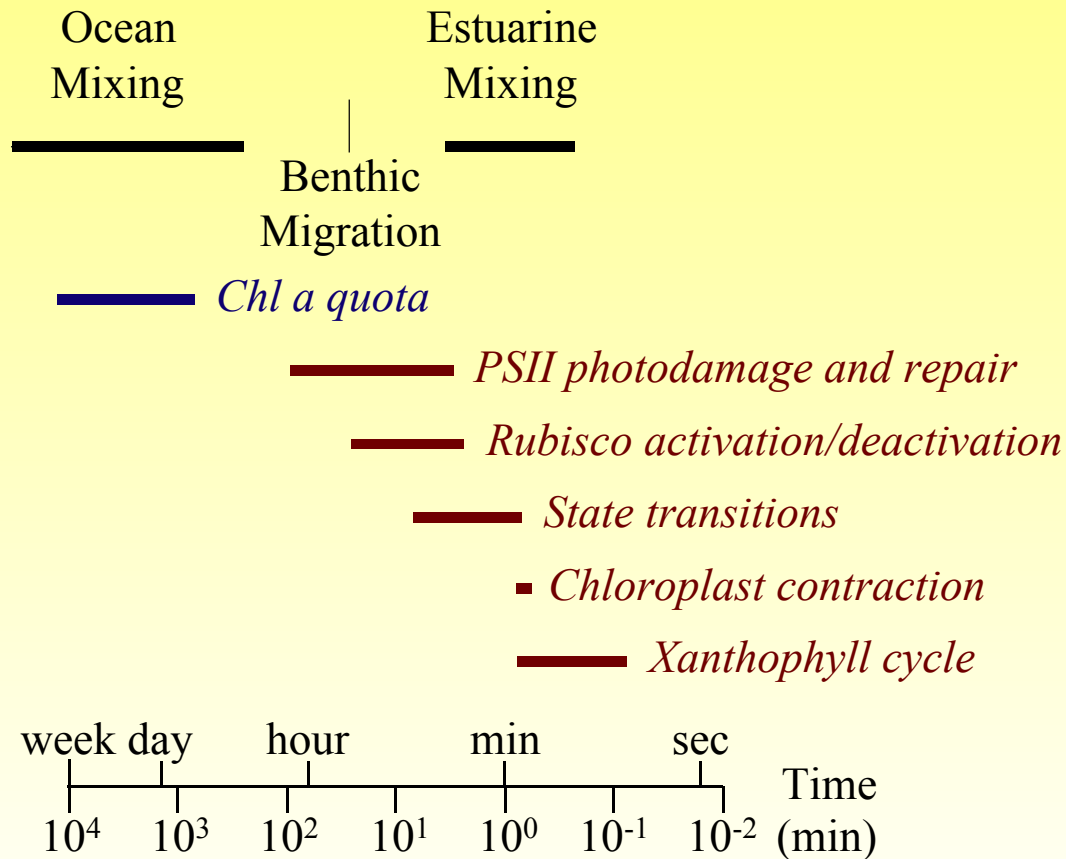
Integrated Chla: 22.5 mg m⁻²



Integrated Chla: 18.9 mg m⁻²



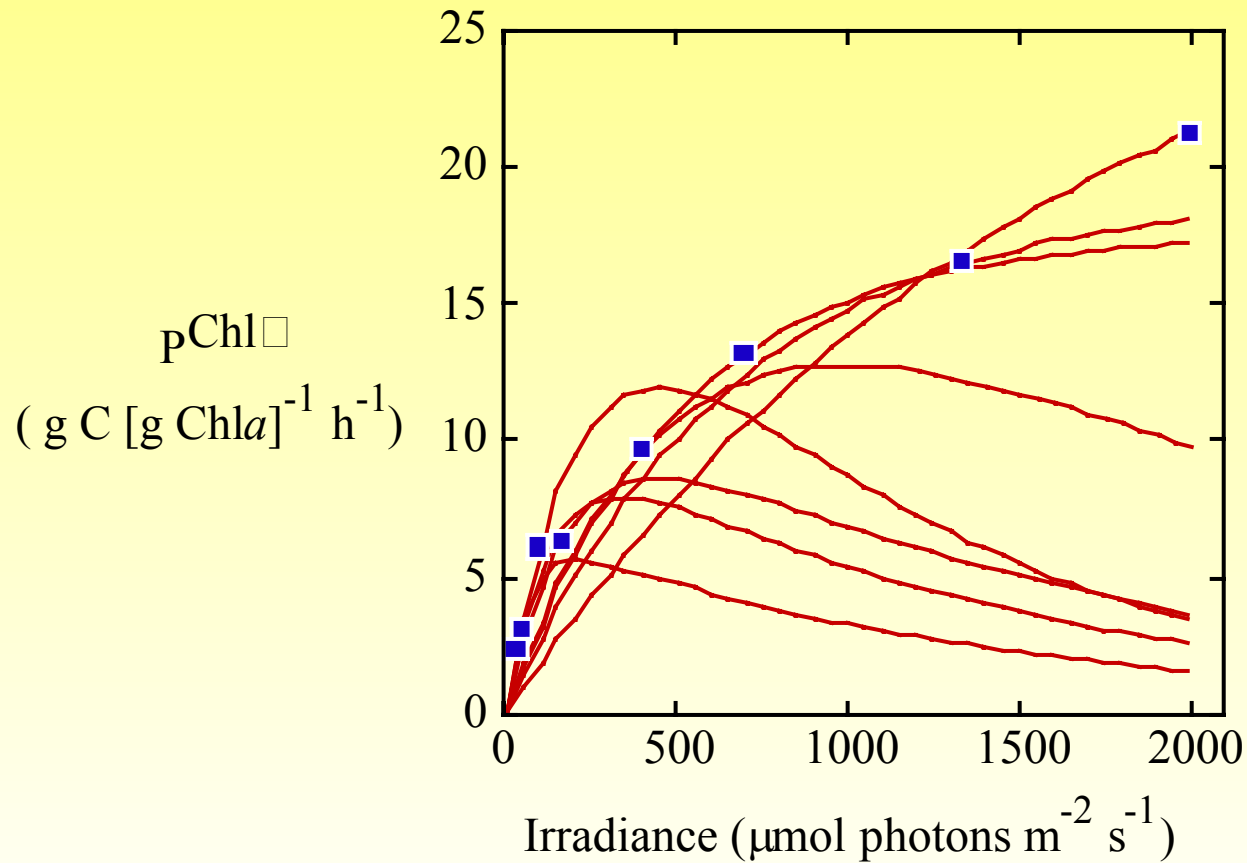
These cover the range of rates of acclimative and dissipatory processes



Photosynthetic responses vary on multiple timescales

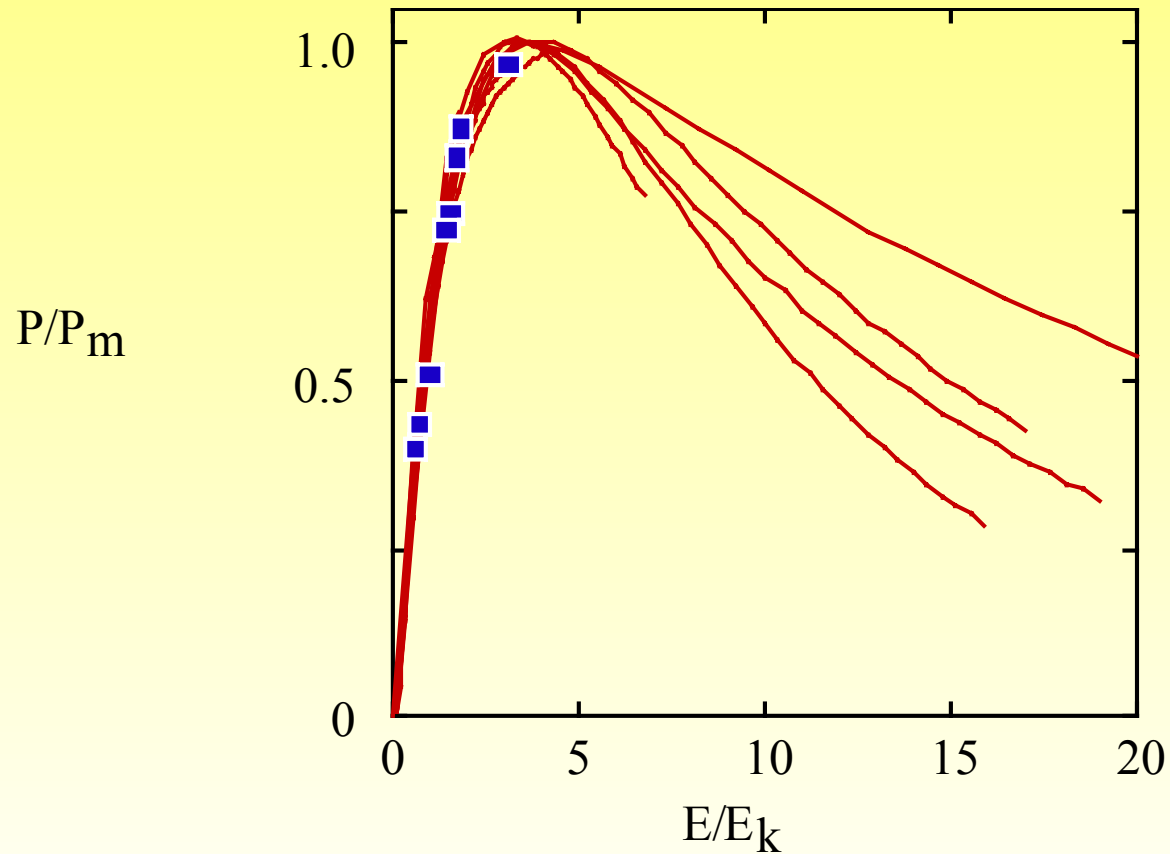
- “Ultimate” regulation
 - Regulation via *quantity* of photosynthetic components
 - Response under fully-acclimated state
- “Proximate” regulation
 - Regulation via *activity* of photosynthetic components
 - Responses to sudden and/or rapid changes in environmental conditions
 - Include both photosynthetic and dissipatory mechanisms

Acclimated photosynthetic rates and P vs E vs T responses...



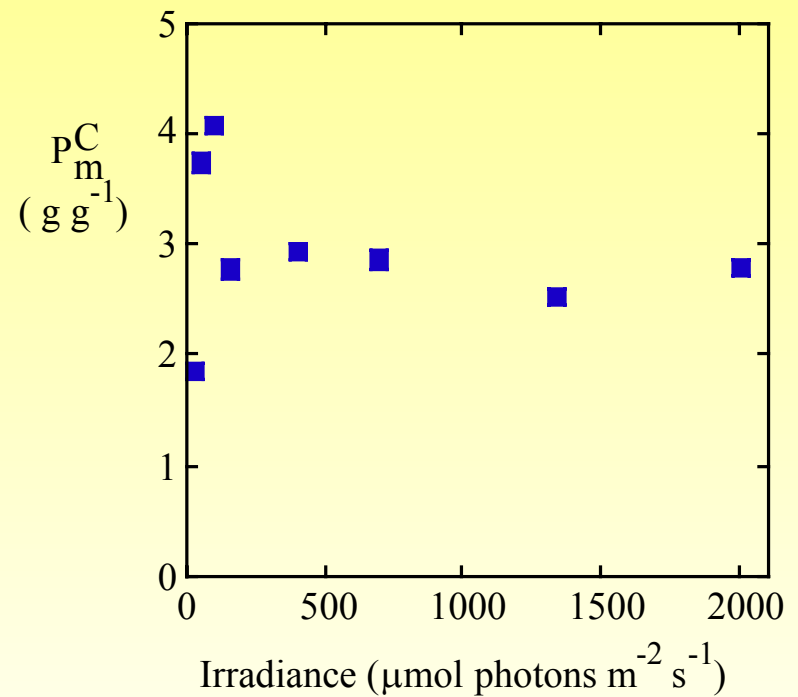
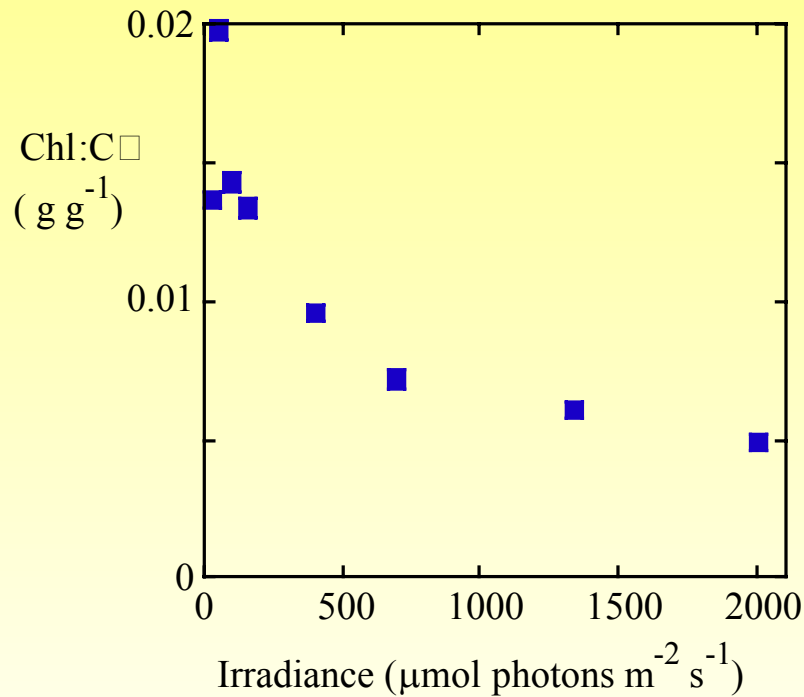
Kana and Glibert (1987)

...differ in magnitude and 'position', but relatively little in form



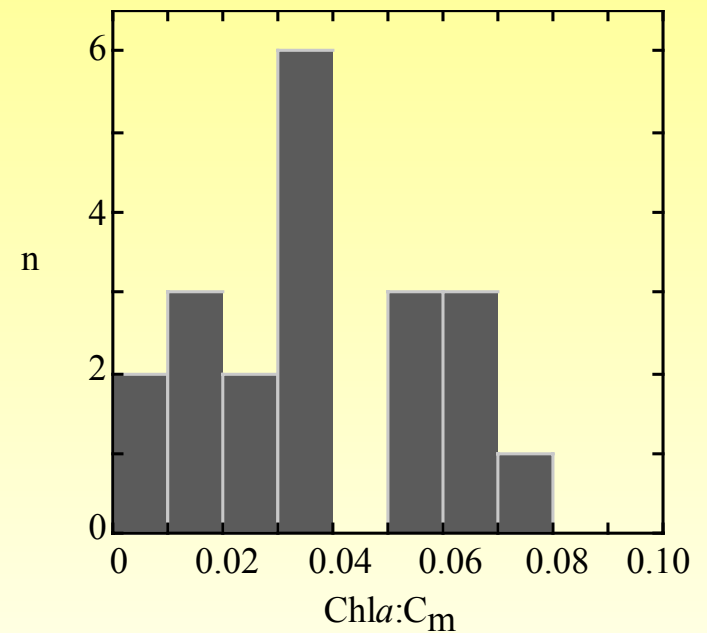
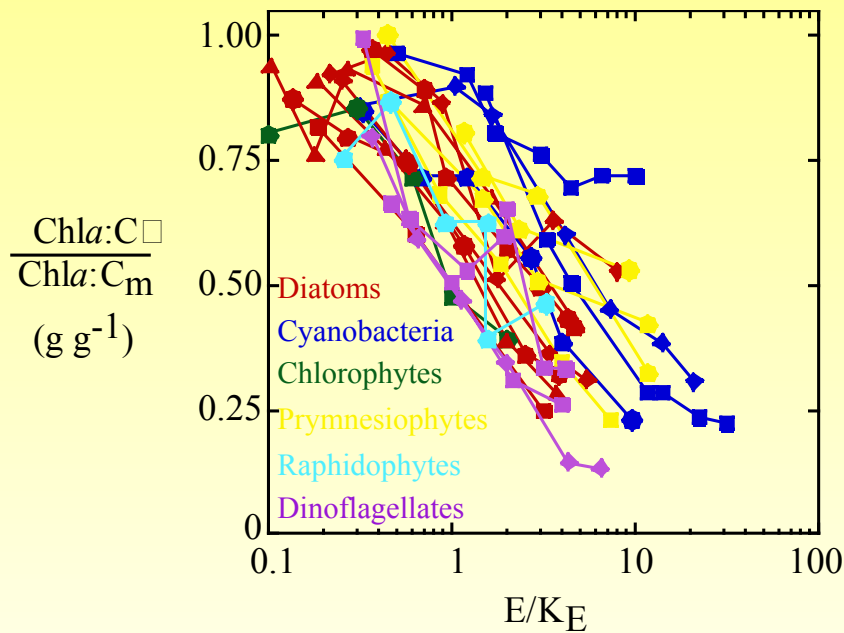
Kana and Glibert (1987)

...variability can be expressed in terms of photosynthetic pigmentation



Kana and Glibert (1987)

The pattern is general in microalgae



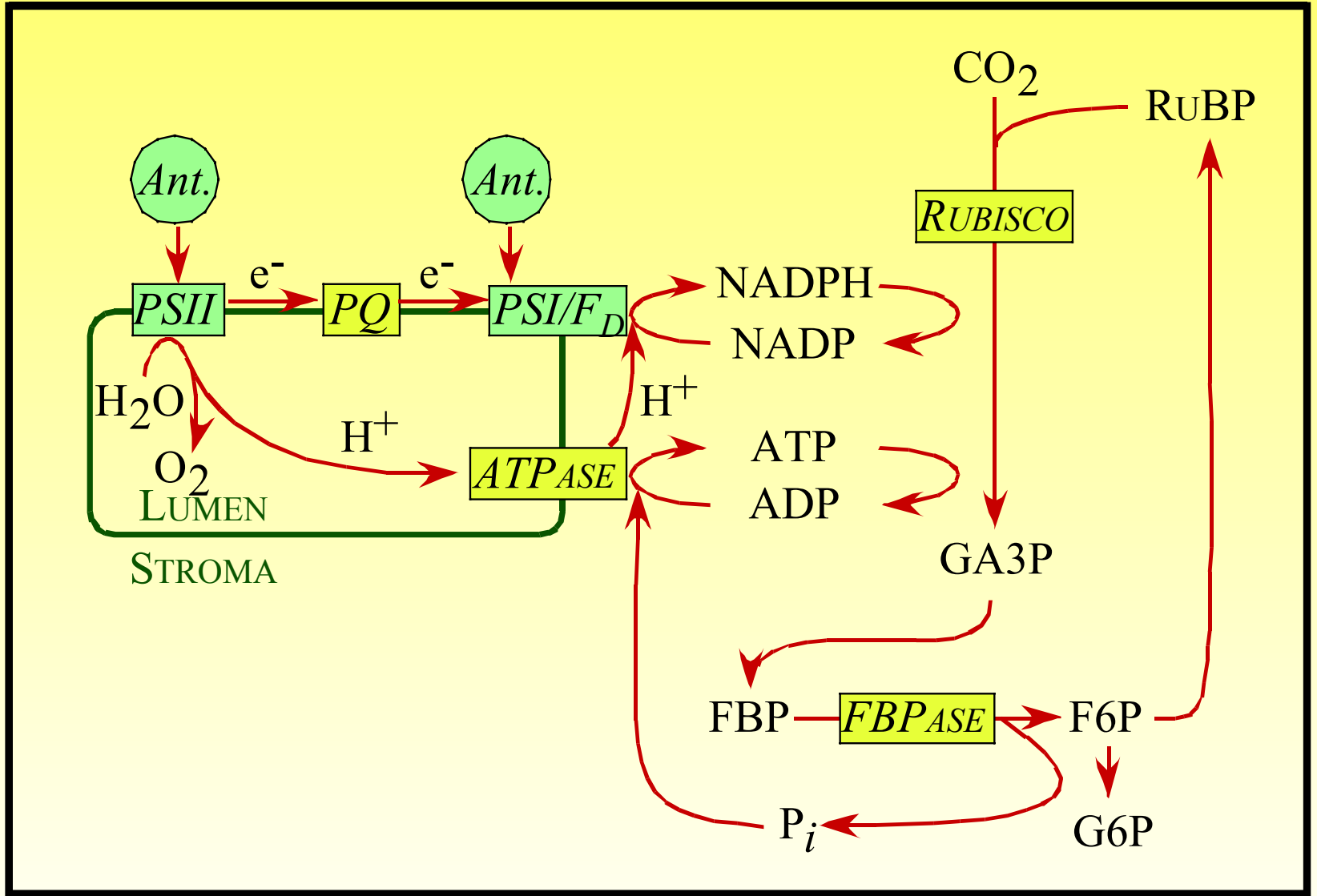
MacIntyre et al. (2002)

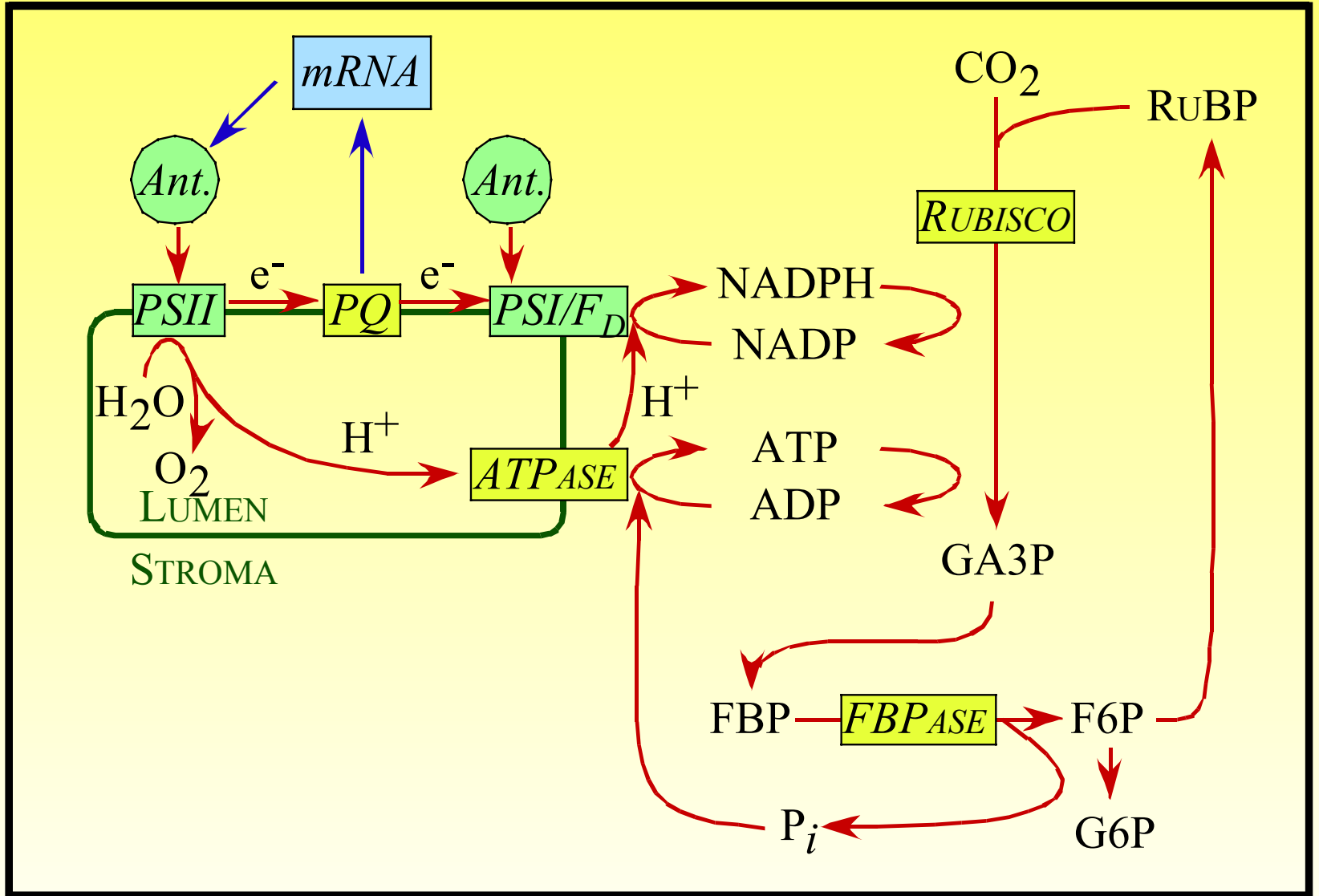
Short-term responses are likely more variable

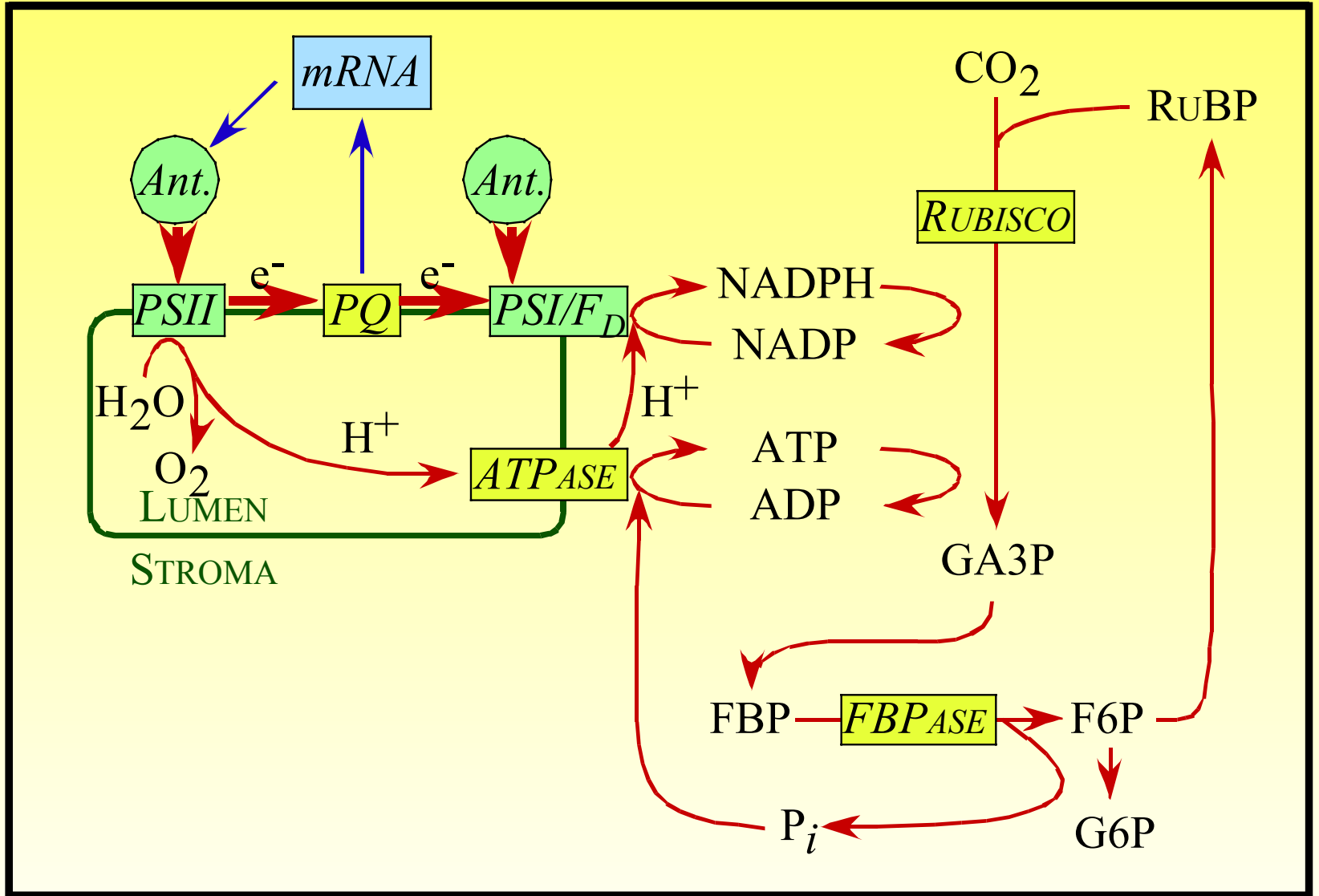
- What are the underlying physiological mechanisms?
- On what time-scales do they operate?
- Are they general?

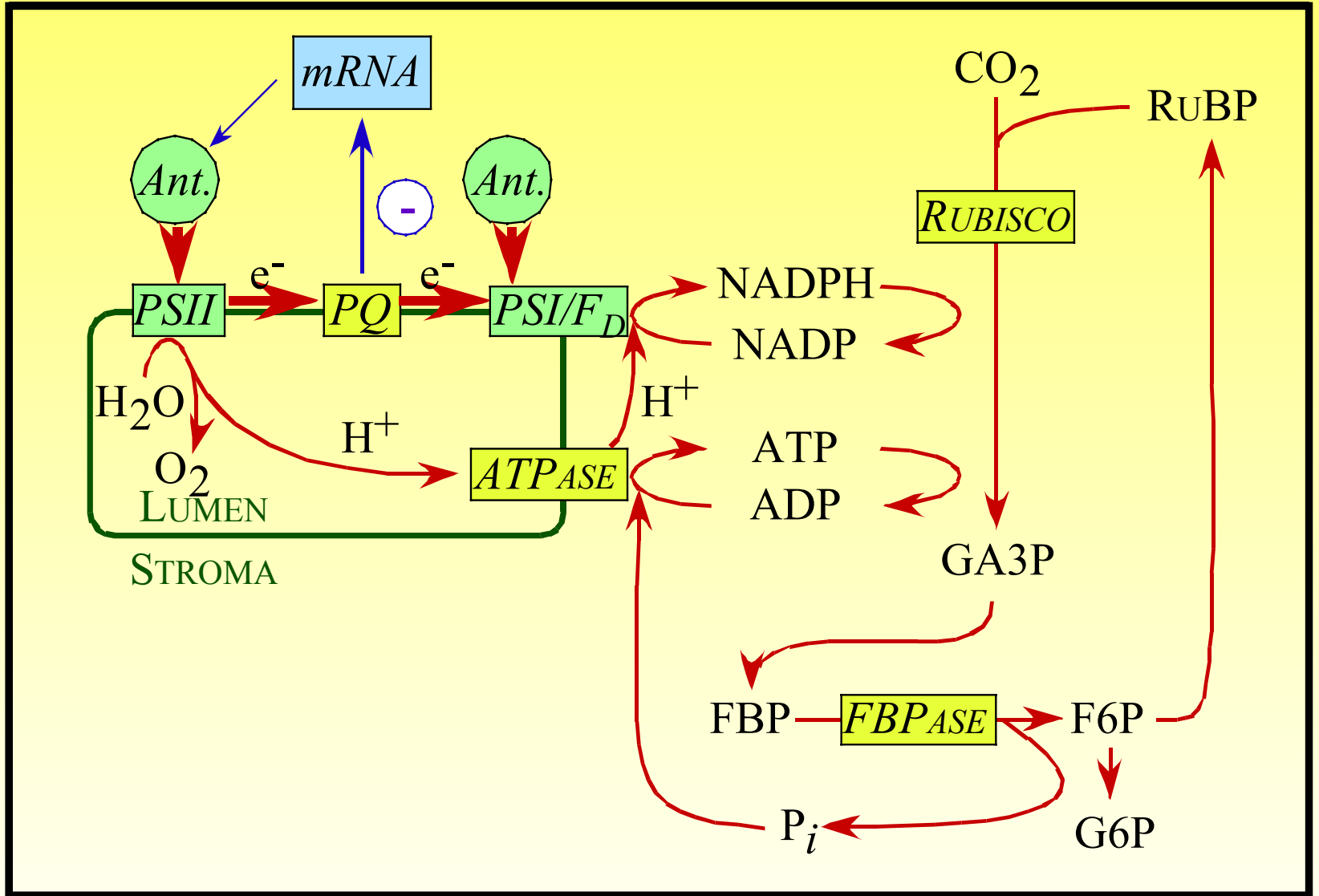
Caveat: the model organisms...



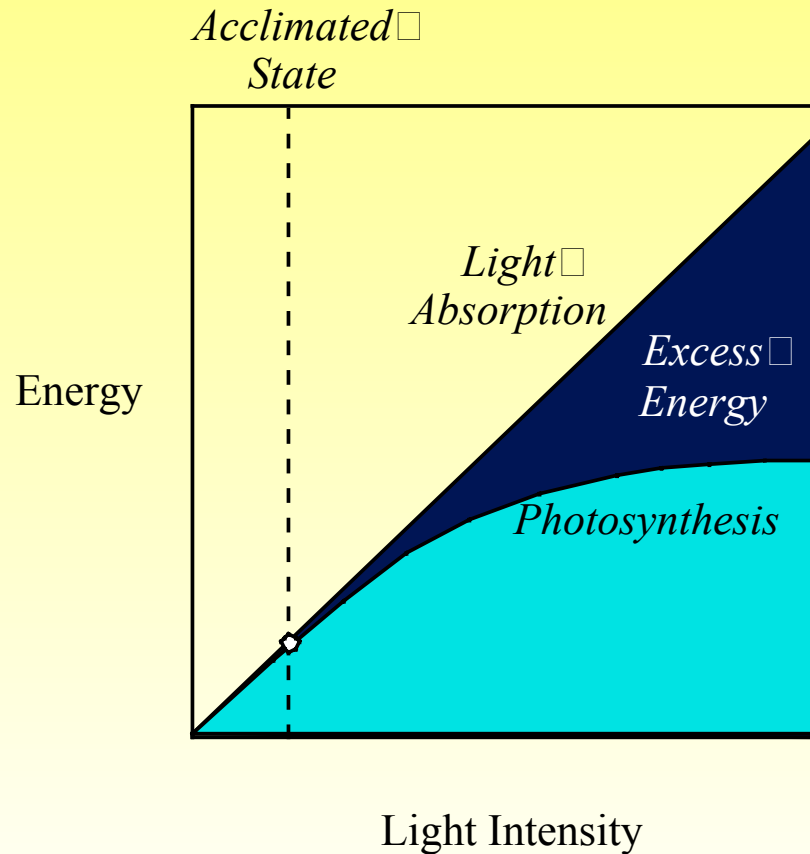




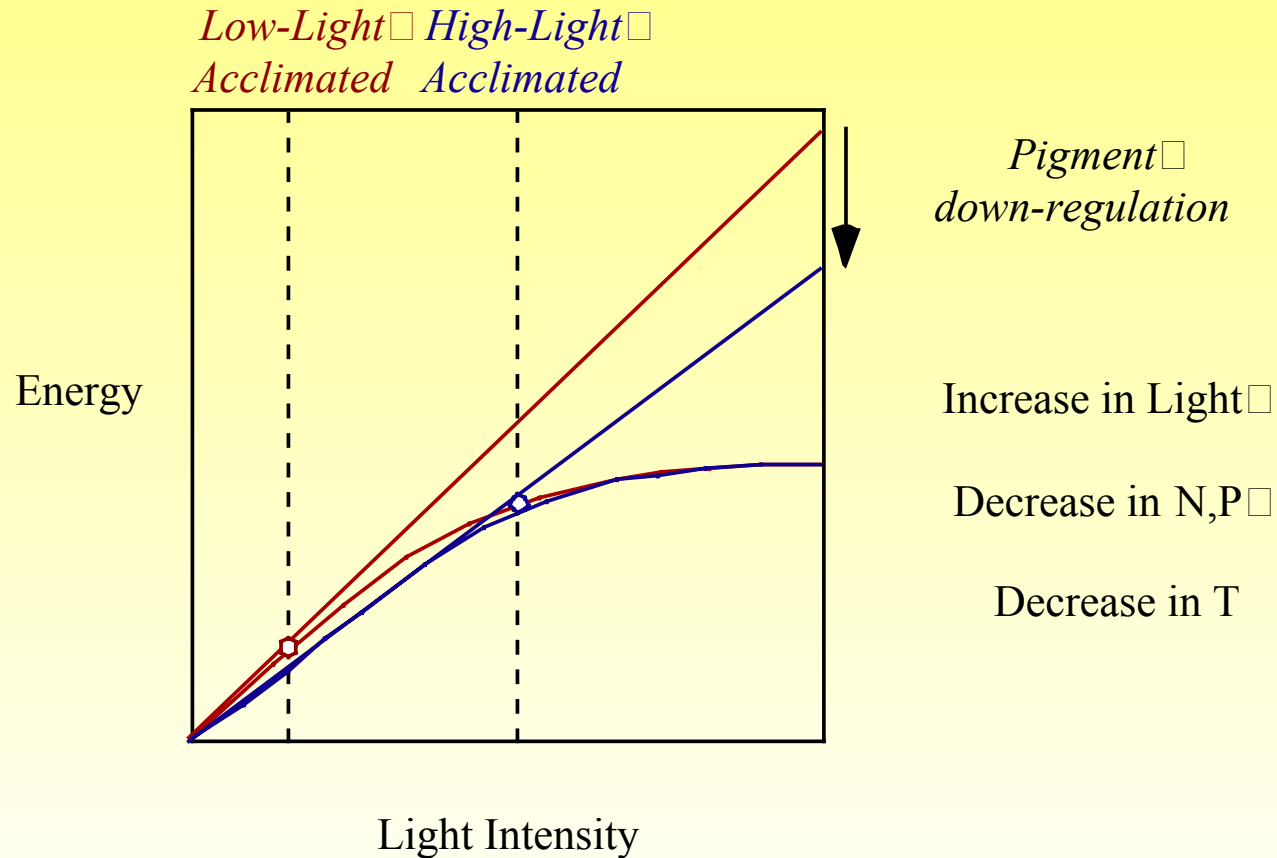




An increase in photon “pressure” results in an excess of excitation energy

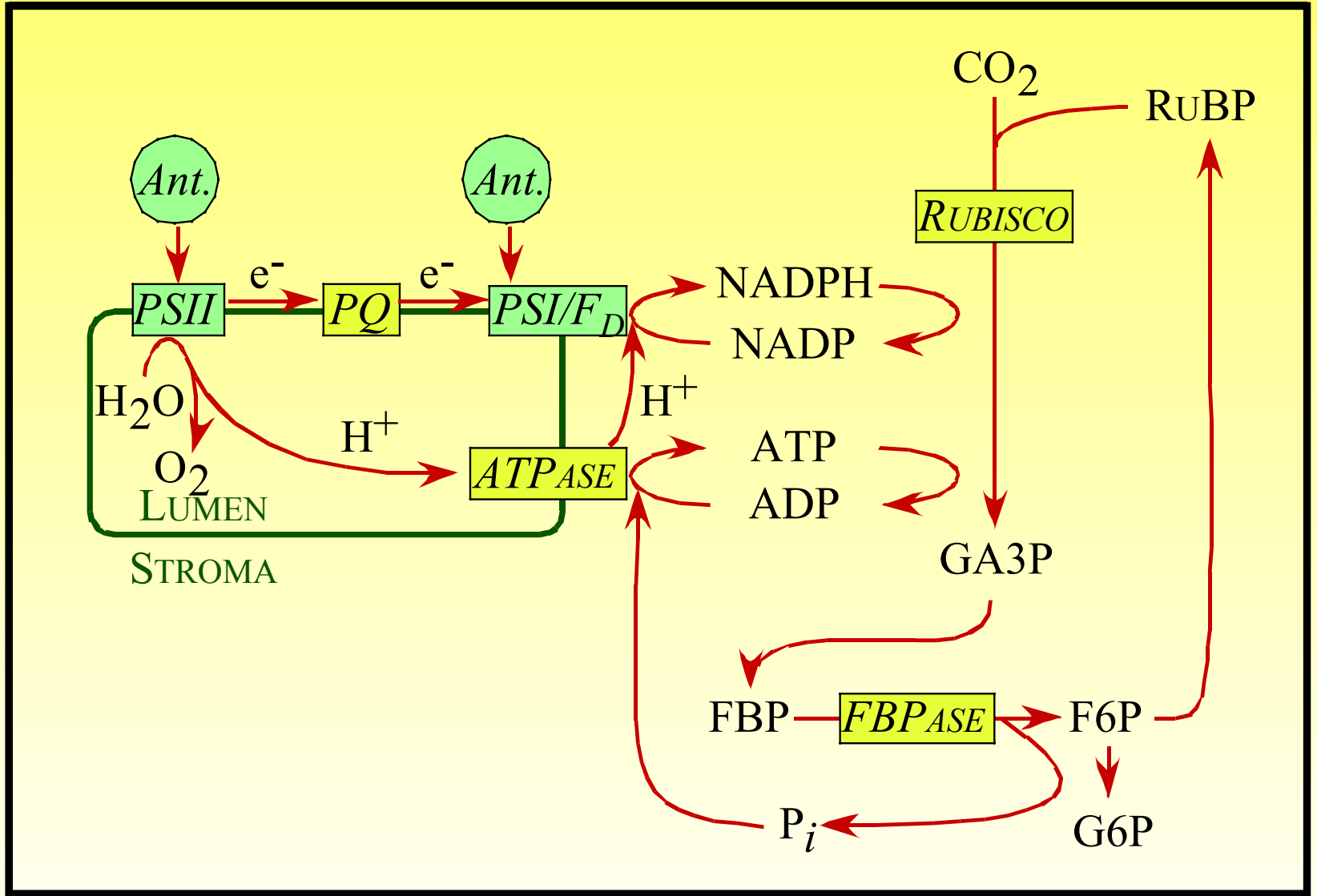


...and down-regulation of pigments & absorption

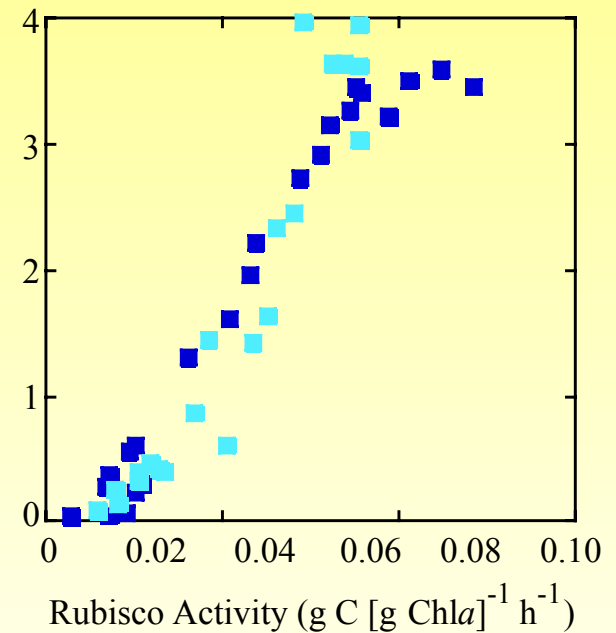
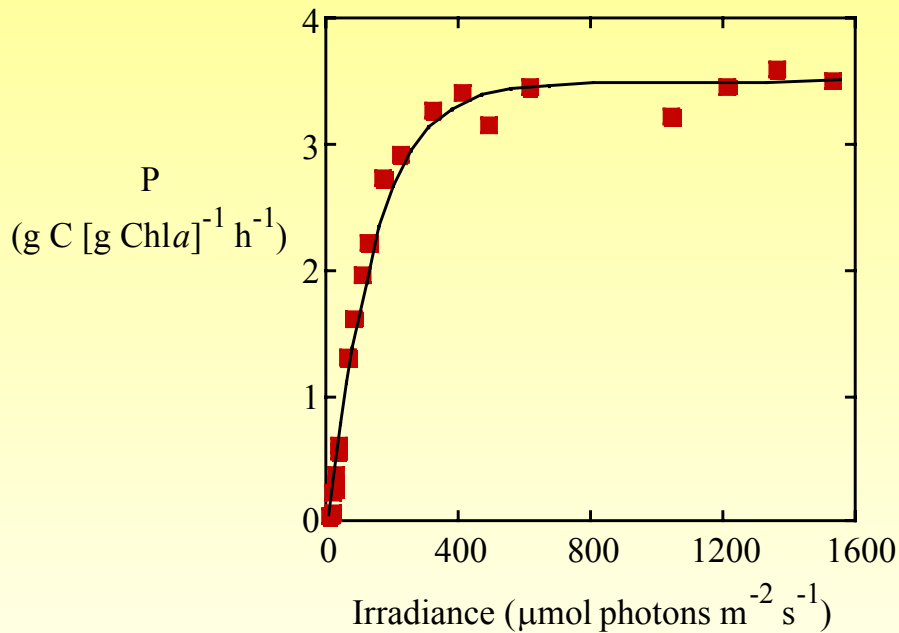


Rapid (“proximate”) responses can be as important

- Pigment regulation is slow (cf. generation time)
- The rate of change of irradiance is relatively fast in most mixed layers
- Over-excitation leads to photoinhibitory damage to reaction centers
- Regulation on short time-scales by photosynthetic induction and dissipatory mechanisms

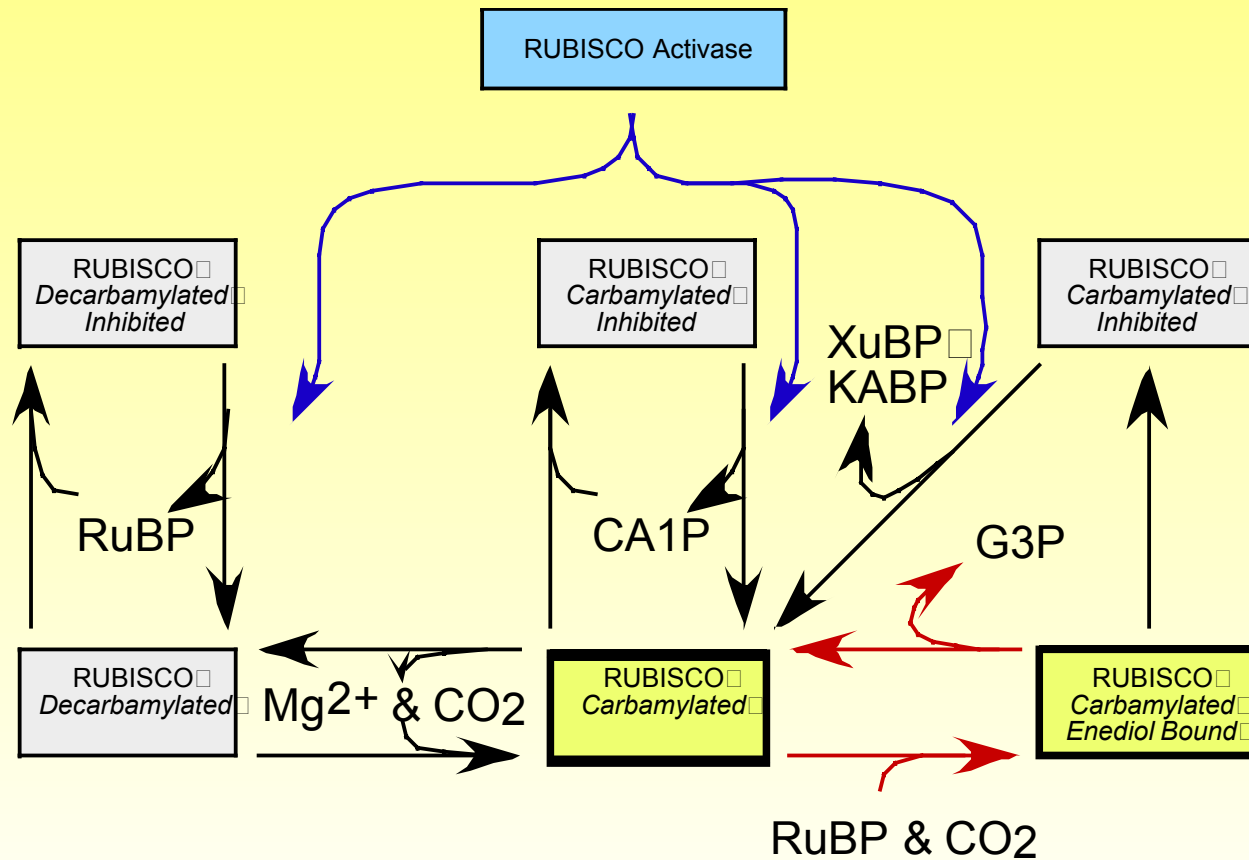


Rubisco activity is regulated in response to short-term variation in irradiance

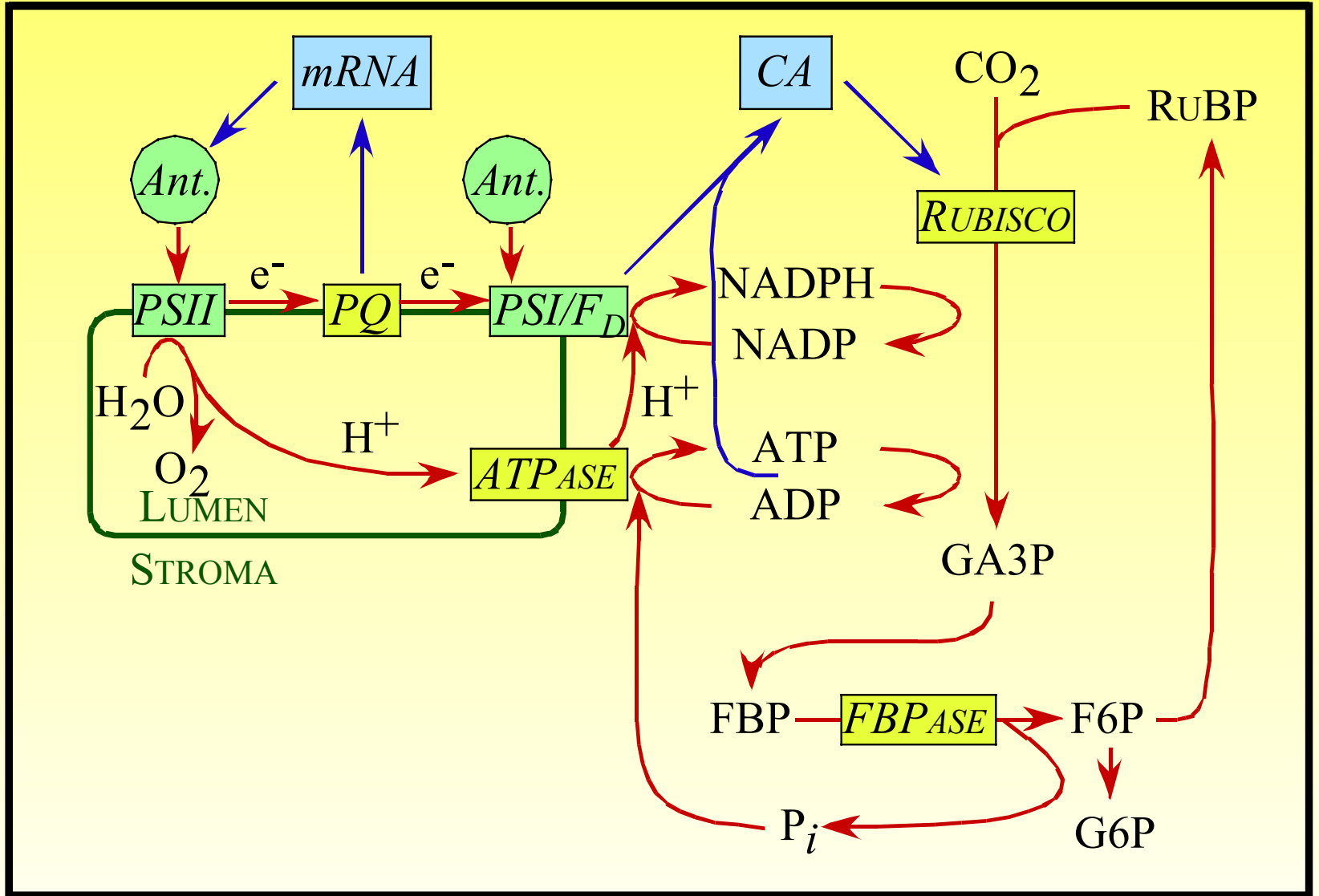


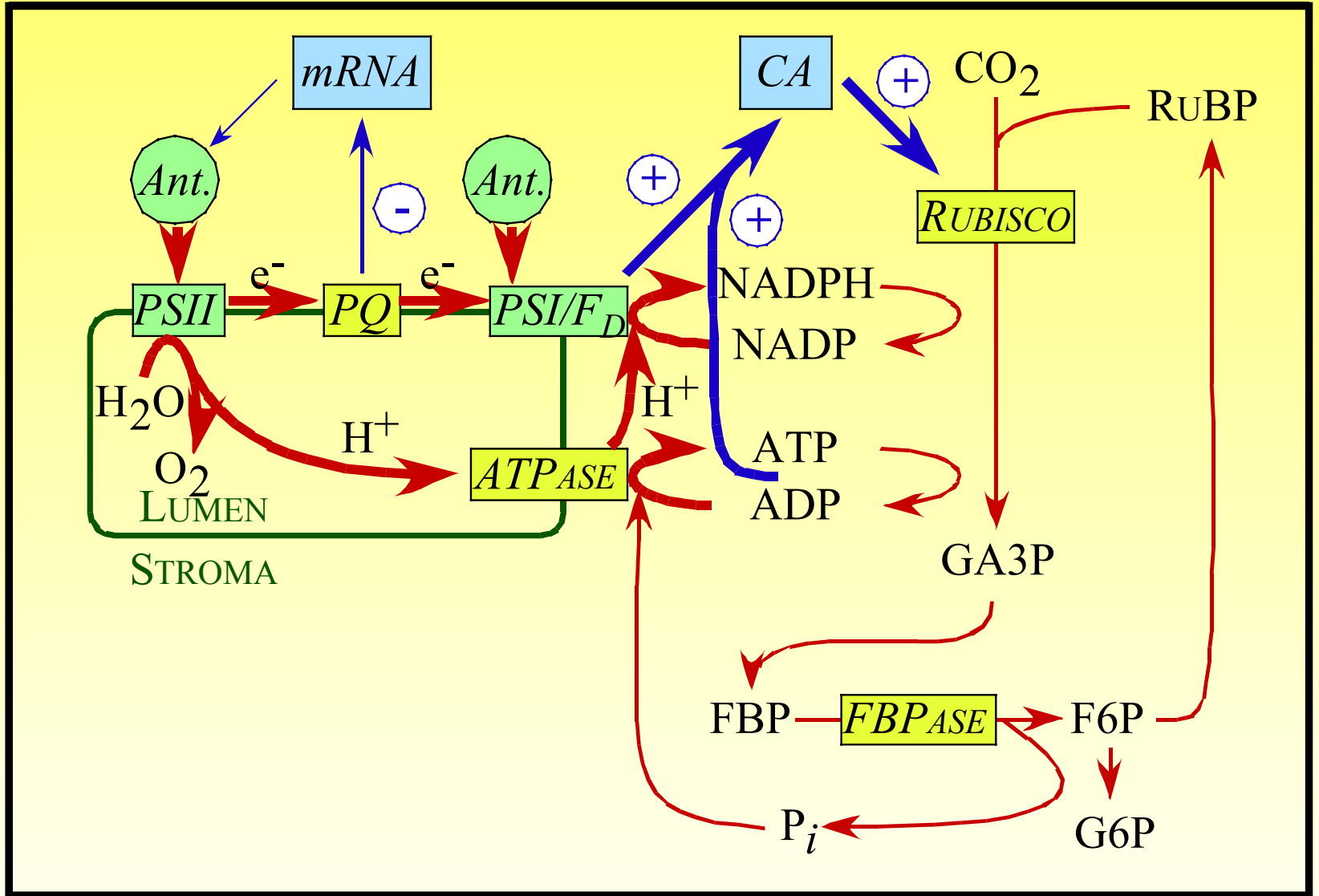
MacIntyre and Geider (1996)

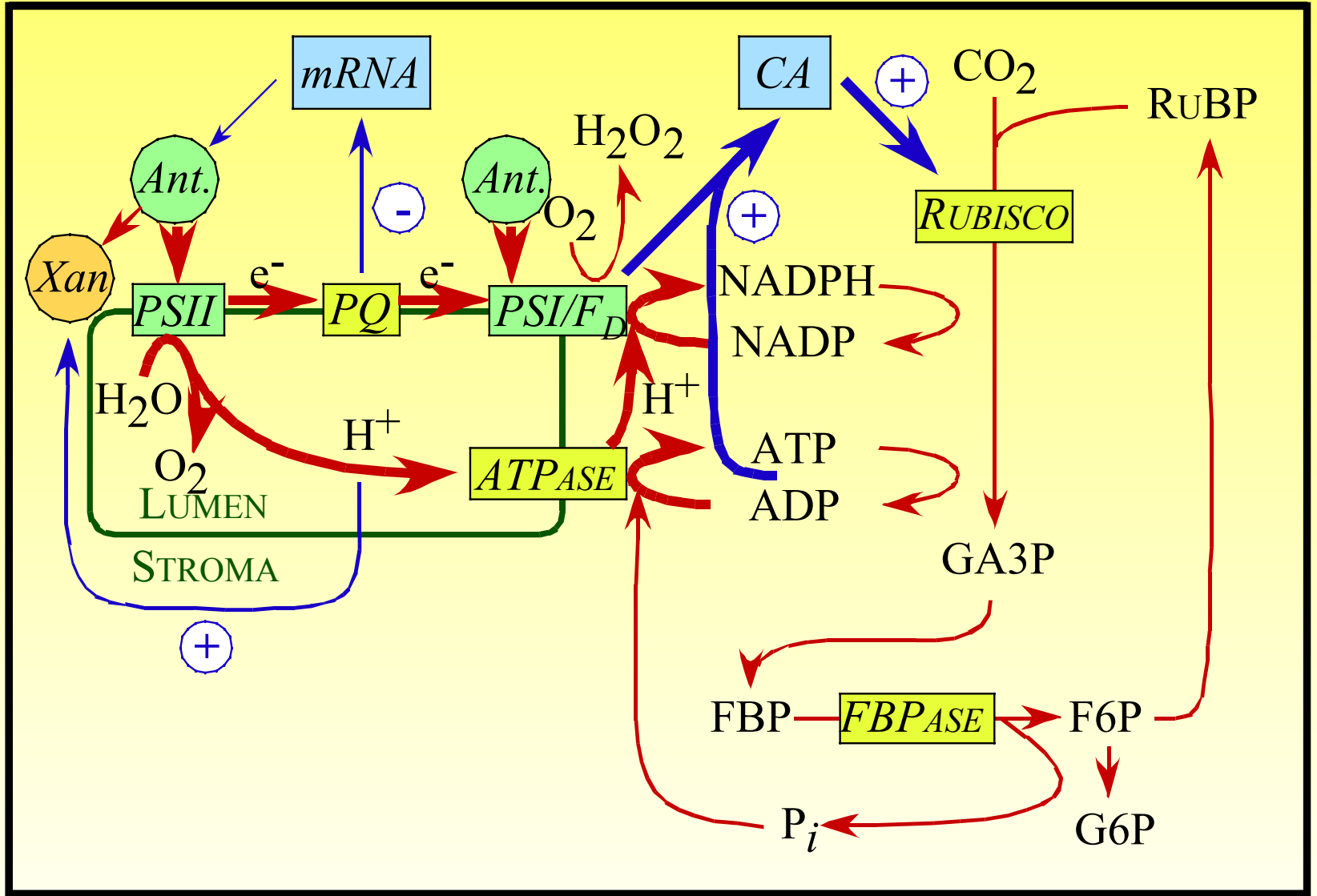
The regulation is complex...

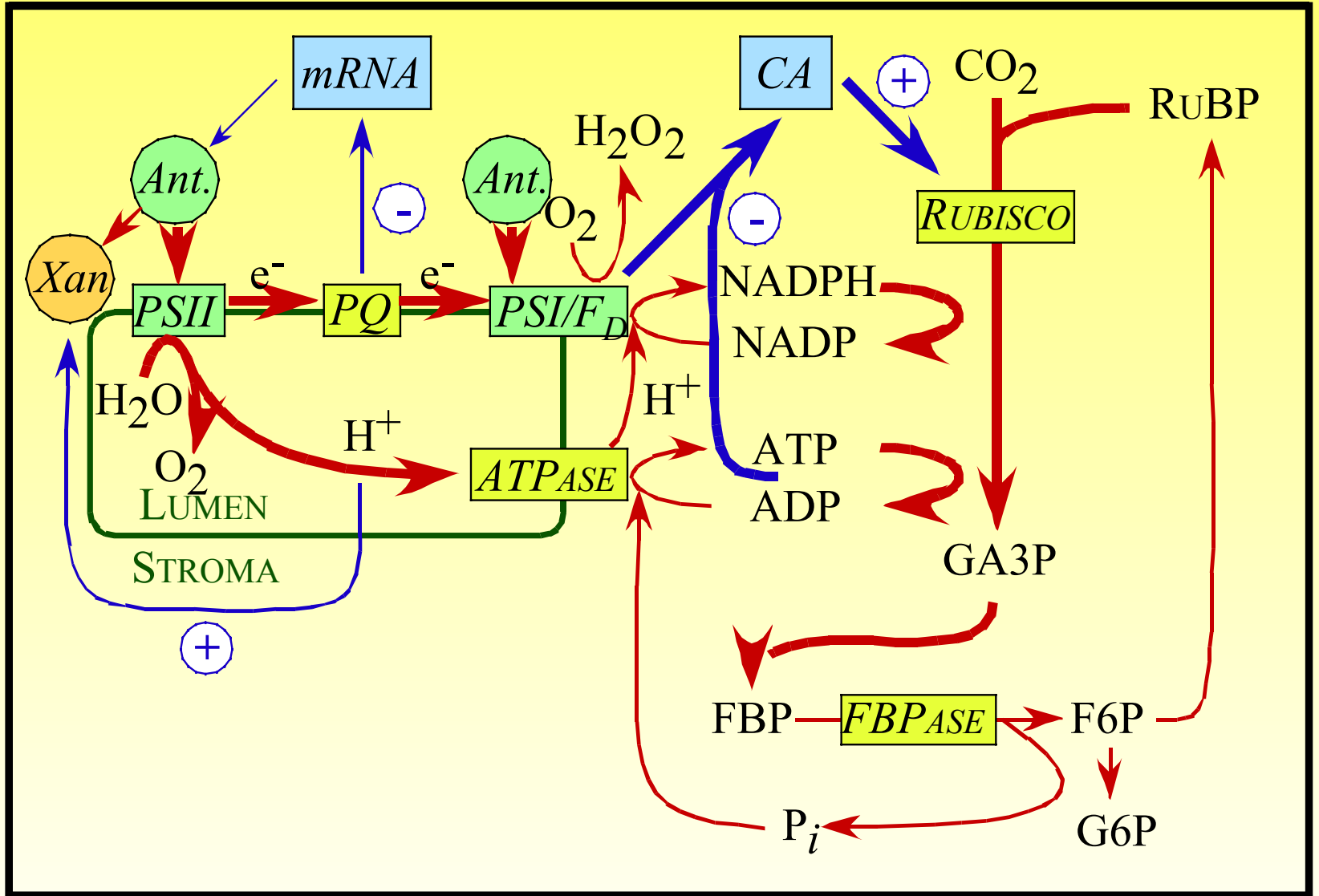


Geider and MacIntyre (2002)

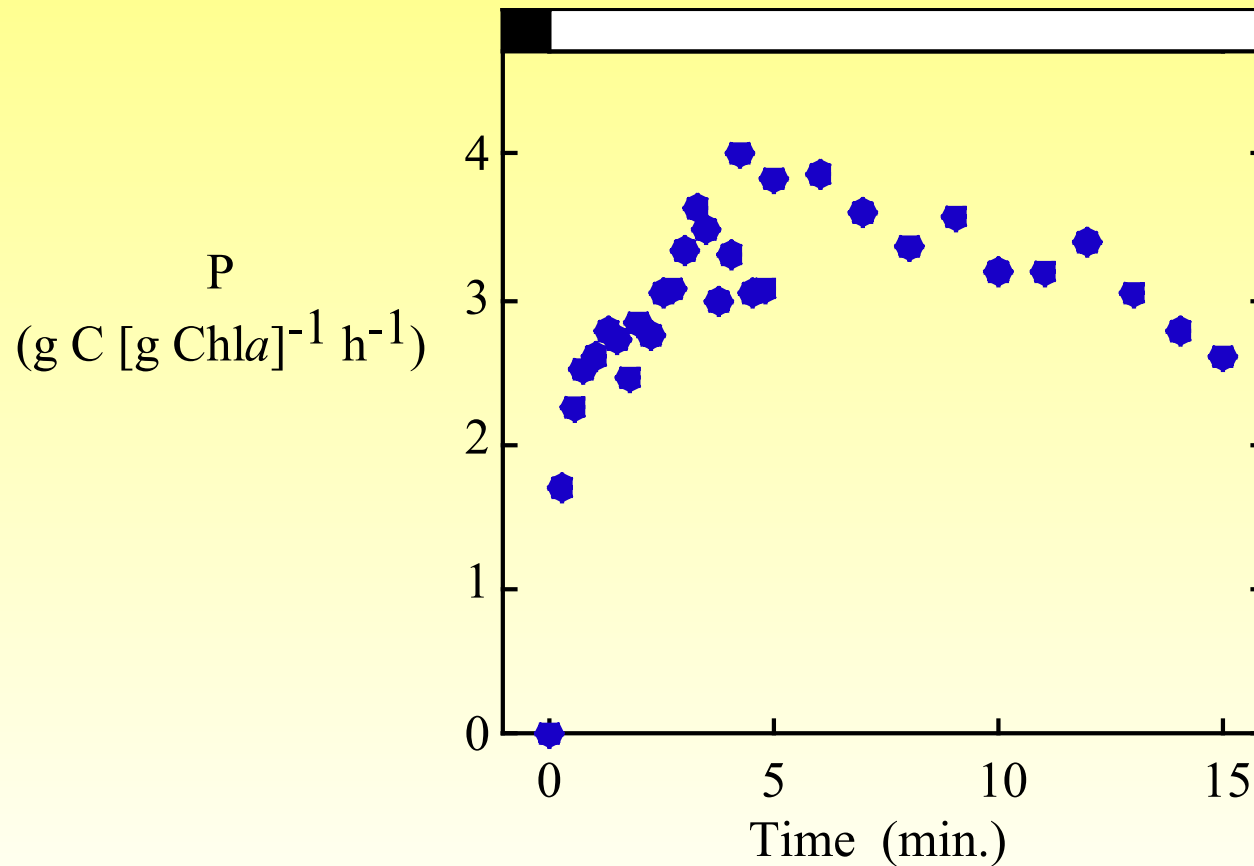




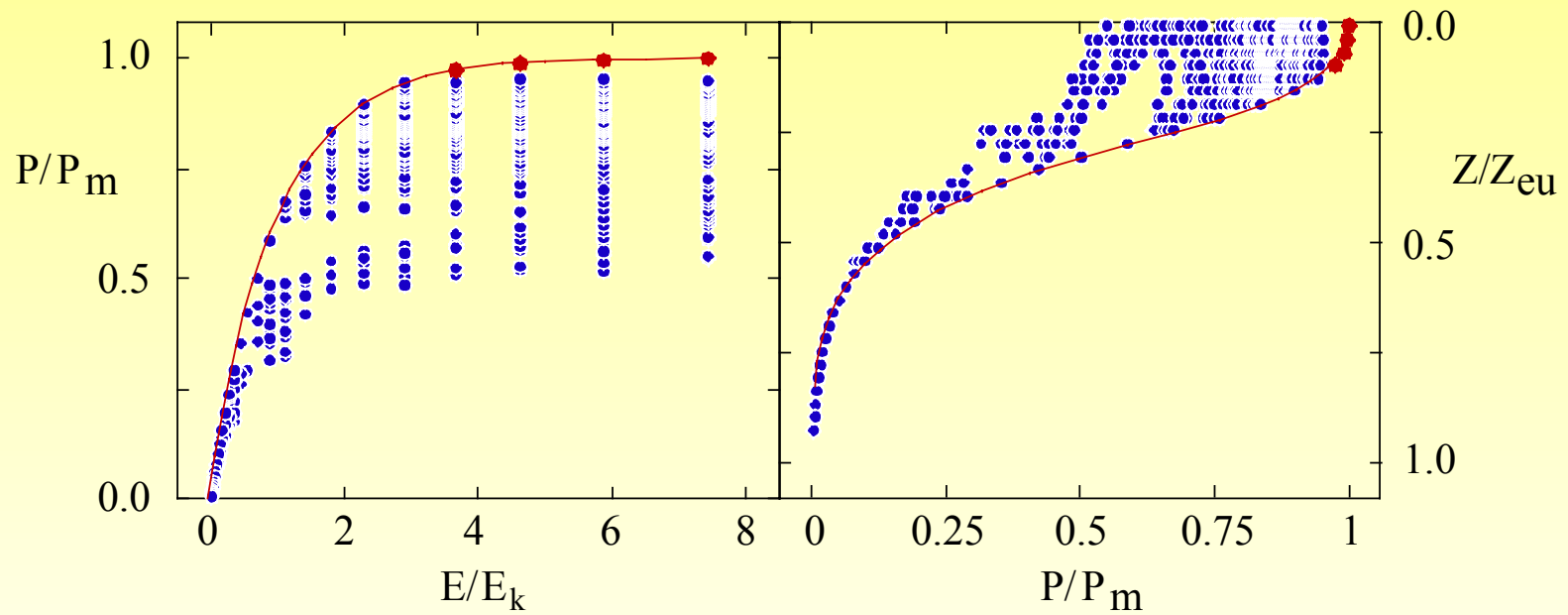




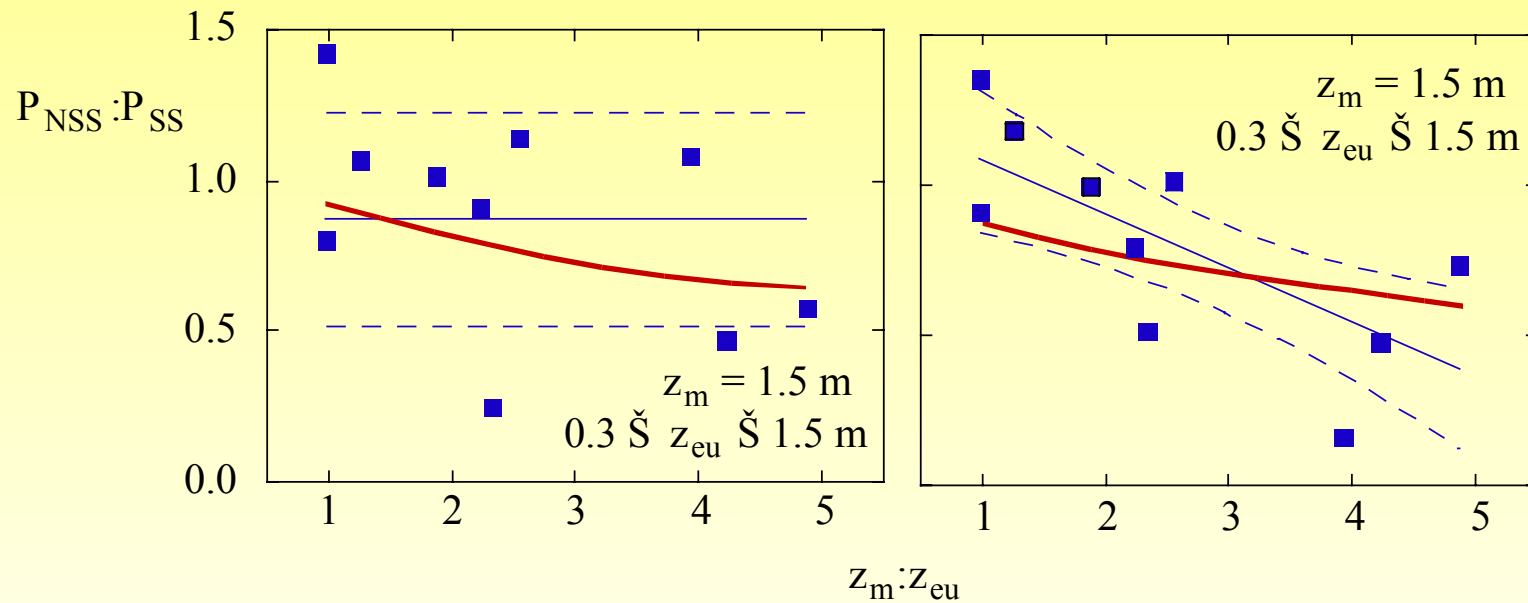
Kinetics of the P vs E vs T response can be complex in rapidly-mixed systems



Modeling Rubisco activation and deactivation kinetics as rate-limiting step

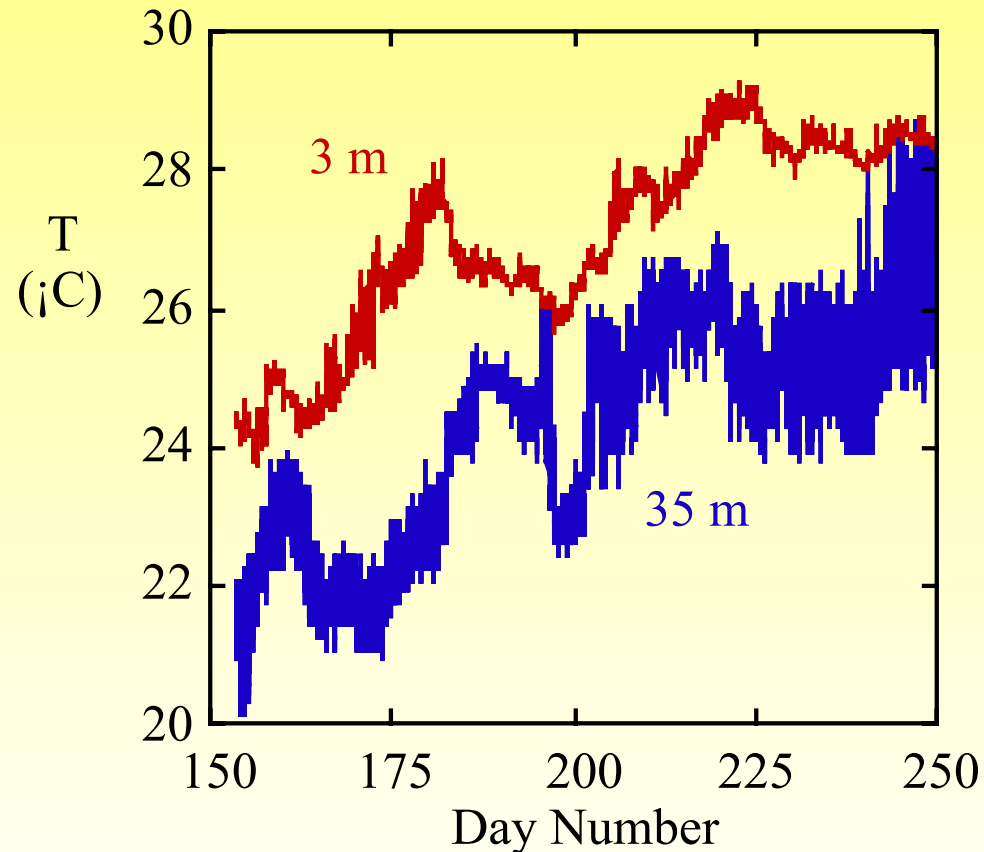


...yields realistic estimates of productivity in moving incubations



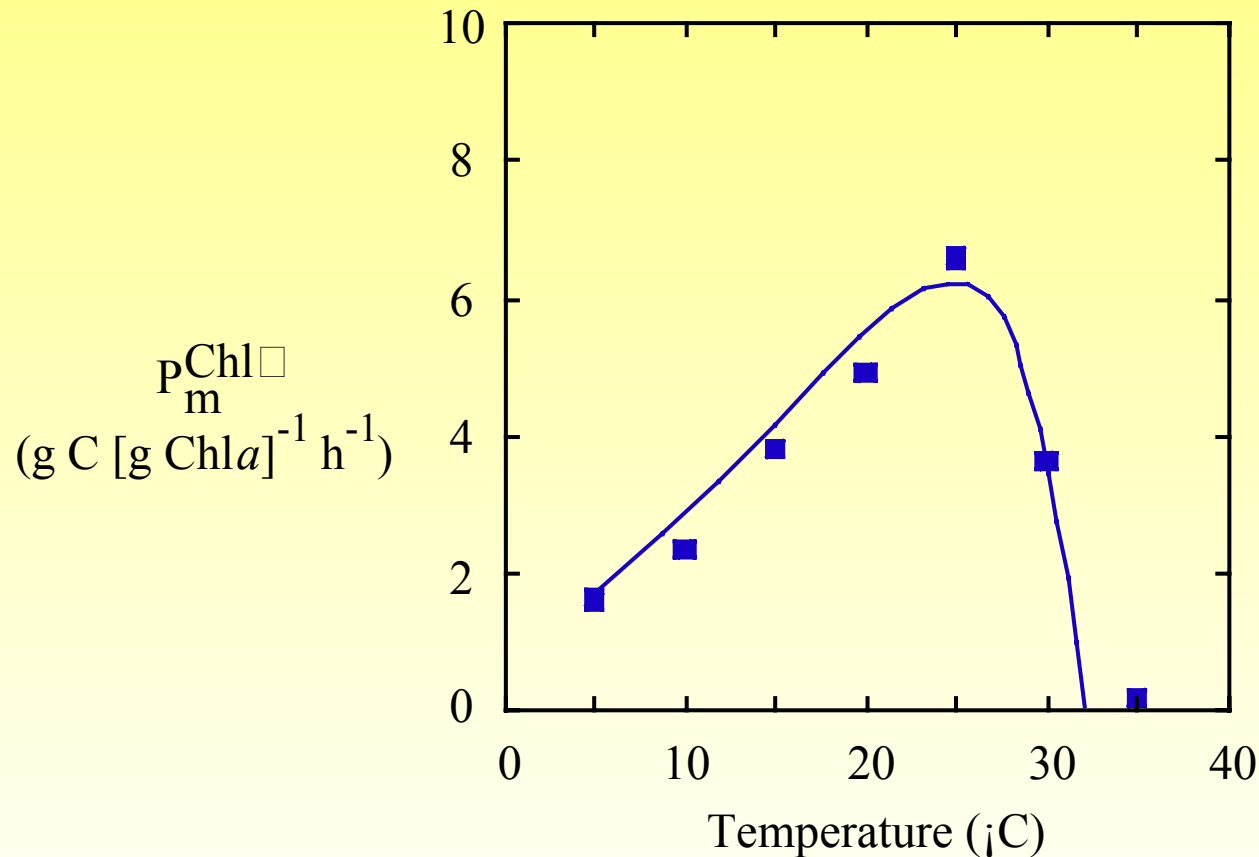
Geider and MacIntyre (1996); Randal and Day (1987)

Temperature fluctuations in the pelagic operate on scale of pigment regulation



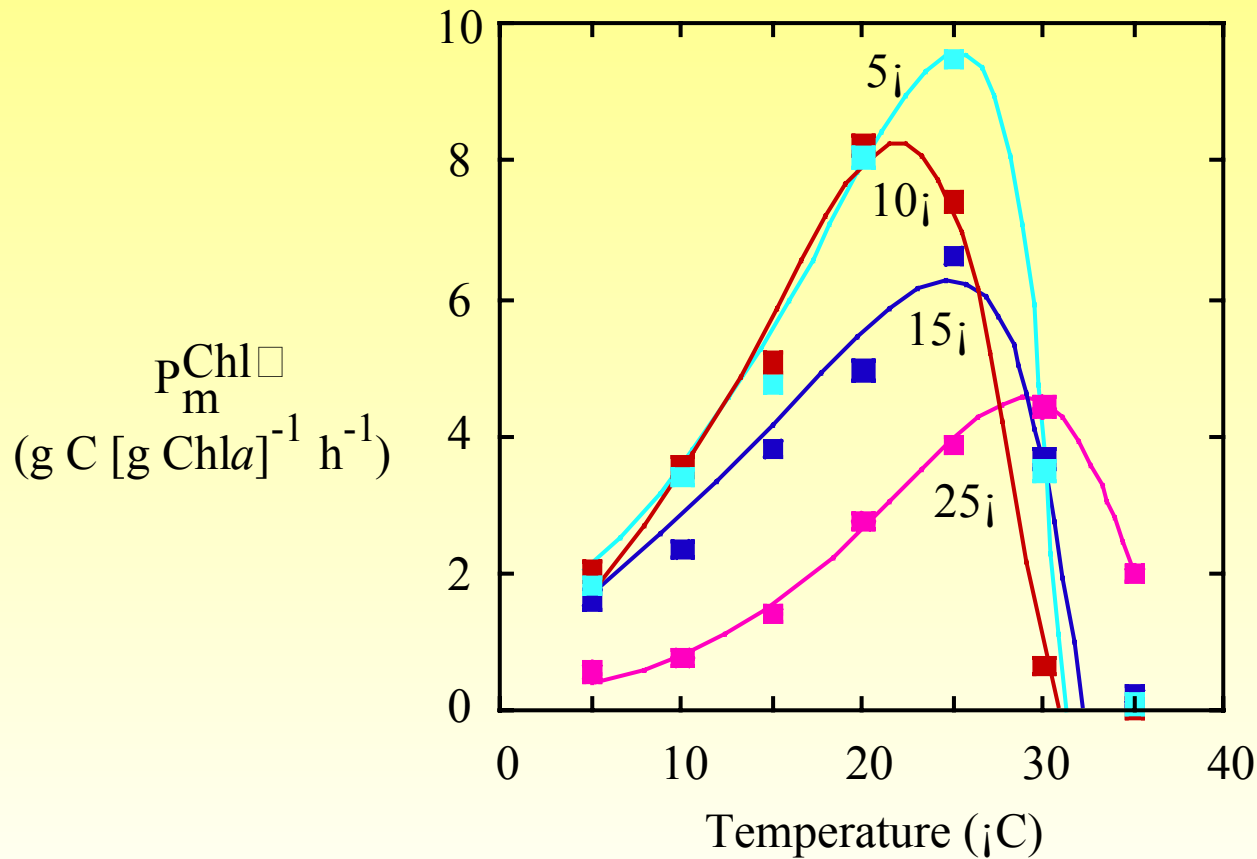
Data: Dickey et al. (Bermuda Timeseries Mooring)

In contrast, temperature fluctuations in the benthos are extreme: $12^{\circ}\text{C} @ 3^{\circ}\text{C h}^{-1}$



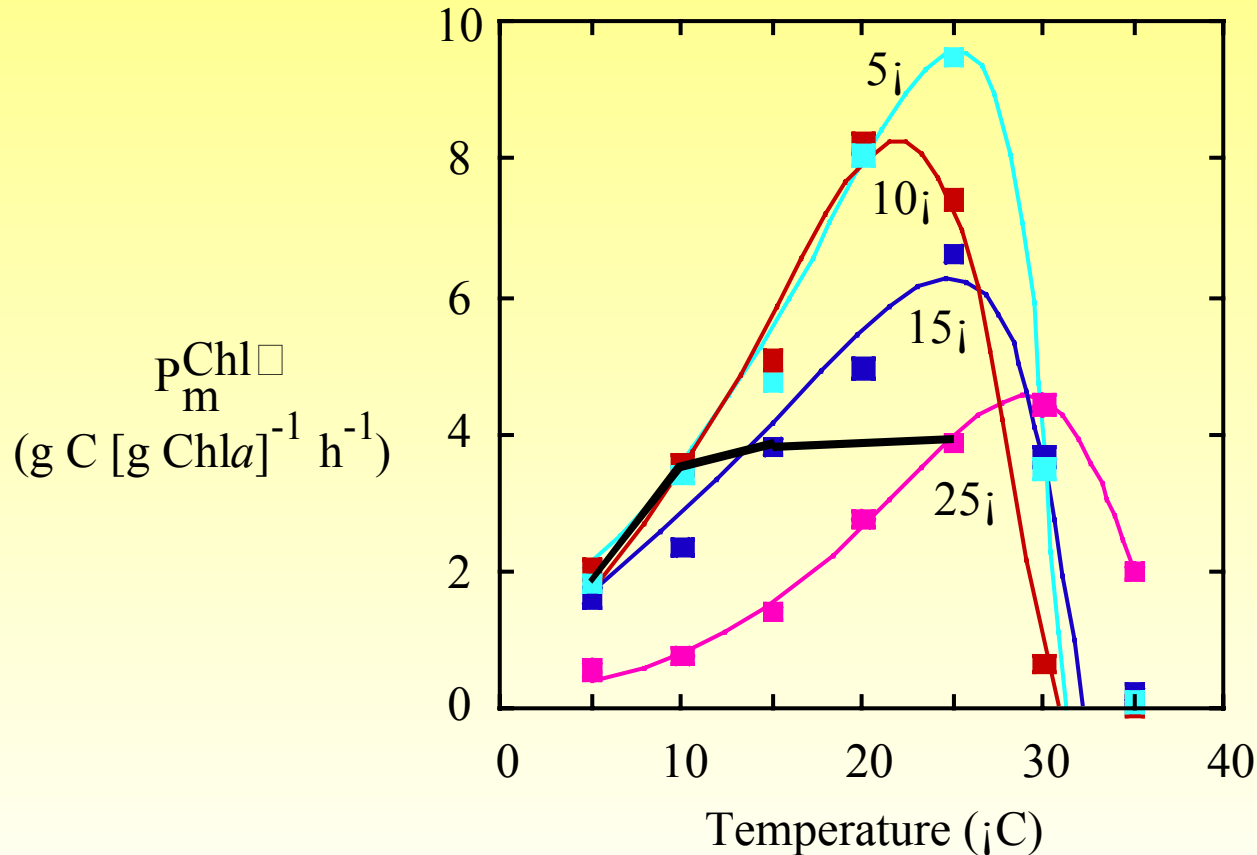
Data: Li and Morris (1982)

Compensatory changes can occur with acclimation



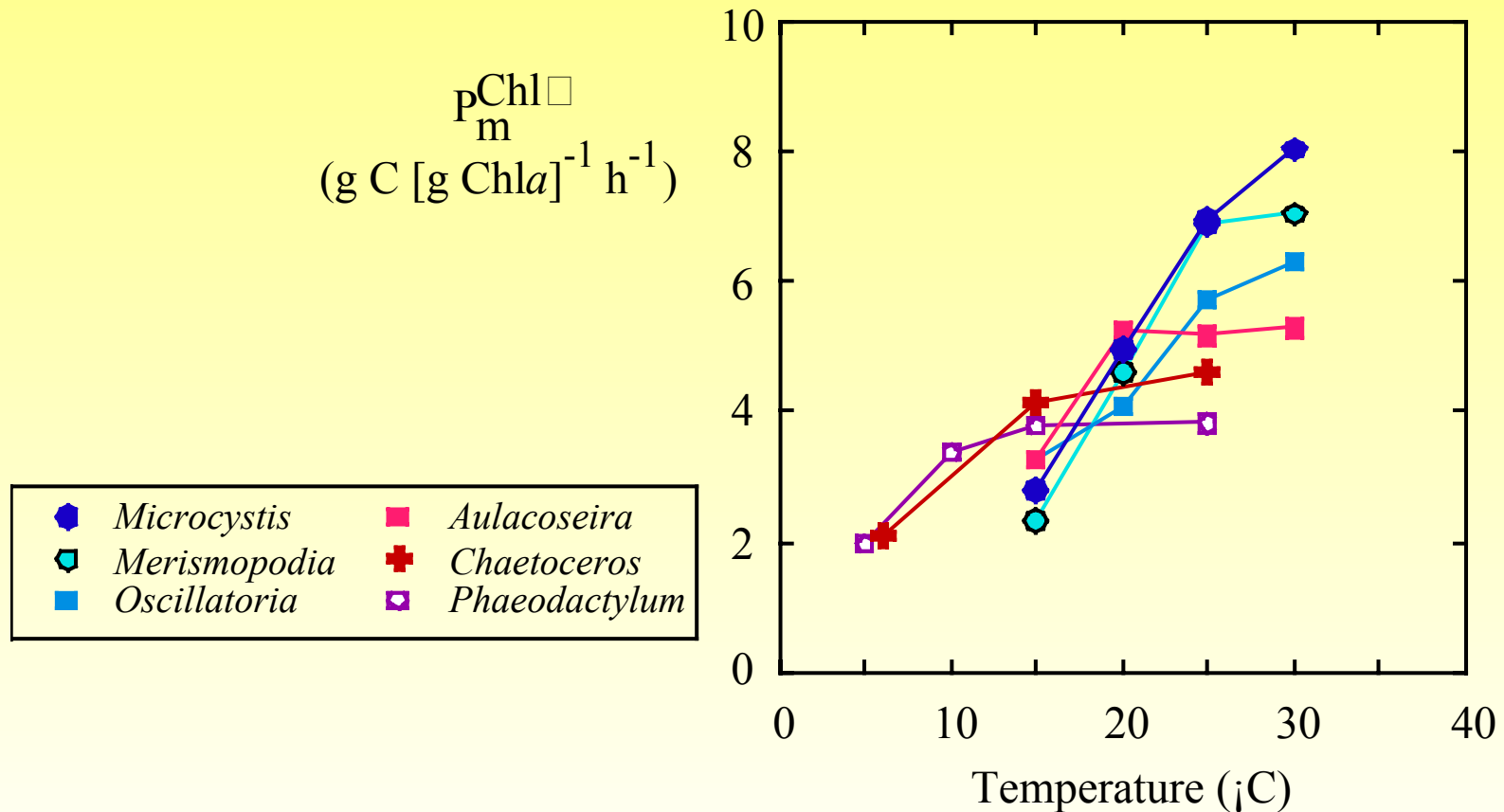
Data: Li and Morris (1982)

...so the effect is minimal under acclimated conditions



Data: Li and Morris (1982)

However, there may be taxonomic differences in acclimated response



Data: Li and Morris (1982); Coles and Jones (2000); Anning et al. (2001)

Microalgae are not spinach

Taxon	Rubisco Pool Size		Rubisco Activity		Rubisco activase		CCM ⁷	
	<i>E</i> ¹	<i>N</i> ²	<i>E</i> ³	<i>N</i> ⁴	<i>Present</i> ⁵	<i>Inferred</i> ⁶	<i>Const.</i>	<i>Induce</i>
Cyanobacteria	?	?	?	?	N?			Y
Chlorophytes	N	Y	Y	Y	Y		N	Y
Diatoms	Y	?	Y	?	?	Y	N	Y
Prymnesiophytes	?	Y	N	Y	?	?	N	Y
Dinoflagellates	?	?	?	?	?	?	Y	Y

References: 1 (Sukenik et al. 1987, Orellana and Perry 1992); 2 (Falkowski et al. 1989, Geider et al. 1998a); 3 (Mouget et al. 1993, MacIntyre et al. 1996b, 1997); 4 (Falkowski et al. 1989, Beardall et al. 1991); 5 (McKay et al. 1991, Süß et al. 1995, Beuf et al. 1999); 6 (Uemura et al. 1998); 7 (Goyal and Tolbert 1990, Berman-Frank et al. 1995, Giordano and Bowes 1997, Nimer et al. 1997, Badger et al. 1998, Nimer et al. 1999, Huertas et al. 2000)

Summary

- Photosynthetic responses occur on multiple time-scales
 - Acclimative responses in pool sizes
 - Inductive/dissipatory responses in activity
- These occur on same time-scales as natural variability
- Many responses are general; some are not
- Taxonomic variability is very poorly described