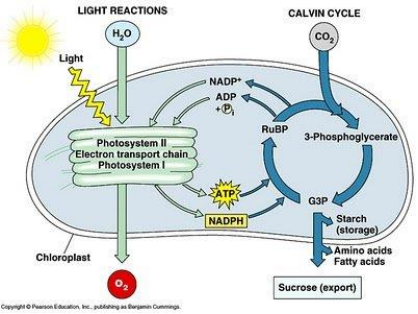
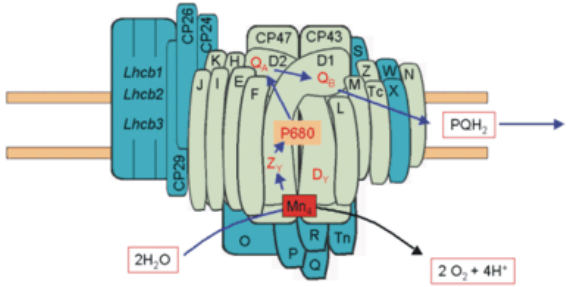


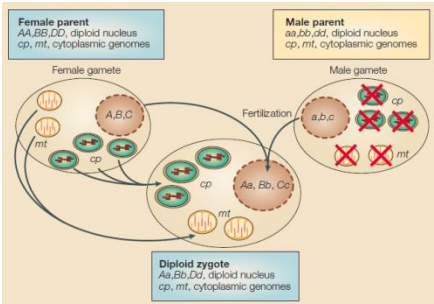




When do we expect biological adaptations to be “optimal” enough to reveal quantum processes?

and

How can we exploit natural variation to study quantum processes in biology?

John (Jack) Werren
Department of Biology
University of Rochester

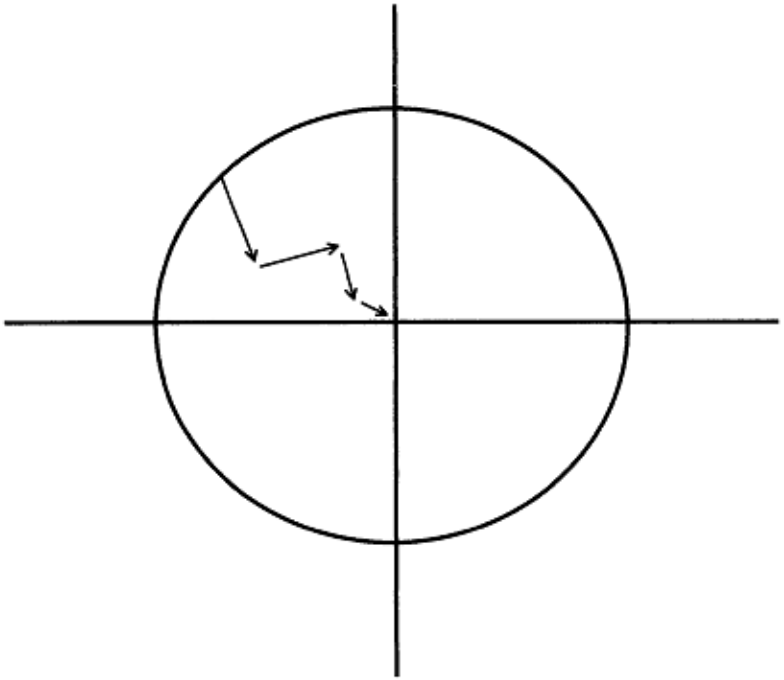


# Outline

- Relevant Population Genetics
- Some Features of Chloroplast & Nuclear Genomes
- Exploiting Natural Variation to Reveal Quantum Processes
- Black Holes, Common Goods Problem, and Quorum Sensing
- Provacative Questions?

What happens as a system evolves toward the Optimum?

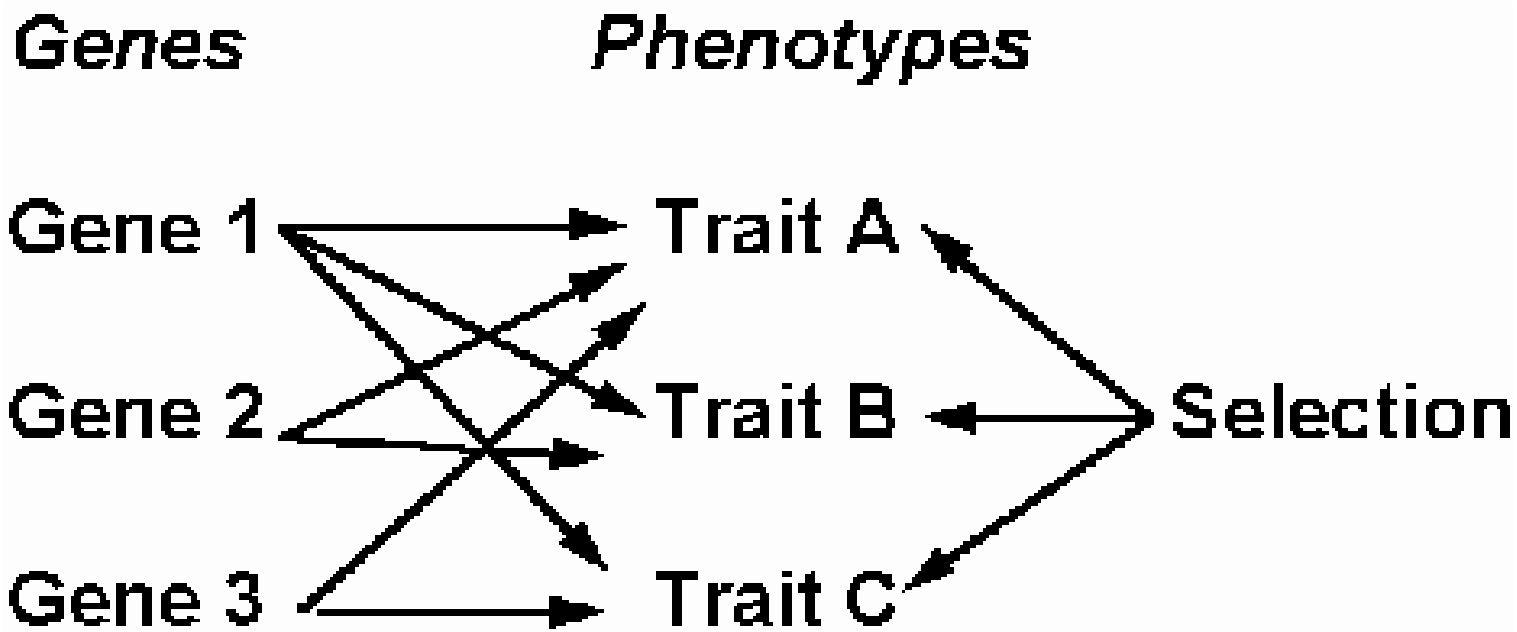
How close can it get?



# Some Relevant Processes that Shape Adaptations

- Mutation
- Selection
- Genetic Drift
- Pleiotropy
- Epistasis
- Recombination
- Functional Trade-offs
- Environment

# Pleiotropy

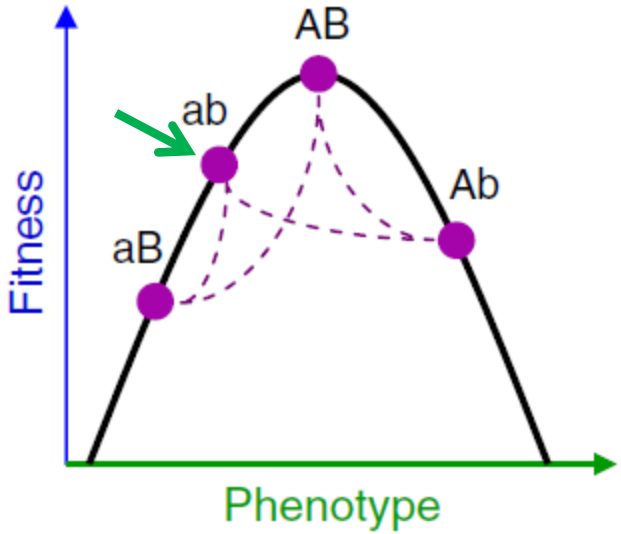



Individual Genes Can Effect Different Traits
Which is being optimized? Genetic Tradeoffs

http://www.ucl.ac.uk/~ucbhdjm/courses/b242/

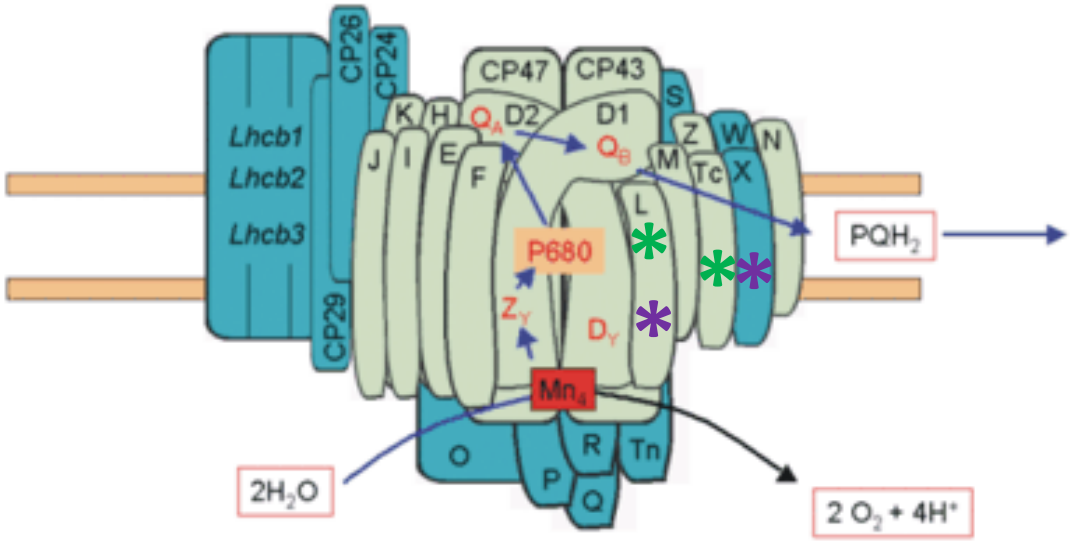
# Gene Interactions (Epistasis)

When Epistasis Can Constrain Achieving an Optimum




When Intermediates have Lower Fitness

Requires double mutations
(requires very large population size)




Interprotein Epistasis

Intraprotein Epistasis

# Mutation-Selection Balance
# In Infinitely Large Populations
# (Single Locus)

$p^* = u/s$ haploids

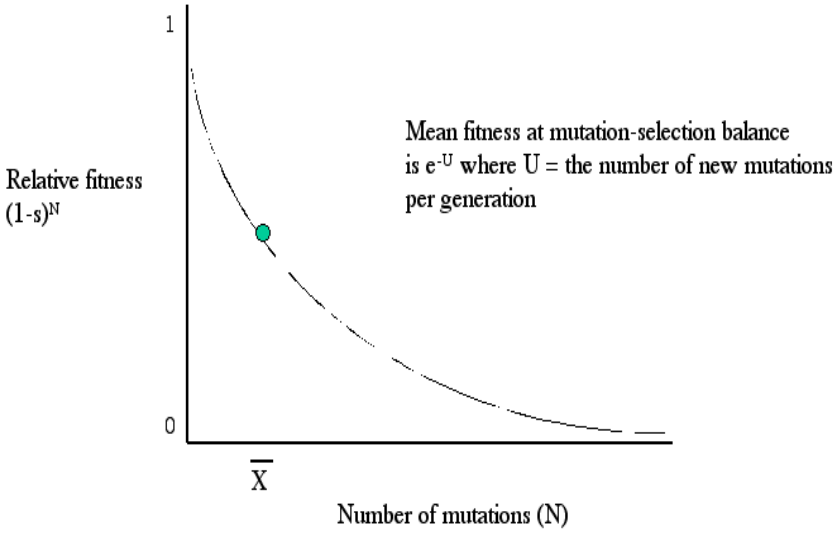
$p^* = \text{sqr}(u/s)$ diploids (recessive allele)

$p^* \sim u/(sh)$ for diploid (intermediate dominant)

p* - equilibrium frequency of the deleterious mutation
u - mutation rate from wild-type to mutant allele
s - fitness reduction of the deleterious allele
(wild-type W = 1 mutant W = 1-s)

Neglects back mutations

# What about mutations in a suite of genes that affect a trait?



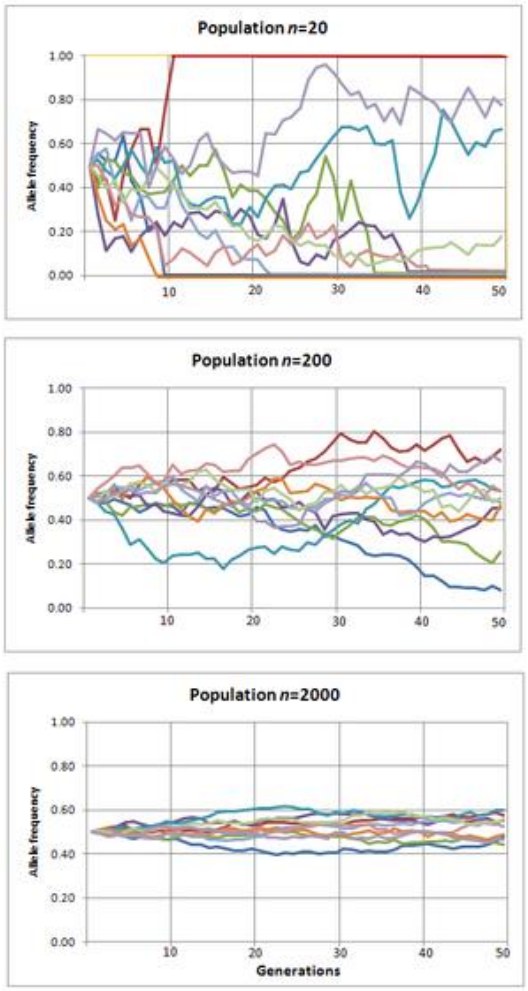

U – total new deleterious mutations per generation

Depends on number of genes causing the phenotype

The more genes, the greater the number of targets for harmful mutations
And the greater the distance of the trait from the optimum due to harmful mutations

www.mpg.de

# Population Size and Genetic Drift Can Limit Adaptation




**Genetic drift** – stochastic sampling of alleles in finite populations will lead to changes in allele frequencies over time.

The larger the population, the slower are changes in allele frequency due to drift.

But even Very large populations experience drift

Drift can also effect the probability positively selected alleles will become “fixed”

“fixed” in genetic parlance means the allele goes to 100% (or nearly so)

# Effective Population Size ($N_e$ )

$N_e$ - Idealized population size that should result in a particular pattern of polymorphism in a population

$N_e << N$ Why?

- Population size fluctuations
- Population substructure & Inbreeding
- Stochastic variation in survival and fecundity
- Selection
- Mating Systems

Table 1 | **Effective population size ($N_e$) estimates from DNA sequence diversities**

| Species | $N_e$ | Genes used | Refs |
|---|---|---|---|
| ***Species with direct mutation rate estimates*** | | | |
| Humans | 10,400 | 50 nuclear sequences | 145 |
| *Drosophila melanogaster* (African populations) | 1,150,000 | 252 nuclear genes | 108 |
| *Caenorhabditis elegans* (self-fertilizing hermaphrodite) | 80,000 | 6 nuclear genes | 41 |
| *Escherichia coli* | 25,000,000 | 410 genes | 146 |
| ***Species with indirect mutation rate estimates*** | | | |
| Bonobo | 12,300 | 50 nuclear sequences | 145 |
| Chimpanzee | 21,300 | 50 nuclear sequences | 145 |
| Gorilla | 25,200 | 50 nuclear sequences | 145 |
| Gray whale | 34,410 | 9 nuclear gene introns | 147 |
| *Caenorhabditis remanei* (separate sexes) | 1,600,000 | 6 nuclear genes | 43 |
| *Plasmodium falciparum* | 210,000–300,000 | 204 nuclear genes | 148 |

Charlesworth 2009

# In General

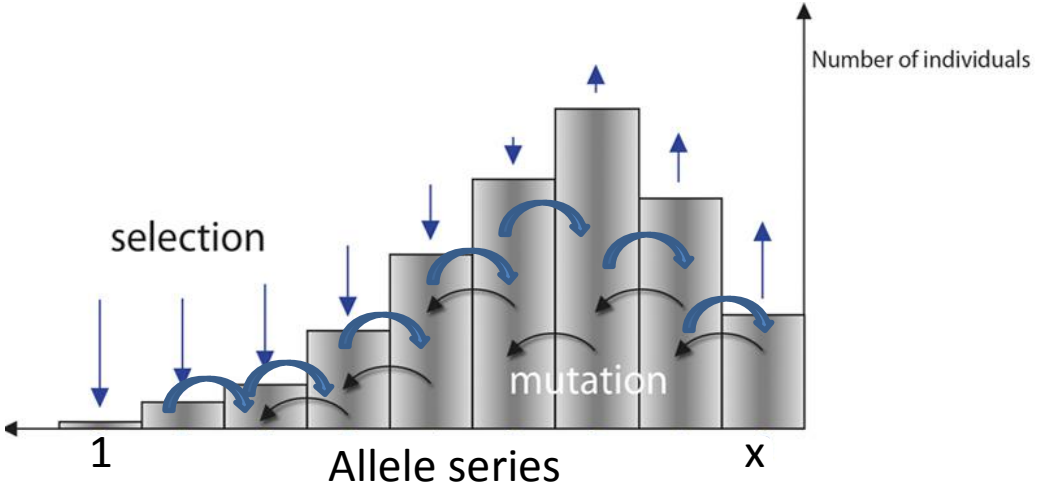
$s >> 1/N_e$ Selection is stronger than genetic drift

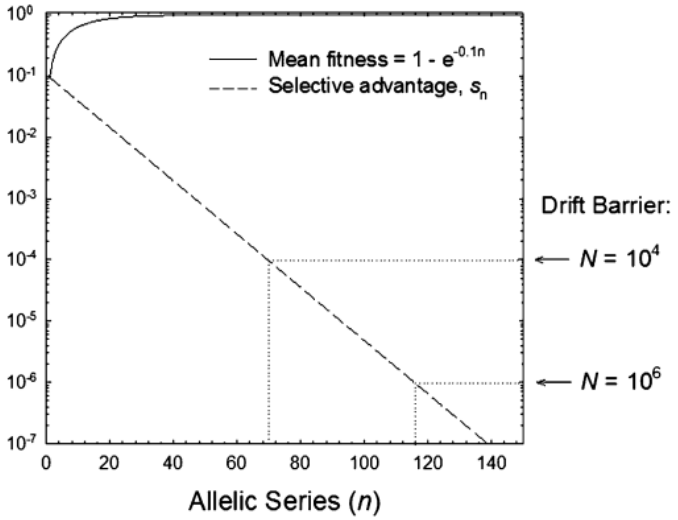
$s << 1/N_e$ Selection is weaker than genetic drift
(selected alleles are effectively neutral)

New mutations, even with strong effect, have a finite probability of being lost by drift

# Combining Mutation, Selection & Drift

(Lynch 2012)



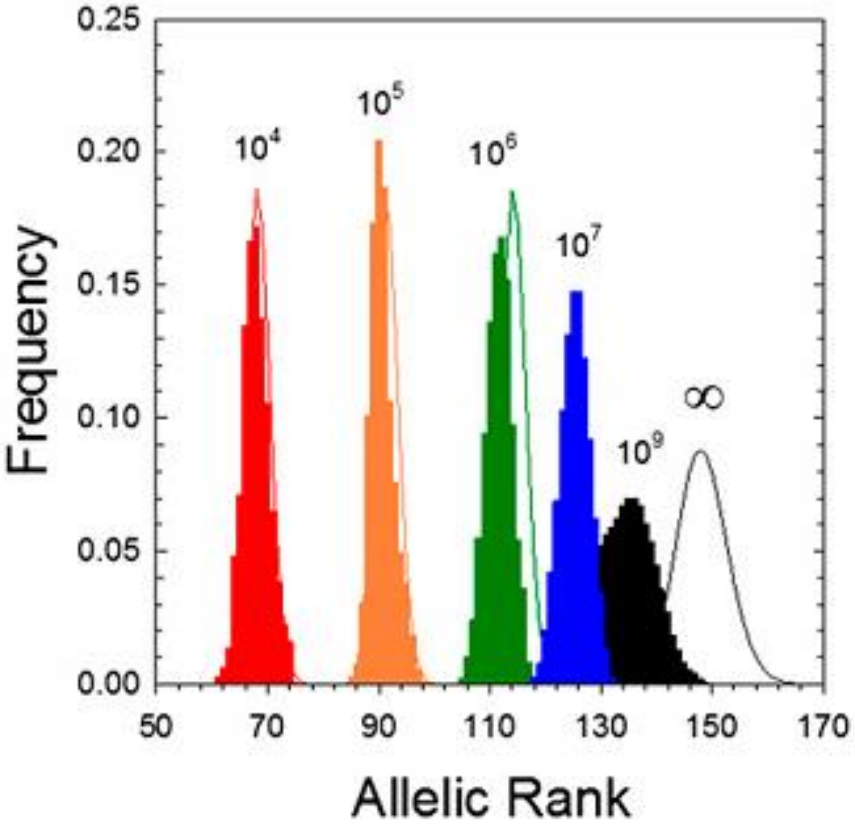

Step-wise mutations
Fitness increment $s_i = e^{-Ki}$

u – rate of beneficial mutations
v - rate of harmful mutations

As the optimum is approached, incremental fitness gains ($s_i$) become smaller

Smaller populations hit the "Drift Barrier" (when fitness gain is effectively neutral) sooner

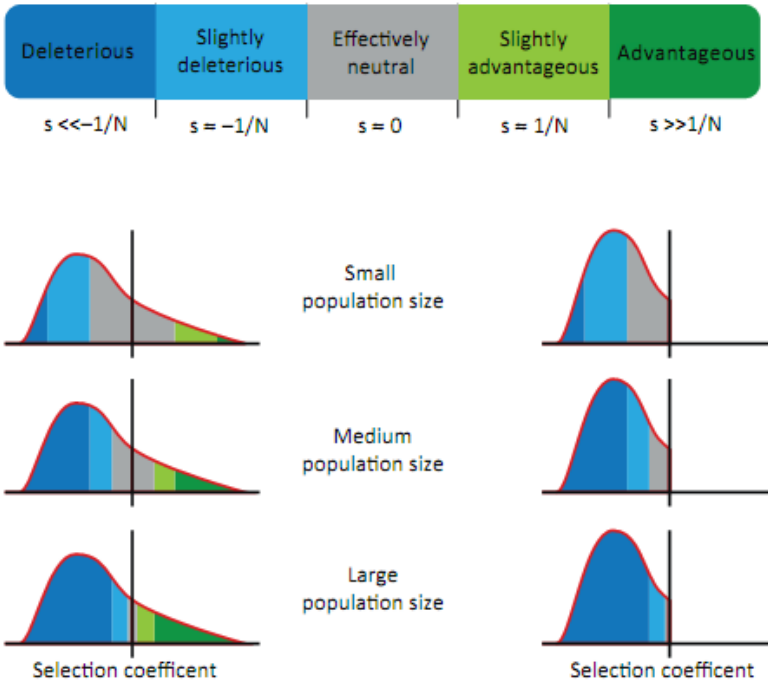
# What Happens?

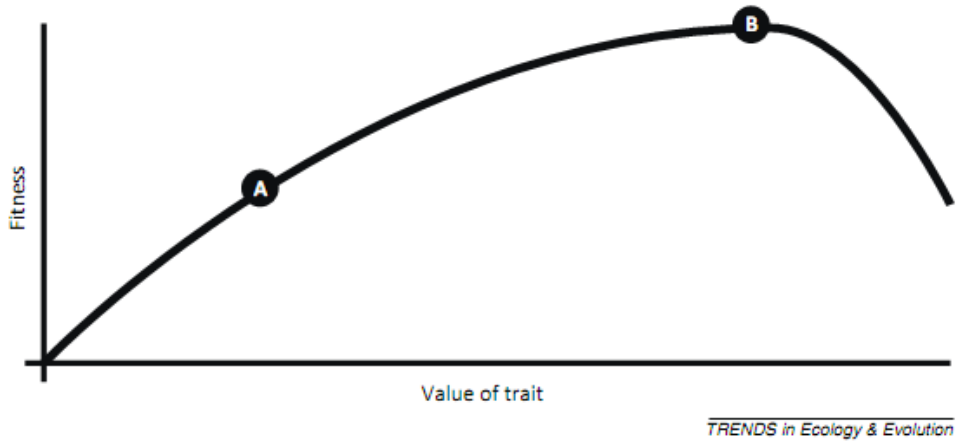



1. System evolves upward until the fitness gain is effectively neutral due to population size Population Size Matters.

2. The model assumes that beneficial and harmful mutation rates are unchanging; however, the relative numbers of beneficial mutations will decline as the optimum is approached

3. The mutation process is unrealistic and there is no recombination in this system




As the optimum is approached, the proportion of mildly deleterious and nearly neutral mutations increases because effect sizes of beneficial mutations become effectively neutral

Lanfear et al. 2014

# General Findings

- Species with larger Ne will show

(a) more adaptive evolution

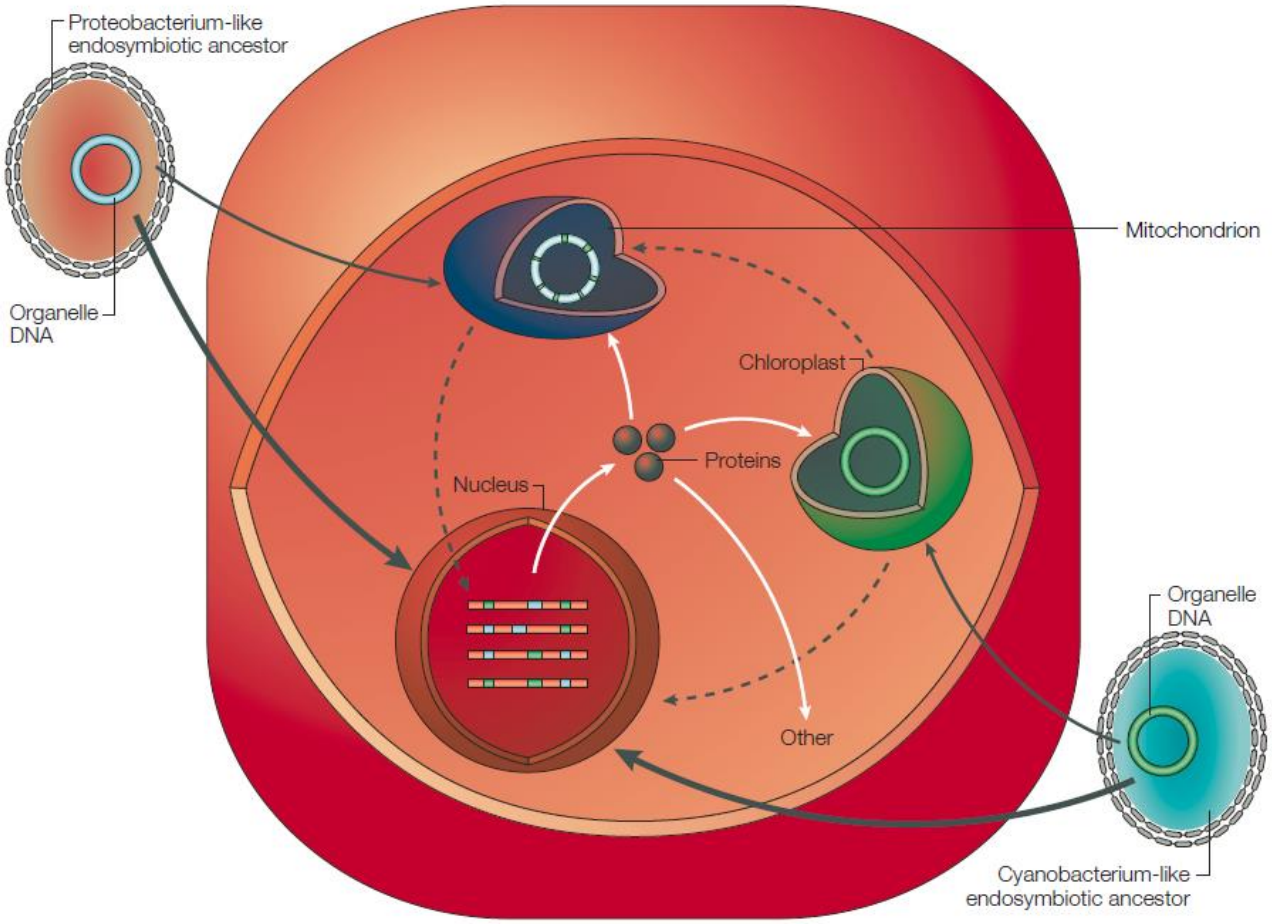
(b) evolve closer to the optimum (s>1/ Ne)

(c) Are less likely to fix mildly harmful mutations

- Species with smaller Ne will show the opposite and are likely to have more rapid divergence in nuclear-cytoplasmic incompatibilities
- Recombining genomes are better at evolving adaptively. Chloroplasts suffer from non-recombining genomes.

# Some Points About Chloroplasts & Their Evolution

# Extensive Transfer of Symbiont & Then Organelle Genes to the Nucleus




Timmis et al 2004

Chloroplasts retain ~100 of their original 2,500 proteins

(Wise 2006)

Photosystem II is composed of nearly 30 different protein subunits encoded by both the chloroplast and the nuclear genomes.

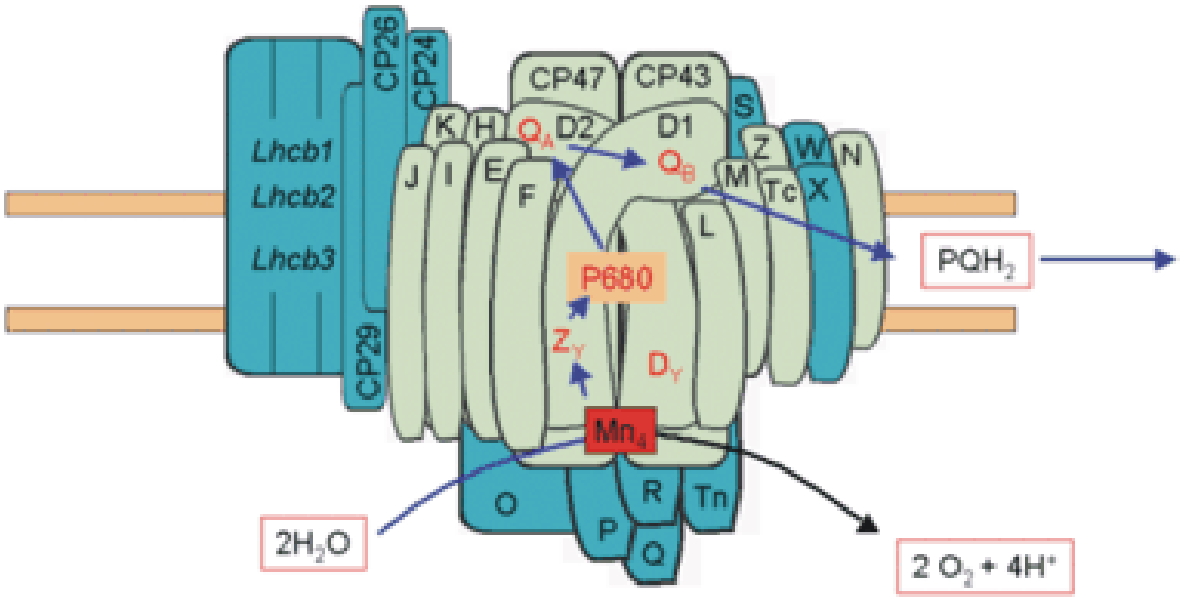
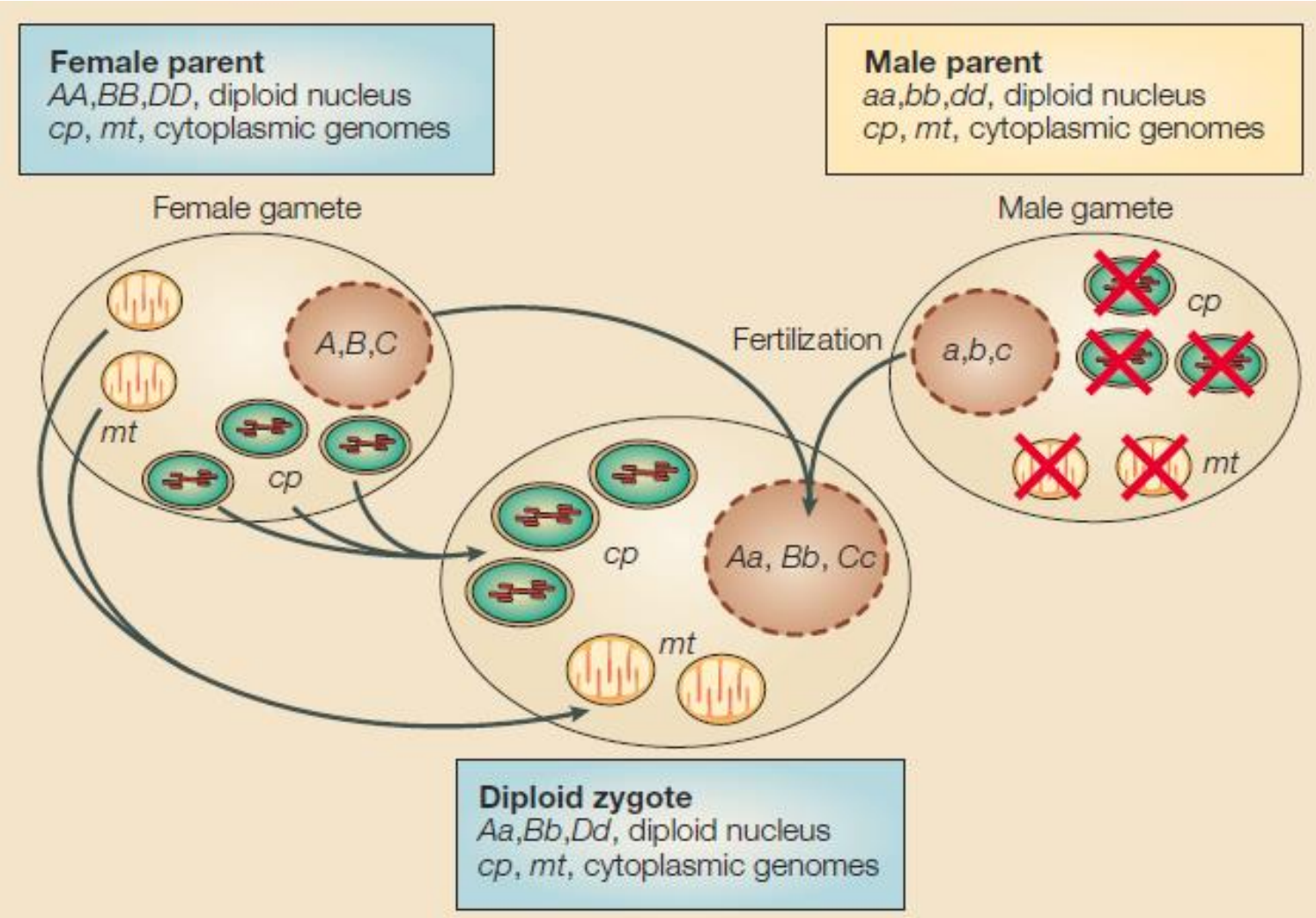



**Fig 1.** *Photosystem II: nuclear-encoded proteins in blue, chloroplast encoded proteins as light blue.* Tikkanen group

Mutation rates differ between Ch & Nuc Genome
Ch genomes are asexual – no recombination

# General Inheritance Patterns of Nuclear and Plastid Genes




Timmis et al 2004

# Chloroplast Inheritance

Chloroplast Inheritance is generally maternal (through the seed)

There are mechanisms to ensure uniparental inheritance of chloroplasts (e.g. active elimination of paternal chloroplasts).

Gymnosperms (e.g. pines and firs) pass chloroplasts paternally.
Some angiosperms are now know to do this as well.

Chloroplast inheritance is often disrupted in hybrids (showing genetic control of inheritance).

## Consequences of Chloroplast Uniparental Inheritance

Smaller Effective Population Sizes -> Drift
**Hitch-hiking** in non-recombining genomes -> fixing mildly harmful mutations

# How Natural Variation Can Be Used to Study Quantum Processes in Biology

# What Are the Advantages of Using Natural Variation?

Mutagenesis

Natural Variants

Sieve of Natural Selection

# Natural Variation is Expected Within Species for Photosystem Efficiency

*Genet. Res., Camb.* (1988), **52**, *pp.* 33–43 *With 7 text-figures* *Printed in Great Britain*



## Quantitative genetic variability maintained by mutation-stabilizing selection balance in finite populations

PETER D. KEIGHTLEY AND WILLIAM G. HILL
*Department of Genetics, University of Edinburgh, West Mains Road, Edinburgh EH9 3JN*

(*Received 25 October 1987 and in revised form 23 December 1987*)

And perhaps for coherence levels and features

# Species and Ecotypes are Likely to Differ in Photosystem Efficiency due to Adaptation To Different Environments

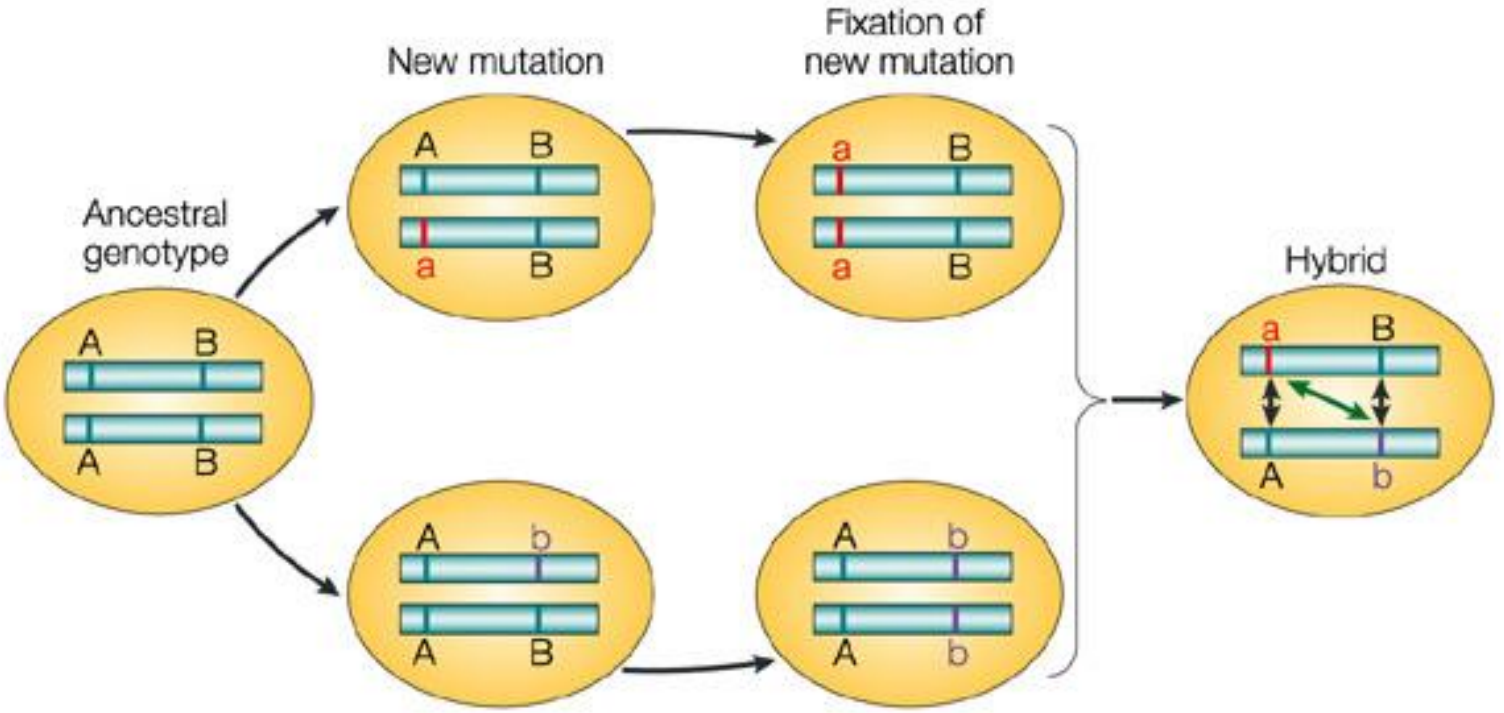
e.g. Low Light Conditions
(Shade Tolerant)

e.g. High Light Conditions
(Shade Intolerant)

..and due to different effective population sizes and mutation rates

# Related Species with Diverging Co-adapted Gene Complexes

## Dobzhansky-Muller Incompatibilities

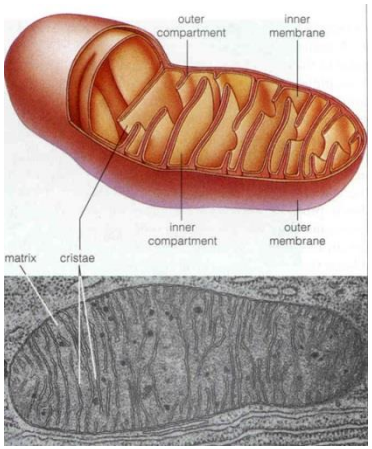


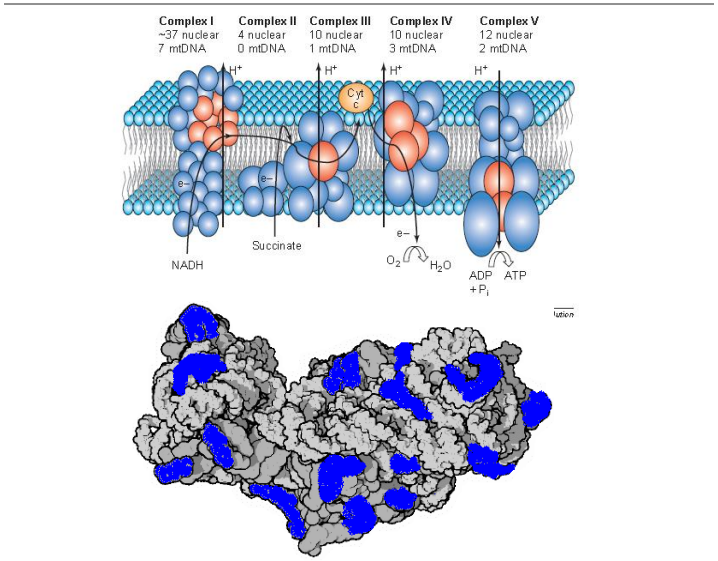

Wu & Ting 2004

Nature Reviews | Genetics

Likely to be a Rich Source for Genetic Tools to Study Quantum Processes

# *Nuclear-Mitochondrial Incompatibilities Common in Nasonia insects*




Oxphos

Mt Ribosome

High mitochondrial mutation rate (~35X higher than nucleus)

Interacting nuclear genes (e.g. Oxphos and RNP) are the fastest evolving genes in related species

Nuclear-Mt incompatibilities are major contributors to reduced fitness of hybrids

Breeuwer & Werren 1995
Oliveira et al 2007
Werren et al 2010

Photosystem II is composed of nearly 30 different protein subunits encoded by both the chloroplast and the nuclear genomes.

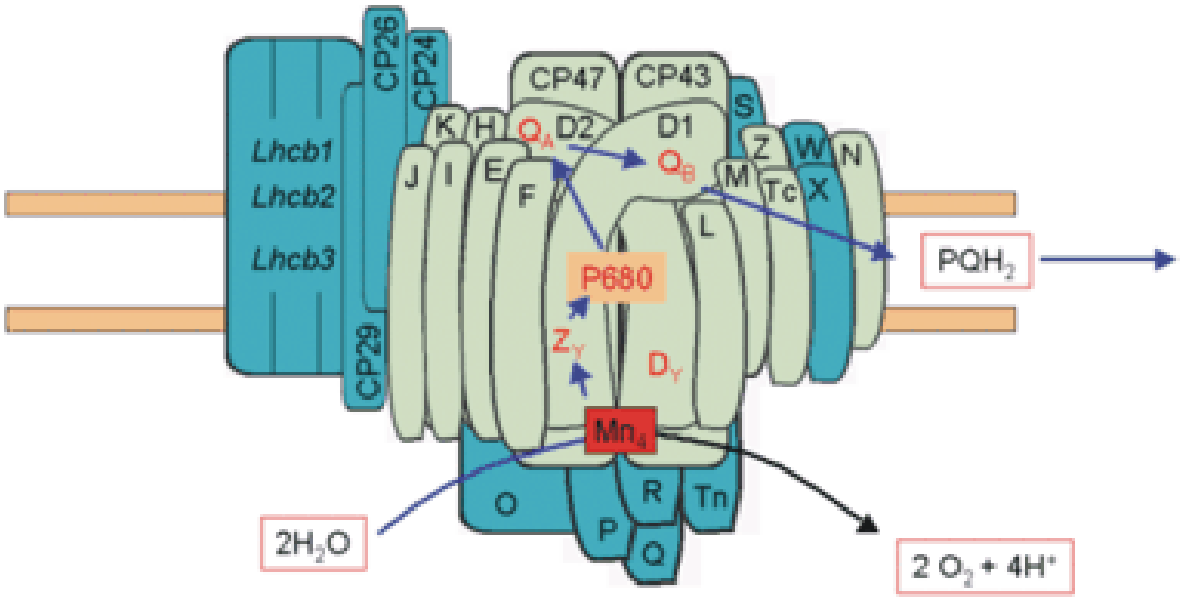



**Fig 1.** *Photosystem II: nuclear-encoded proteins in blue, chloroplast encoded proteins as light blue.* Tikkanen group

Uniparental (Asexual) Inheritance in Chloroplasts

Reduces effective population size and increases fixation of mildly deleterious mutations by hitch-hiking when beneficial mutations spread

Accelerates Nuclear-Chloroplast coevolution & DZ Incompatibilities.

# Relative Mutation Rates of Chl, Mt and Nu differ considerably among different groups

| | |
|---|---|
| Chlamydomonas and Mesostigma | Chloroplast = Nucleus = Mitochondria |
| Most seed plants | Mitochondria < Chloroplast (3x) < Nucleus (10X) |
| Red algal (Porphyra ) | Chloroplast = Nucleus < Mt (3x ) |
| Phaecystis (Red algal derived plastid) | Nucleus < Chloroplast (3x) < Mitochondria (10x) |

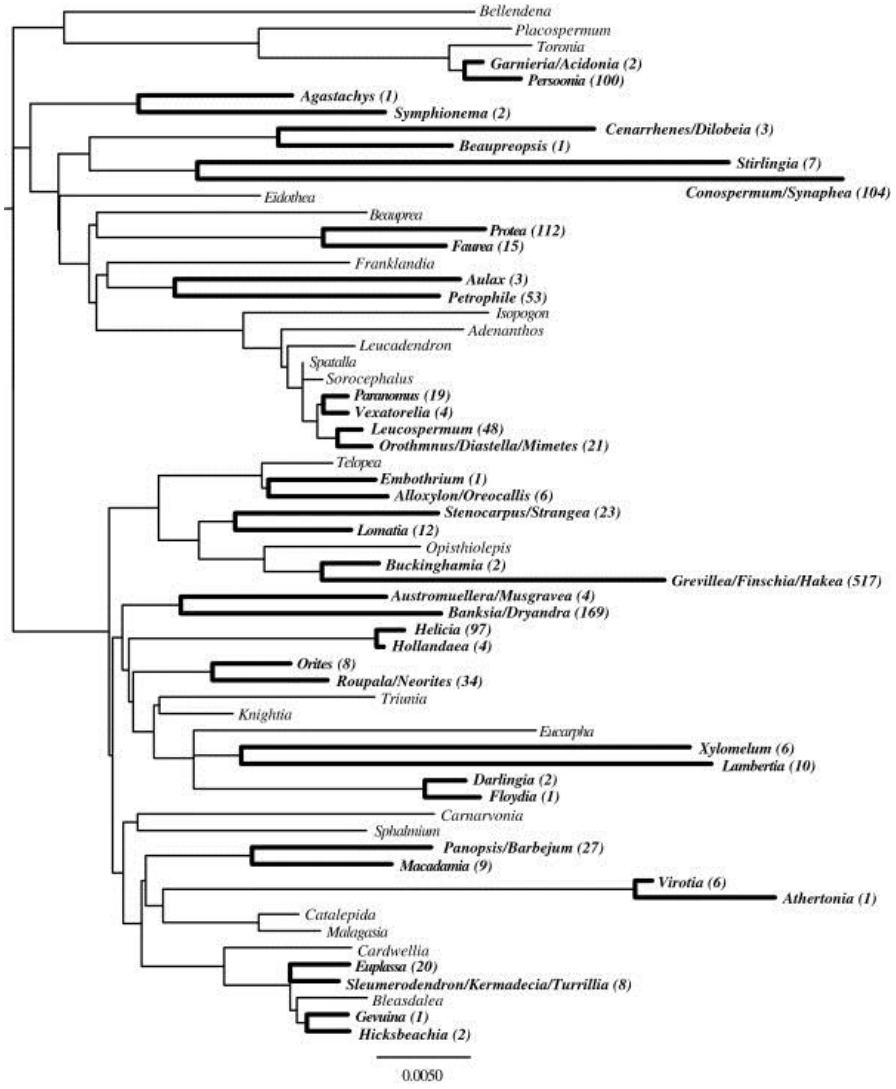
Smith et al 2013

This variation is rather amazing.
Will Effect Rates of Evolution in the Photosynthesis Machinery

## Effective Population Size of Nucleus and Chloroplast Can Differ Remarkably Even Between Closely Related Species

| | $N_c/N_n$ | |
|---|---|---|
| *Arabidopsis thaliana* | 1.0 | Inbred Species |
| *Arabidopsis lyrata* | 0.5 | Outbred Species |

# Chloroplast Mutation Rates Vary Widely Between Species And Correlate With Diversification of Plant Lineages




Duchene & Bromham 2013

Lineages with higher chloroplast mutation rates have higher speciation rates!!

Maybe due to more rapid accumulation of D-M Incompatibilities between nuclear and chloroplast geneomes

A resource for studying genetics of photosystem efficiency

# Black Holes, Common Goods, & Quorum Sensing

Schwab & Herbert 2004

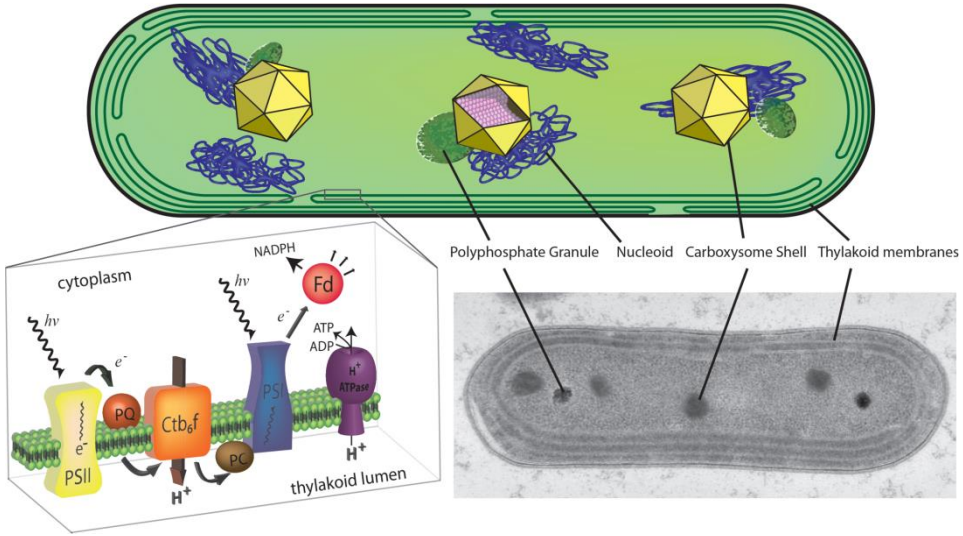
How Selection May Shape Heat Production versus Photosynthesis
In Phototrophic Purple Sulfur Bacteria

"Common Goods" problem.

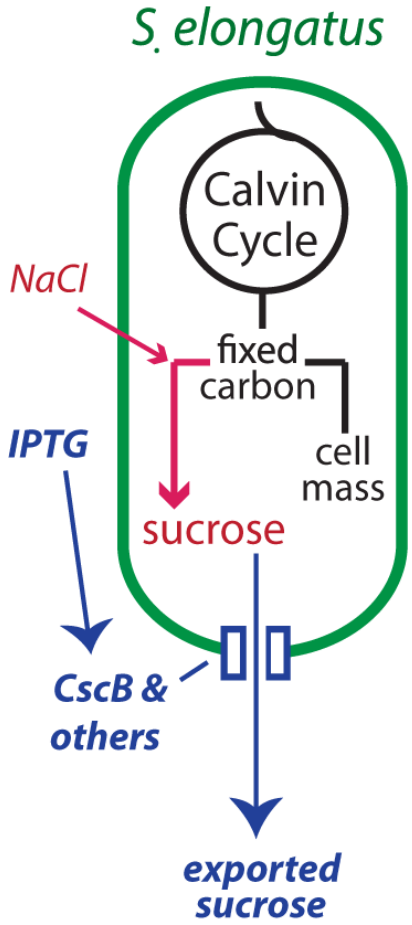
NOT ENOUGH TIME

# Bioengineering Cyanobacteria as Photosynthetic "Factories" for Sugars

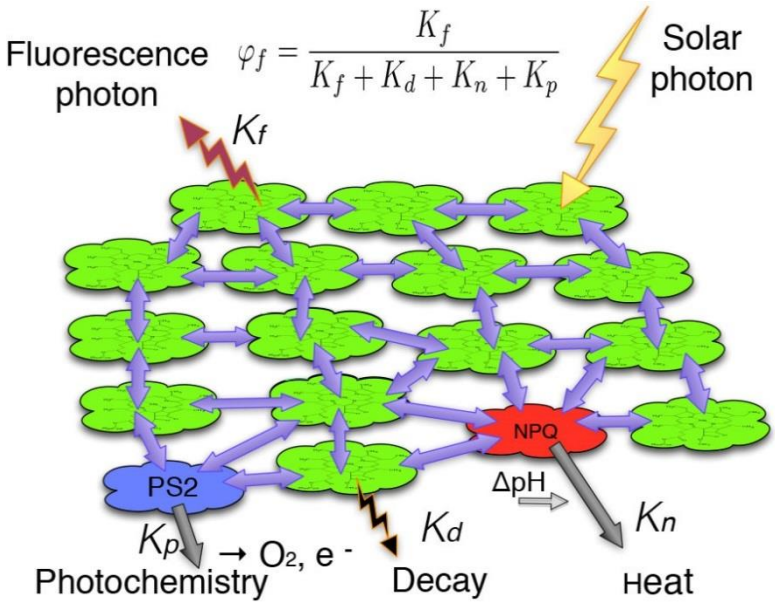
Danny Ducat (MSU)




*Synechococcus engineered to export sucrose*

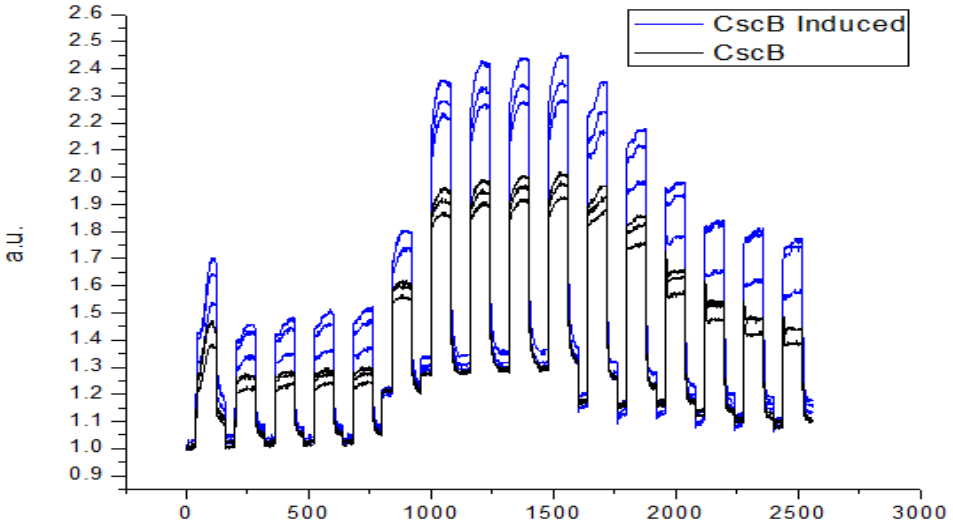


Used Chlorophyll Fluorescence as a proxy of photosynthesis efficiency




Frankenberg, Christian, et al. 2013. SPIE

Increased Phi2 is consistent with an enhancement in photosynthetic efficiency in sucrose-secreting cyanobacteria




So, Sucrose in Cell Appears to Inhibit Photosynthesis.

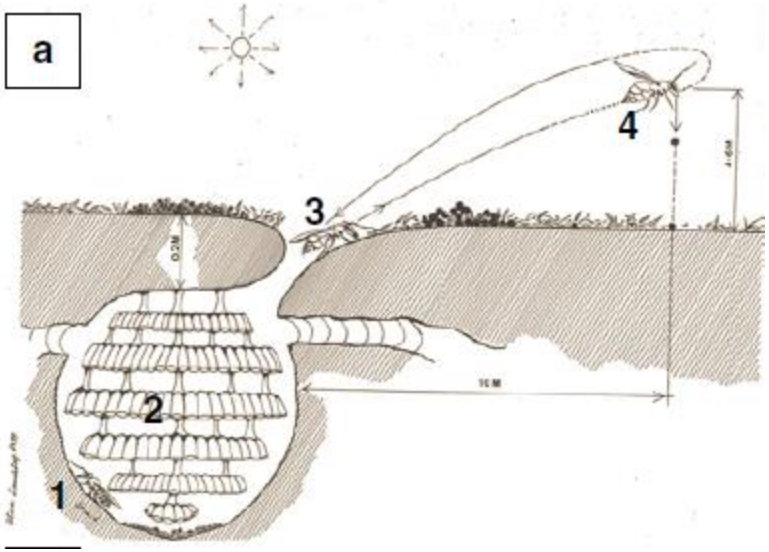
Use of Engineered Cells Removes This Inhibition

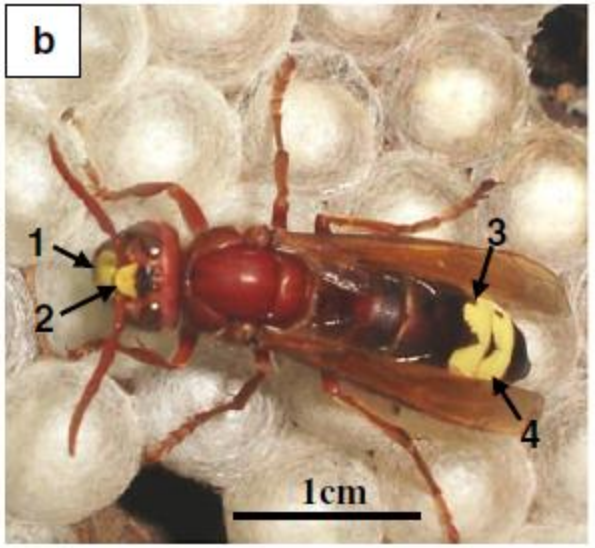
**Experiment** – Select Cells for Higher Levels of Photosynthesis Efficiency

**Question** – Will Quantum Coherence Increase?

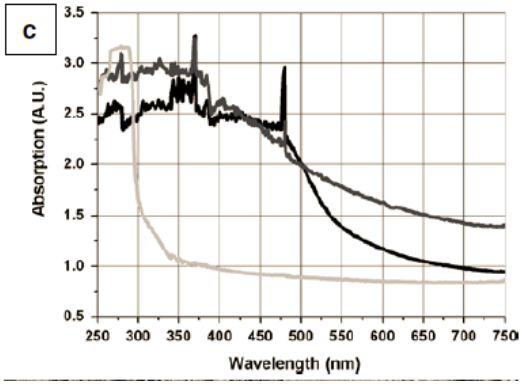
# Solar energy harvesting in the epicuticle of the oriental hornet (*Vespa orientalis*)

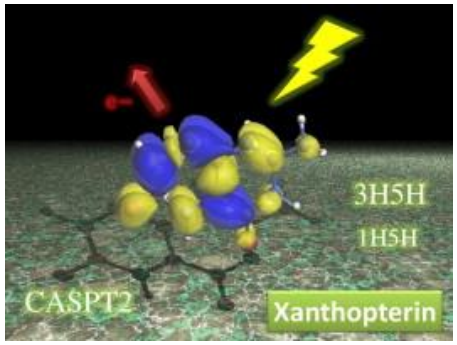
Plotkin et al 2010

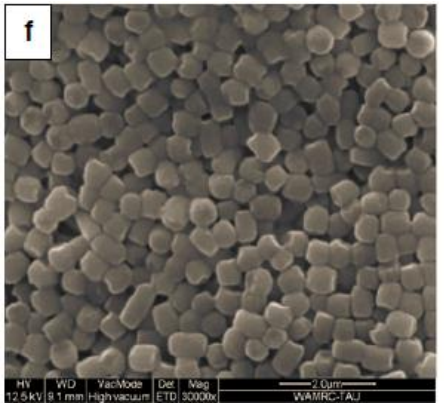


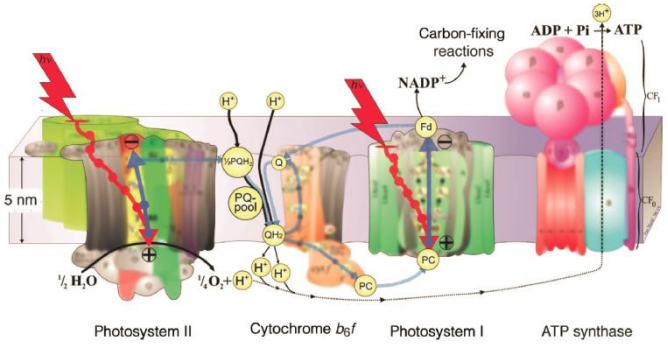




Xanthopterin

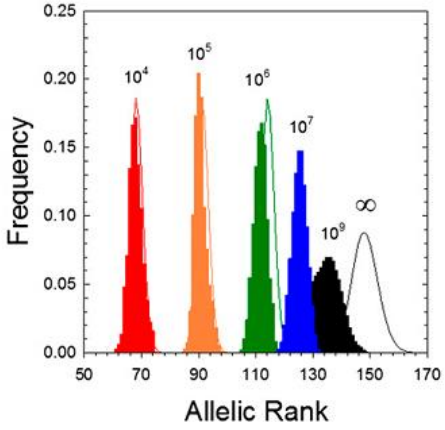


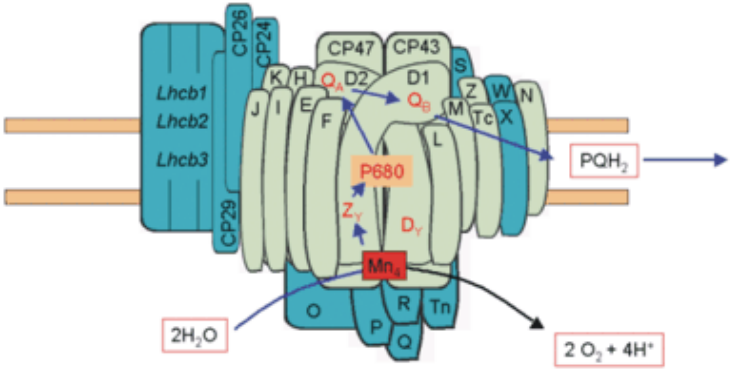



Quantum Processes

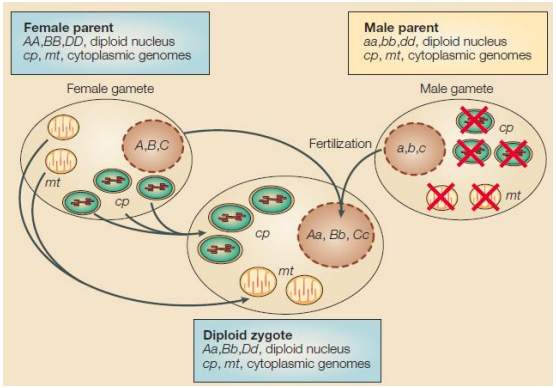



Variation

Adaptation




CytoNuclear Interactions



# Conclusions

I. IF quantum processes are important in photosynthesis efficiency,

Then species will differ in level of quantum efficiency based on differences in

- effective population size
- recombination and inbreeding
- Environment (e.g. low light adapatation)

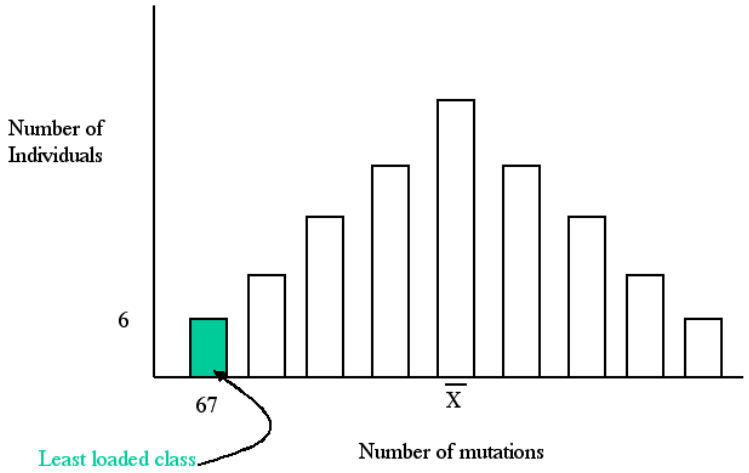
II. Natural variation can be used to test the role of quantum process in photosynthesis

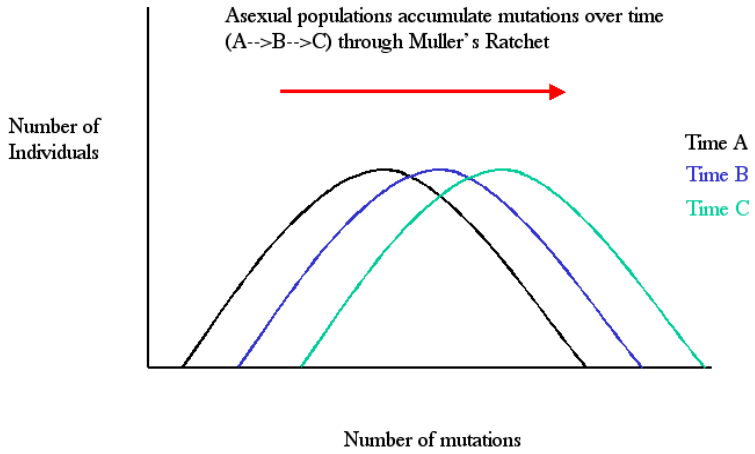
- Dobzhansky-Muller incompatibilities

IV. Interesting experiment to see if photosynthesis efficiency can be improved by experimental evolution. Does this result in increased coherence?

# EXTRAS

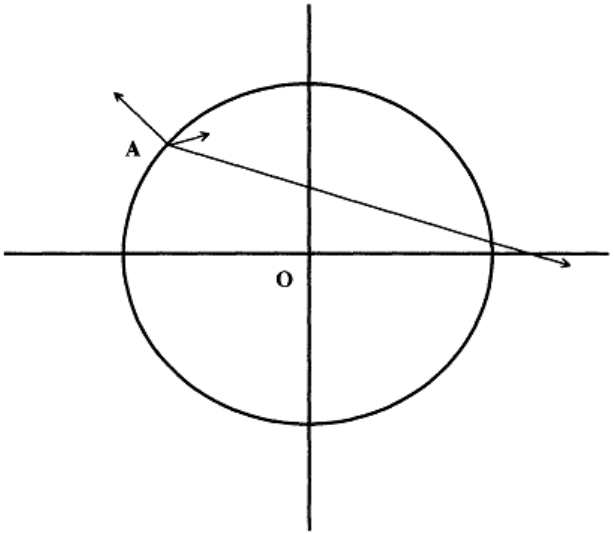
# Muller's Ratchet in Non-Recombining Lineages e.g. Chloroplasts



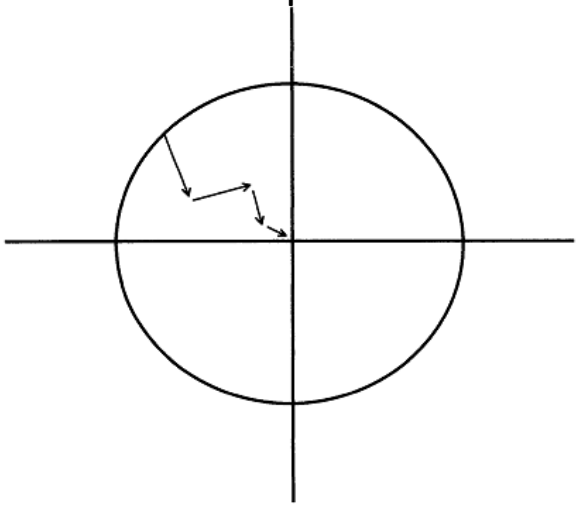




http://courses.bio.indiana.edu/S318-Lively/

Fisher's Two Dimensional Landscape of Adaptation

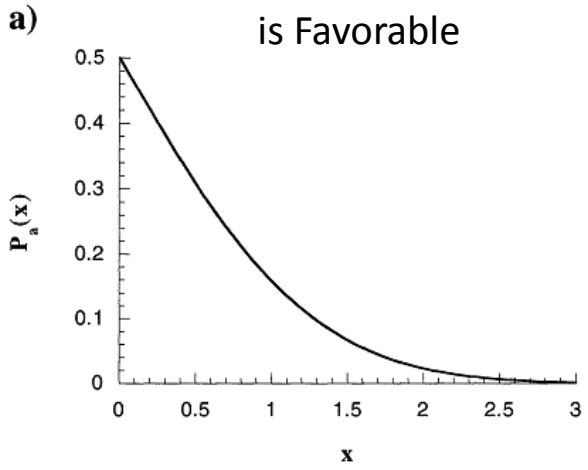



Adaptive Walk Toward The Optimum

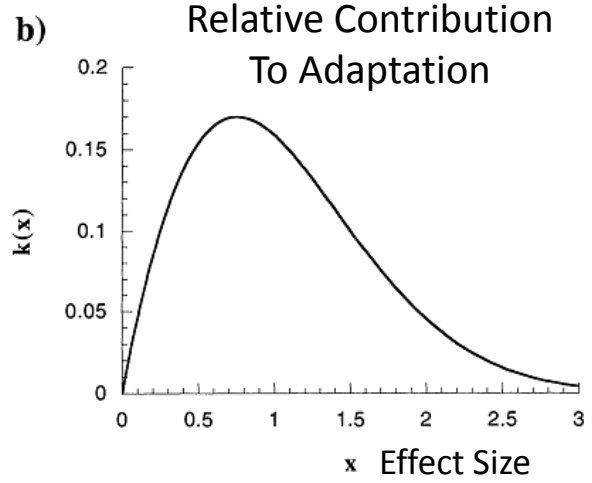


Orr 1998

Prob. a Mutation is Favorable




Relative Contribution To Adaptation




As the optimum is approached, the fitness benefit of each succeeding mutation becomes less

# Black Holes, Common Goods, & Quorum Sensing

1 m thick layer of phototrophic bacteria. The dominant phototrophic purple sulphur bacteria identified as members of the genera *Thiocapsa* and *Allochromatium* contain spirilloxanthin as a major photopigment which strongly absorbs light wavelengths between 480 and 550 nm but is relatively inefficient in channelling captured light energy to the photosynthetic reaction centres in these bacteria. We postulate that the excess captured light energy is dissipated as heat which would account for the observed increase in temperature.

Schwab & herbert 2004

How did it evolve? Benefit of heat exclusion of competitors?

"Common Goods" problem.

# The Common Goods Problem

Heat is a “common good” that could benefit all members of the population

If producing heat is costly, won’t individuals that do not produce it benefit without incurring the costs?

Therefore, is heat production really a “population adaptation” or merely a byproduct?

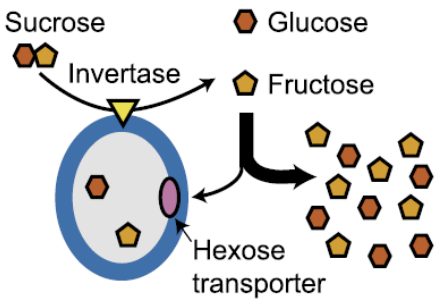
## Two Questions Evolutionary Genetics Ask About “Population Adaptations”

Will the “population adaptation” increase when rare in the population?

Is the “population adaptation” vulnerable to “cheaters” when in the majority?

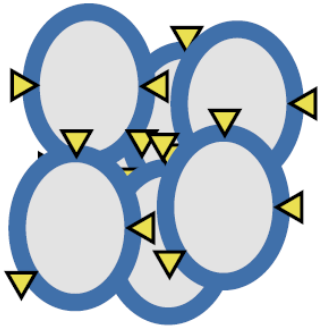
# Example from Yeast

At low cell density in low sucrose concentrations, yeast cells cannot capture enough glucose and fructose to grow.

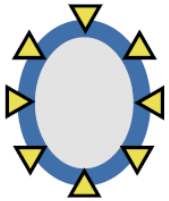



Three engineered strategies for growth in low sucrose:

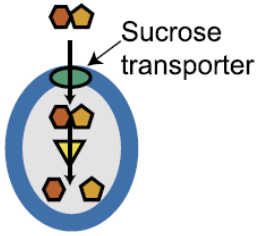
1. Form multicellular clumps.



2. Make more invertase.

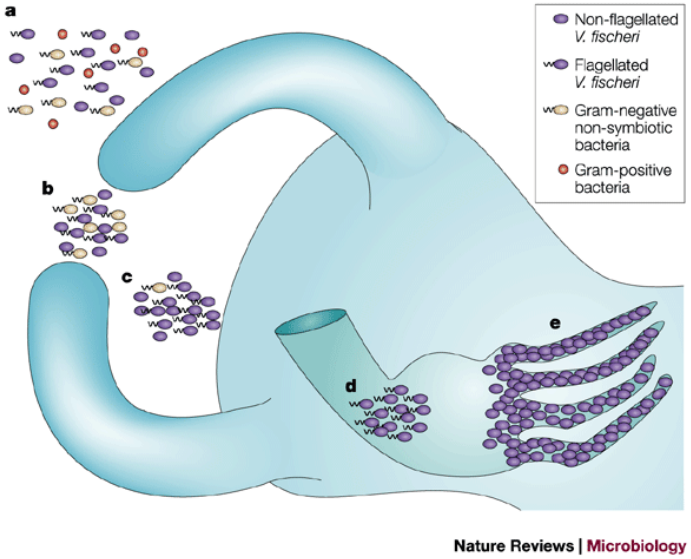


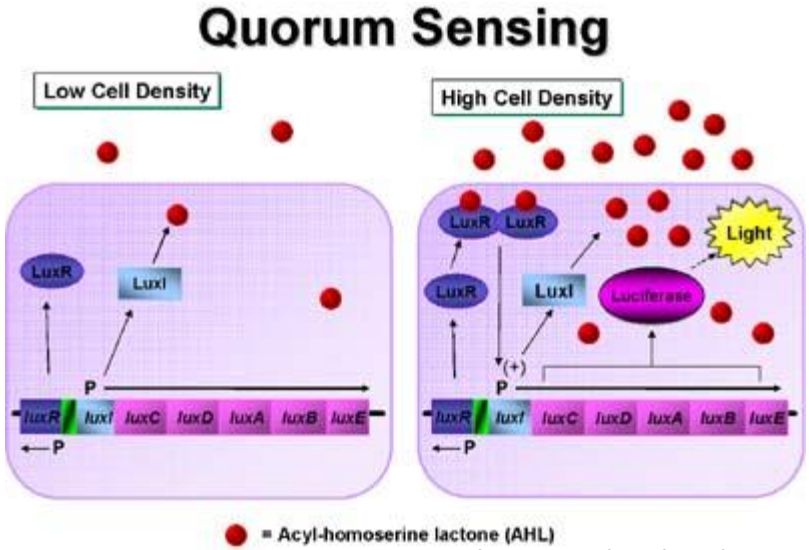
3. Import sucrose.




Koshwanez et al 2013

# Quorum Sensing




www.cheme.caltech.edu

Nyholm & McFall-Ngai 2004

# In the Black Hole

# We may find

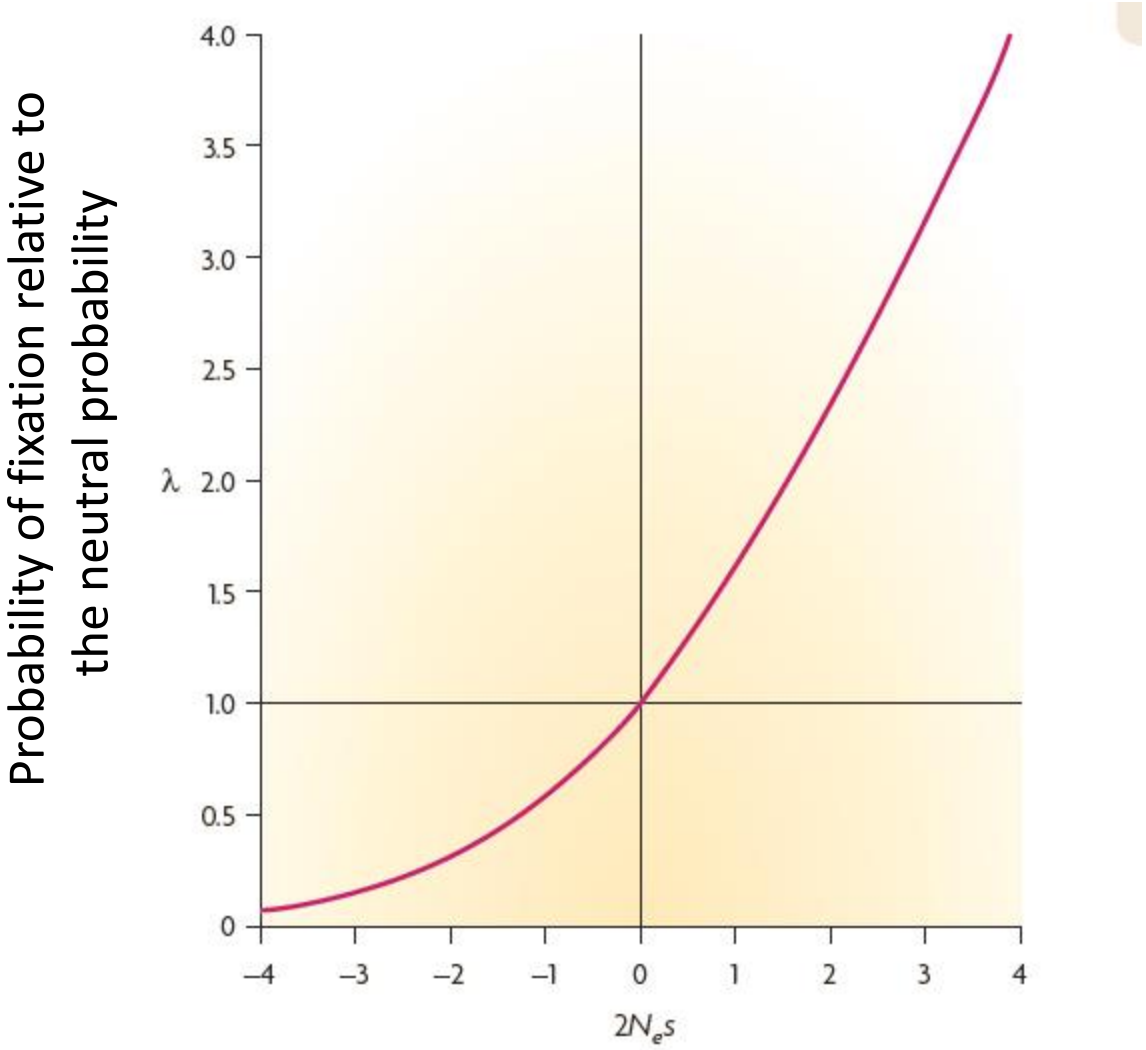
Genetic variants for heat production (“cheaters”) & photosynthetic efficiency

Facultative adjustments in photosystem through quorum sensing – shift from highphoto efficiency to heat production under crowding.

# Some “Provacative” Questions

- What limits plant growth? Is it photon capture or downstream processes? How does this impact evolution of efficiency?
- What are the roles of associated proteins in PSI and PSII in coherence?
- Does coherence increase efficiency of photosynthesis and if so how? (Anna 2014)
- Can we use D-Z incompatibilites and other natural variants to reveal the function of quantum processes in photosynthesis?
- What factors can explain variation in the quantum efficiency of photosynthesis in different organisms (e.g. population size, adaptation to different light environments, plastid and nuclear mutation rates)?
- Can we engineer photosystems to remove constraints, and if so will coherence increase?

# Probability of fixation of a new mutation

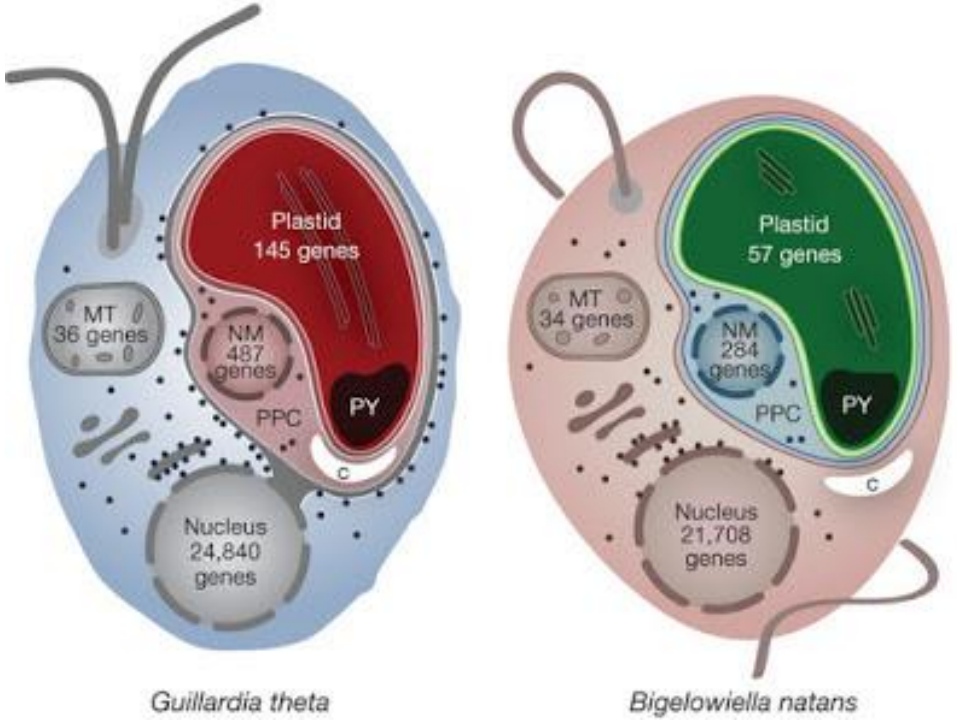



Charlesworth 2009

# Genomes of Two Protists

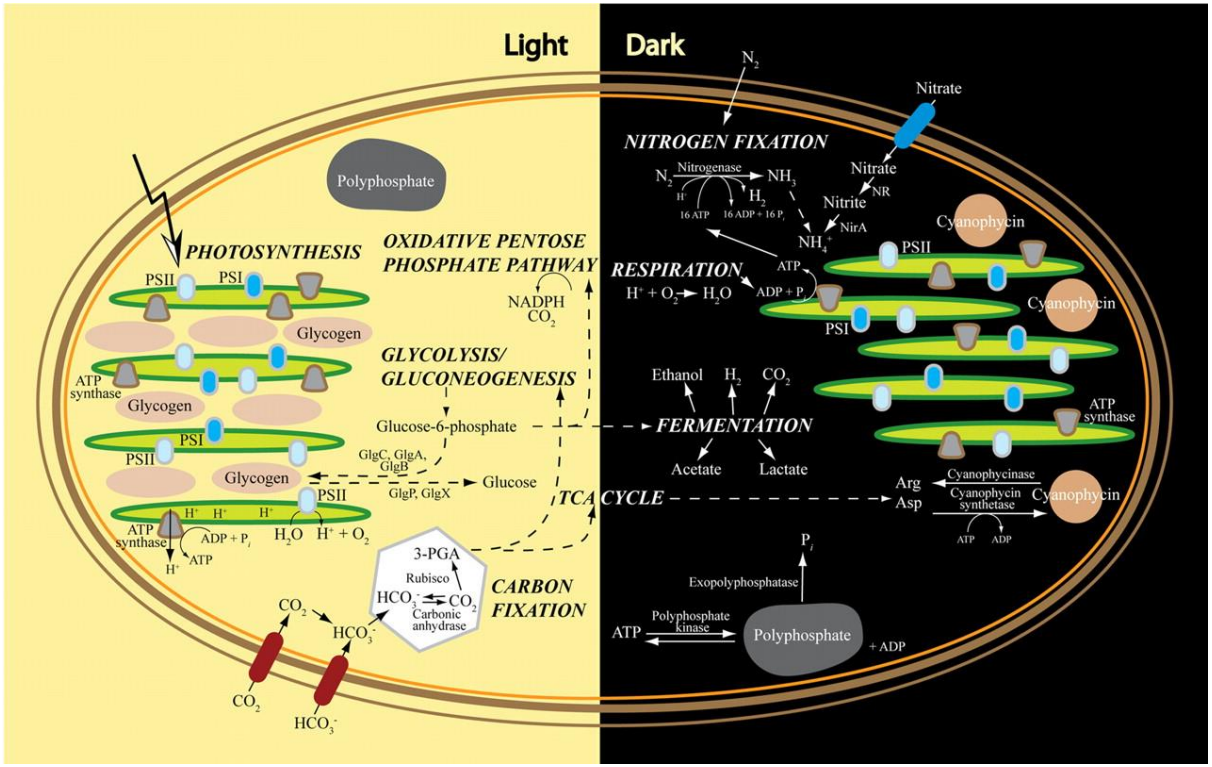
*Guillardia theta*
*Red algae*

*Bigelowiella natans*
Green algae



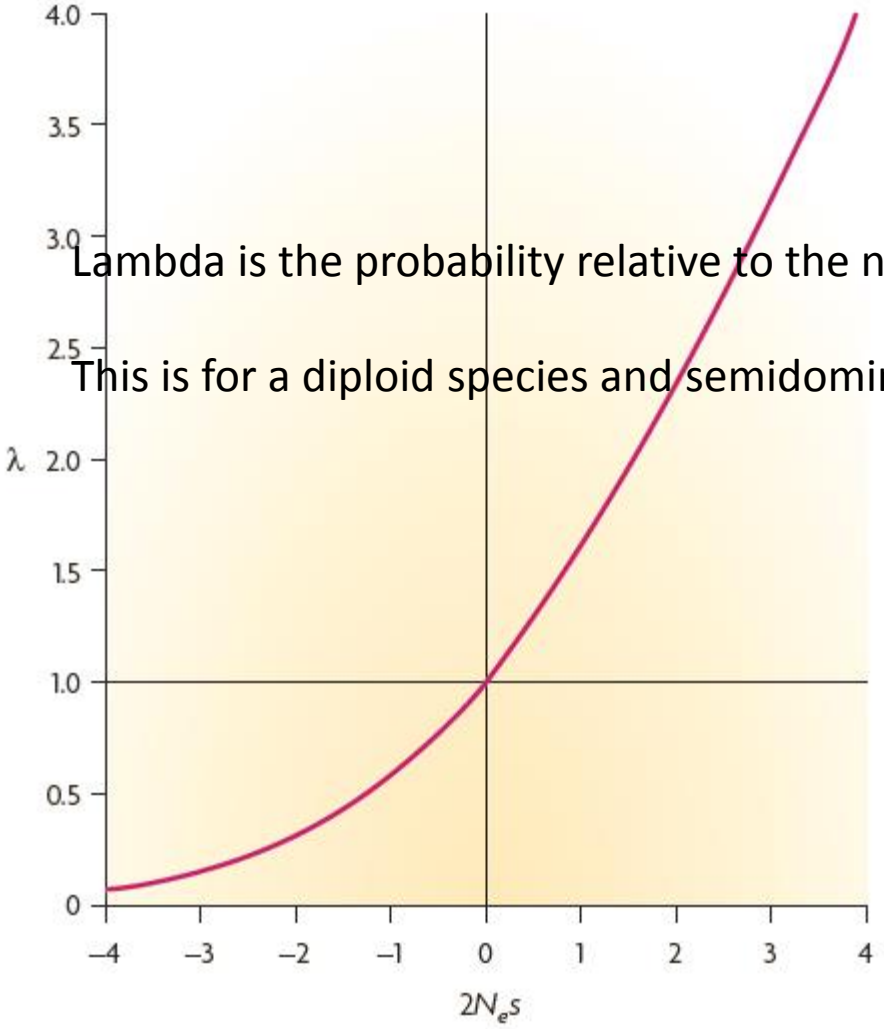

Acquired algal symbionts
Reduction in Algal Genomes - Nucleomorph (ca 300-500 genes)
Transfer of Algal genes to the nucleus

# Functional Trade-offs




e.g. Function in low light versus high light conditions
Photosynthesis versus other functions in the cell

Prob of fixation of a new mutation




Lambda is the probability relative to the neutral proba

This is for a diploid species and semidominant mutatic

The probability of fixation of a mutation is the cha
it will spread through the population and become
finite population, even deleterious mutations can
fixed by drift, and favourable ones can be lost. The
some fairly complex calculations[17,19,64] can be illust
with the simple case of selection at a biallelic auto
locus with semi-dominance, such that the relative
of $A_1A_1$, $A_1A_2$ and $A_2A_2$ are 1, 1 + 0.5$s$ and 1 + $s$, resp
$s$ is the selection coefficient, and is negative if $A_2$ is
deleterious and positive if it is advantageous.

If the population size is $N$, and the effective popu
size is $N_e$, the probability that a newly arisen mutat
from $A_1$ survives in the population and eventually
$A_1$ is given by:

$$Q \approx \frac{N_e s}{N} \frac{1}{\{1 - \exp(-2N_e s)\}}$$

The dependence of $Q$ on $N_e s$ is illustrated in th
λ is the fixation probability of a semi-dominant
expressed relative to the neutral value (1/2$N$). T
given by $Q$ (from the equation above) divided by
This also represents the evolutionary rate of sub
of mutations with selection coefficient $s$, relativ
rate for neutral mutations[8].

Charlesworth 2009

# Key Questions for Discussion

What limits plant growth? Is it the efficiency of photon capture and conversion, or is it the much slower and temperature sensitive processes of C, N, and S-Metabolism?

**Why do mitochondria and chloroplasts retain their own set of genes**

CoRR Hypothesis: Regulation of crucial genes by the redox state of the gene products within the organelle

Hydrophobicity Hypothesis: Hydrophobic regions of some proteins make them difficult to target back to the mitochondria or chloroplast

Genetic code divergence

Review- Daley & Whelan 2005

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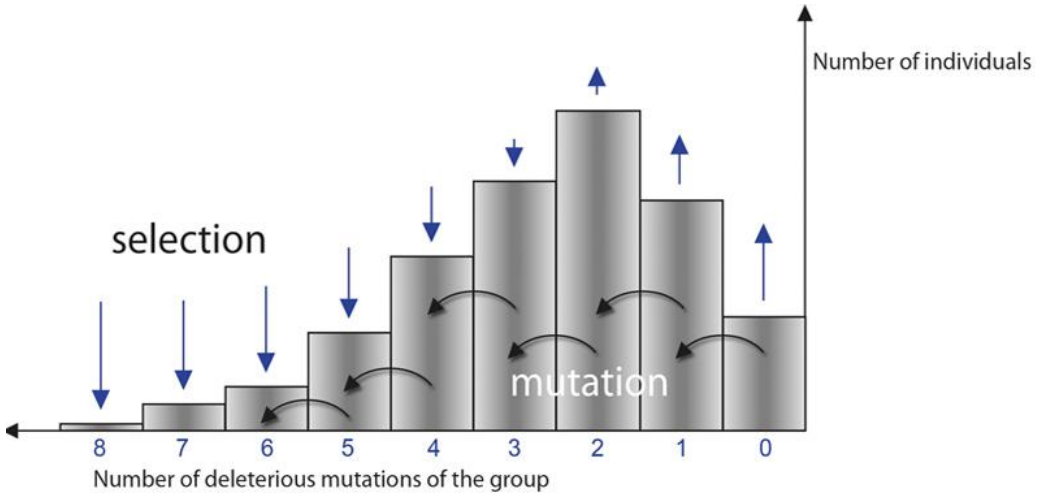
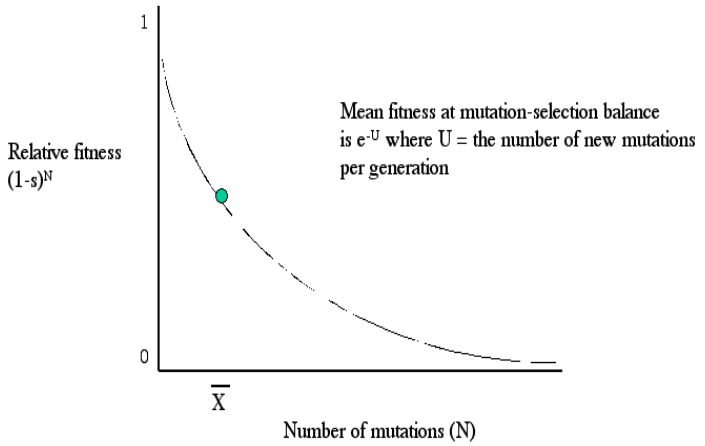
Organelle Competition Hypothesis: Organelles that have retained core gene set are better able to replicate and be transmitted, and therefore outcompete those loosing the core gene set.

Cyto-nuclear conflict Hypotheis: Genetic interests of organelle and host are not identical. Organelles are selected to retain genes that enhance their transmission. E.g. CMS in plant mitochondria.




U – total new deleterious mutations per generation

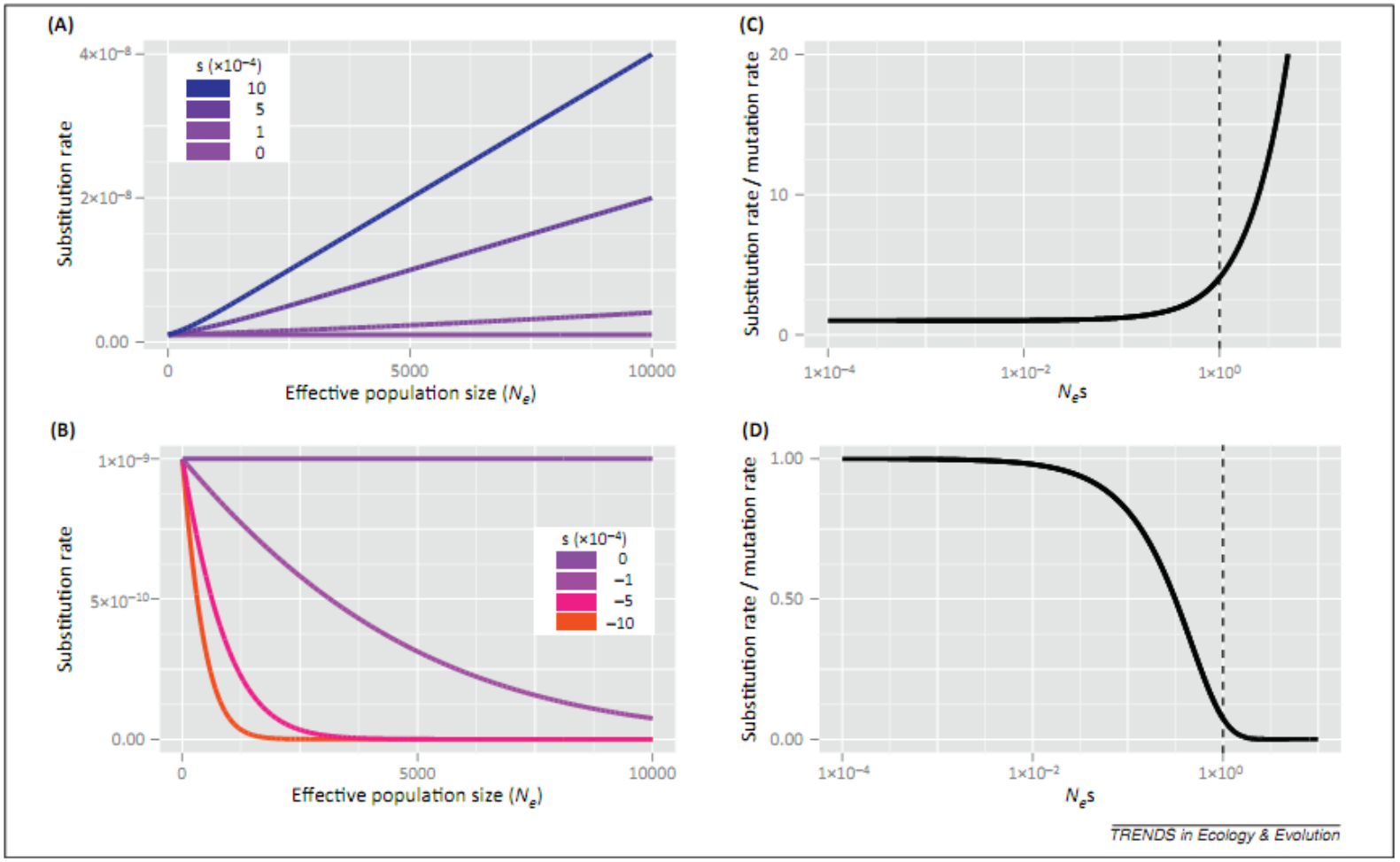



**Figure 1.** The relationship between substitution rate (in substitutions per site per year) and effective population size ($N_e$) under genetic drift and natural selection (the $N_e$RR) [8]. These relationships were calculated assuming a mutation rate of $1 \times 10^{-9}$ mutations per site per year, approximately that found in humans. **(A,B)** show the substitution rate of mutations for a range of positive (A) and negative (B) selection coefficients (denoted 's'). **(C,D)** show the same data, but in this case the y-axis shows the substitution rate relative to the mutation rate, and the x-axis shows the product of $N_e$ and the selection coefficient for positive (C) and negative (D) mutations respectively. A dashed line highlights where $N_e s = 1$, below which mutations are often considered 'effectively neutral'. Note that genetic drift predicts a flat $N_e$RR for neutral mutations, where s = 0.00 in (A,B). In (C,D), this is reflected by the substitution rate equaling the mutation rate, giving a value of 1 on the y-axis, when $N_e s = 0$.

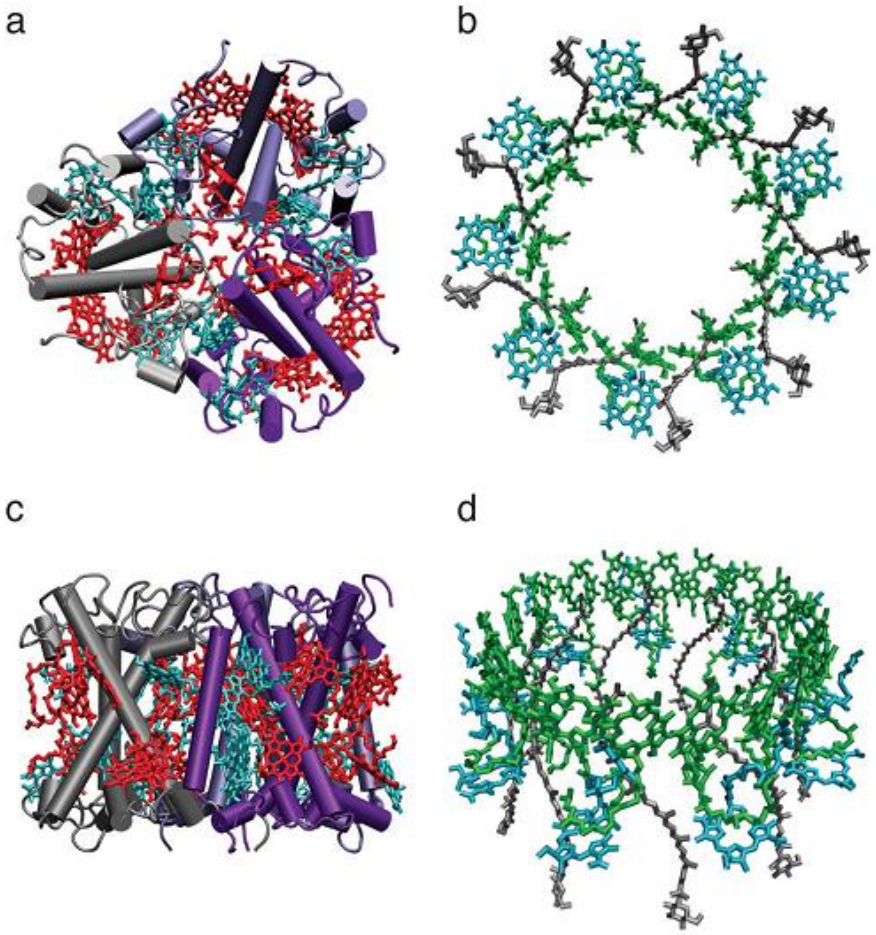
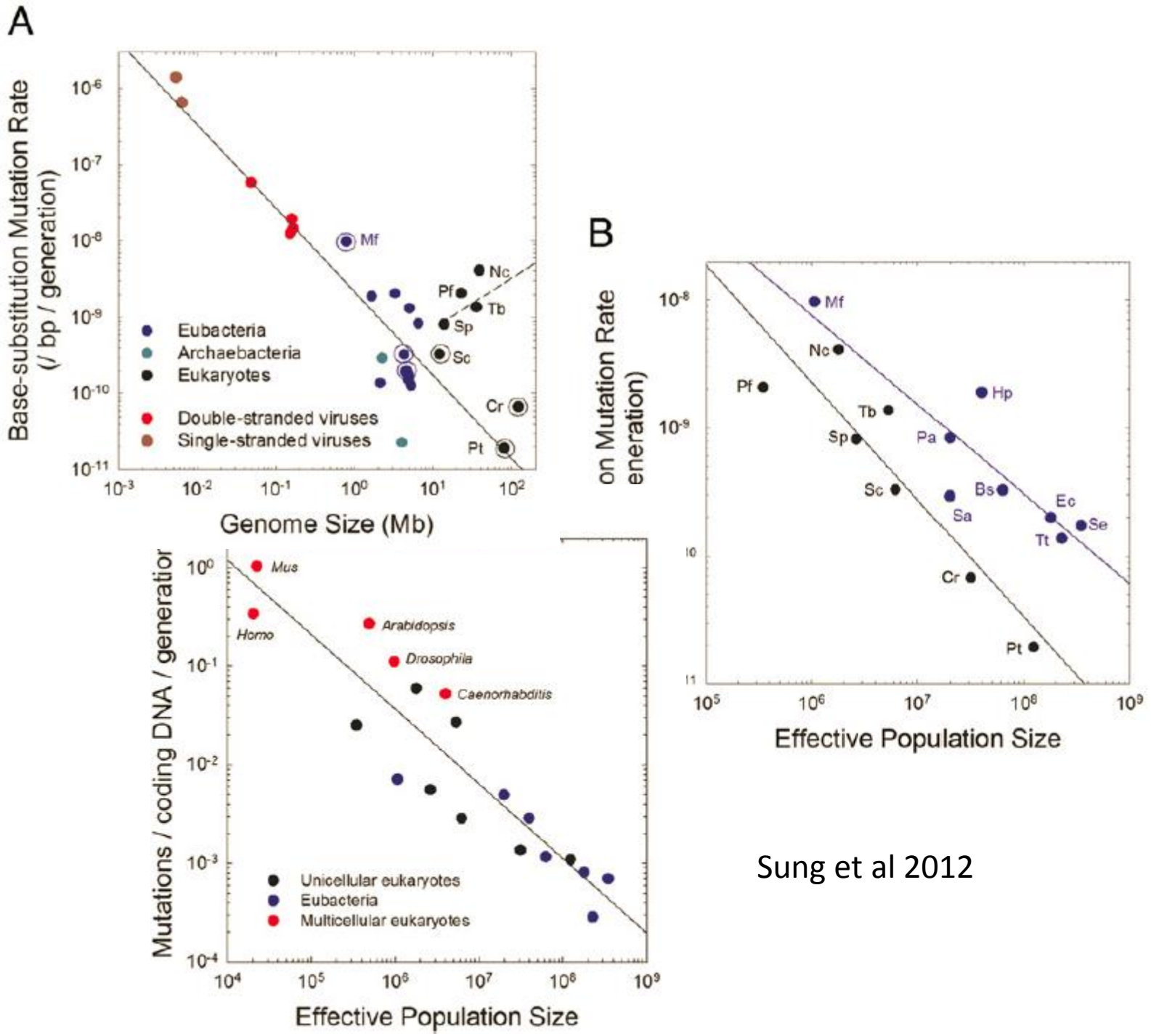



*Figure 6. Structural models of (a, c) LHCII from peas (Standfuss et al. 2005); the red molecules are chlorophyll a, and the blue molecules are chlorophyll b. (b, d) LH2 from* Rhodopseudomonas acidophila *strain 10050. Here, the green bacteriochlorophyll a molecules compose the B850 ring, and the light blue ones compose the B800 ring. The carotenoids are drawn in gray.*




Sung et al 2012

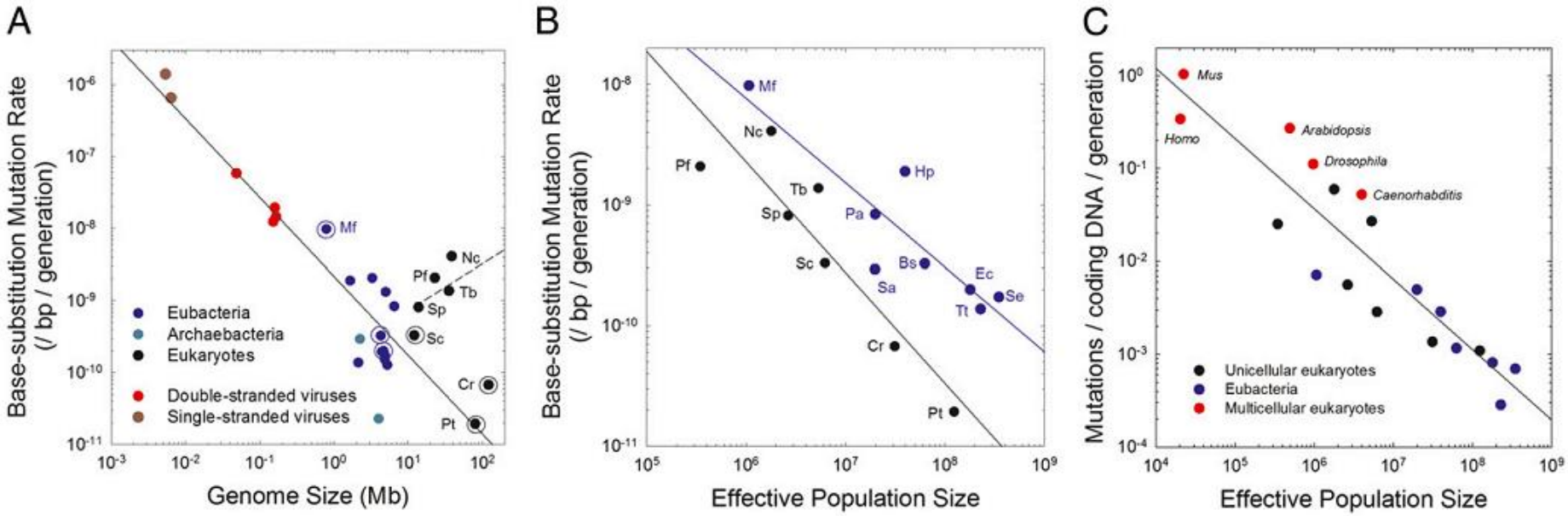
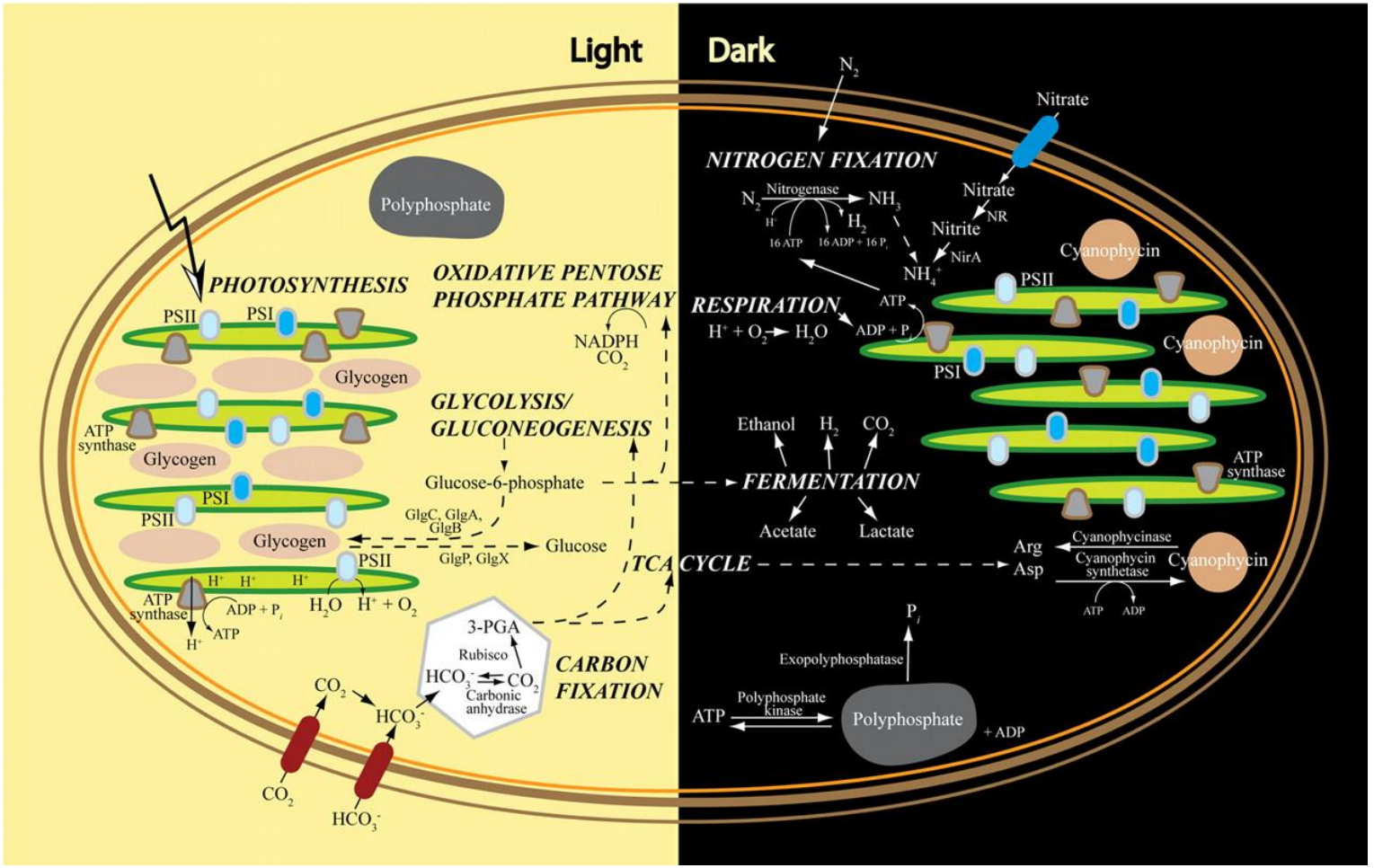
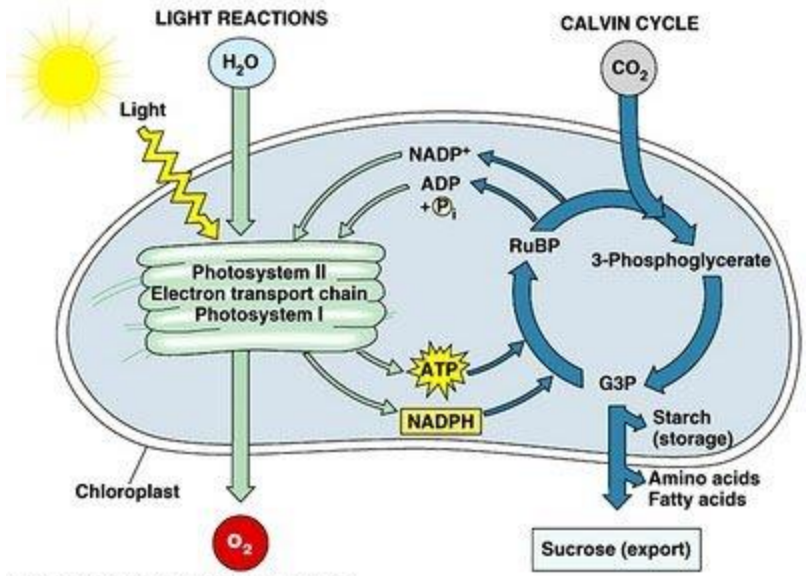



**Fig. 1.** (*A*) Relationship between the base-substitutional mutation rate/site/cell division and genome size. The regression includes all points except the four uppermost eukaryotes, for which the mutation-rate estimates are based on reporter constructs, $\log_{10}u = -8.663–1.096\log_{10}G$, where $u$ is the mutation rate, and $G$ is the genome size in megabases ($r^2 = 0.872$, $df = 21$). Points surrounded by a circle are based on mutation-accumulation experiments involving whole-genome sequencing; all others are based on reporter constructs. For euykaryotes: Cr, *Chlamydomonas reinhardtii*; Nc, *Neurospora crassa*; Pf, *Plasmodium falciparum*; Pt, *Paramecium tetraurelia*; Sc, *Saccharomyces cerevisiae*; Sp, *Schizosaccharomyces pombe*; Tb, *Trypanosoma brucei*. The prokaryote reported in this study, *Mesoplasma florum*, is denoted as Mf. The dashed regression line to the lower right includes multicellular eukaryotes (not shown) (4). (*B*) Relationship between the base-substitutional mutation rate/site/cell division and the effective population size ($N_e$) extrapolated from silent-site diversity. Eukaryotic regression (black): $\log_{10}u = -3.145–0.916\log_{10}N_e$ ($r^2 = 0.831$); prokaryotic regression (blue): $\log_{10}u = -3.920–0.699\log_{10}N_e$ ($r^2 = 0.794$). Labeled prokaryotic data points: Bs, *Bacillus subtilis*; Ec, *Escherichia coli*; Hp, *Helicobacter pylori*; Mt, *Mycobacterium tuberculosis*; Pa, *Pseudomonas aeruginosa*; Sa, *Sulfolobus acidocaldarius* (archaea); Se, *Salmonella enterica*; Tt, *Thermus thermophila*. (*C*) Relationship between genome-wide mutation rate/cell division for coding DNA and $N_e$. Regression: $\log_{10}(uG_e) = 3.109–0.757\log_{10}N_e$ ($r^2 = 0.844$). The data for multicellular eukaryotes (red) are summarized in Tables S8, S9, and S10, which are slight updates from the data previously summarized (4).

# What Limits Plant Growth?



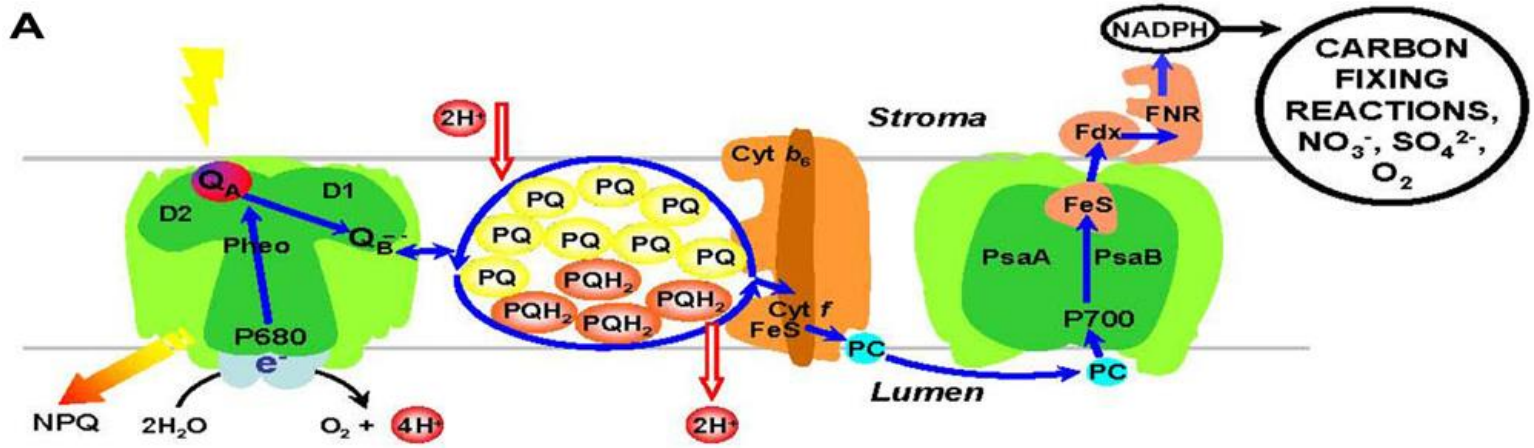
# Dobzhansky-Muller Incompatibilities



An Important Problem: What limits plant growth?
Is it the efficiency of photon capture and conversion, or is it the much slower and temperature sensitive processes of C, N, and S-Metabolism?

Question laid out nicely by Hüner et al., 2012

Consequently, photosynthetic organisms are predisposed to maintain a balance between the rates of light energy trapping through extremely fast (femtosecond to picosecond time scale) but temperature-insensitive photophysical and photochemical processes of light absorption, energy transfer, and charge separation that generates electrons within the photosynthetic reaction centers versus the much slower but very temperature-sensitive processes of C, N, and S-metabolism (Figure 1), and ultimately growth and development that utilize the photosynthetic reductants. To overcome this disparity in reaction rates and temperature sensitivity, non-photochemical quenching mechanisms (NPQ) have evolved to dissipate any excess energy not used in photosynthesis as heat either through antenna quenching via the xanthophyll cycle (Demmig-Adams and Adams, 1992; Horton et al., 1996, 2008; Demmig-Adams et al., 1999) and/or reaction center quenching through PSII charge recombination (Krause and Weis, 1991; Walters and Horton, 1993; Hüner et al., 2006) to protect the PSII reaction center from over-excitation and ensure survival in a fluctuating light environment (Figure 1). The balance between energy trapping versus energy utilization and/or dissipation is called photostasis.




Hüner et al., 2012

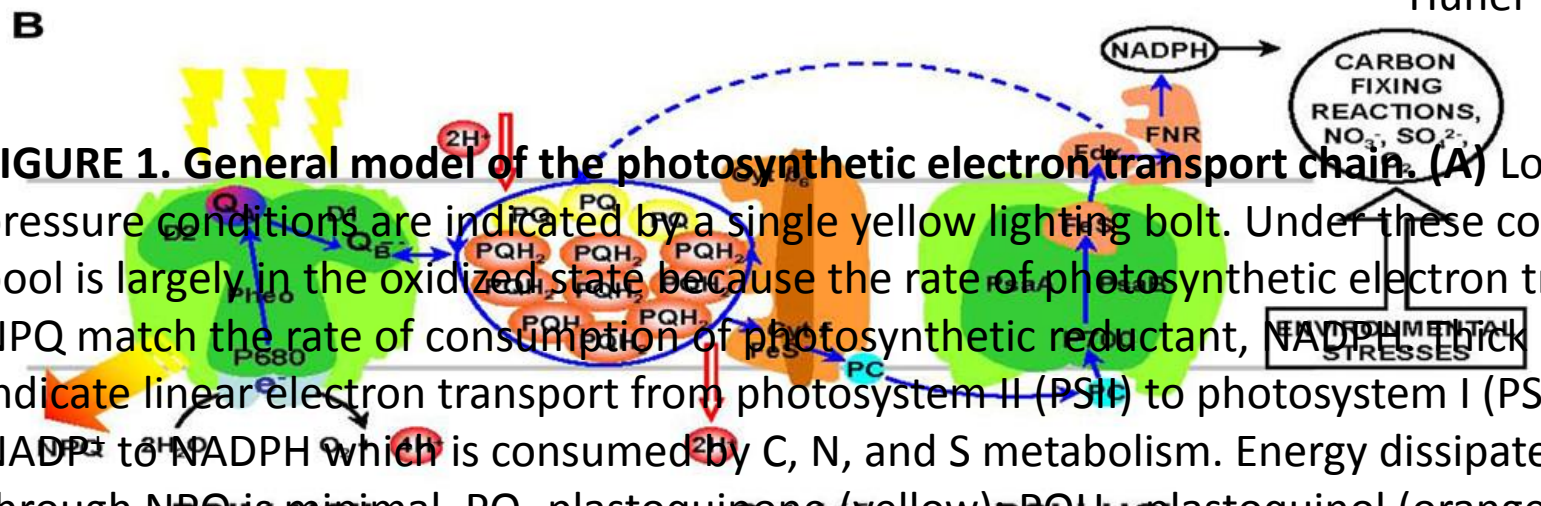



**FIGURE 1. General model of the photosynthetic electron transport chain. (A)** Low excitation pressure conditions are indicated by a single yellow lighting bolt. Under these conditions, the PQ pool is largely in the oxidized state because the rate of photosynthetic electron transport plus NPQ match the rate of consumption of photosynthetic reductant, NADPH. Thick solid blue arrows indicate linear electron transport from photosystem II (PSII) to photosystem I (PSI) to reduce $NADP^+$ to NADPH which is consumed by C, N, and S metabolism. Energy dissipated as heat through NPQ is minimal. PQ, plastoquinone (yellow); $PQH_2$, plastoquinol (orange). **(B)** High excitation pressure conditions can be generated by either high light (3 lightning bolts) or by environmental stresses such as low temperature or nutrient stress which inhibit rates of metabolism. Under these conditions, the PQ pool is largely reduced to plastoquinol and energy dissipated through NPQ is increased. Consequently, rates of linear electron transport between PSII and PSI decrease (thin solid blue arrows) and enhance rates of PSI cyclic electron transport (broken blue arrow).

Anna et al 2014

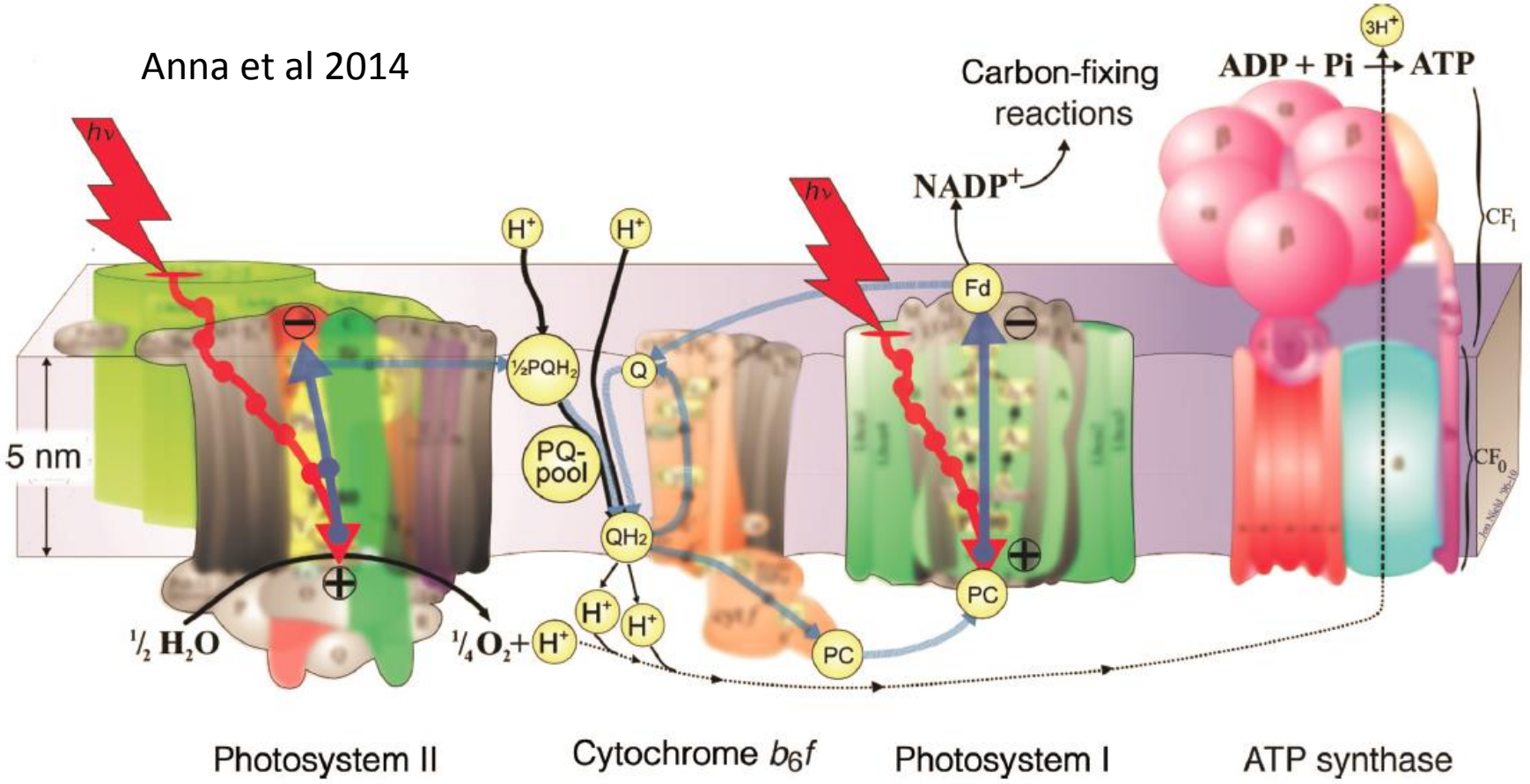
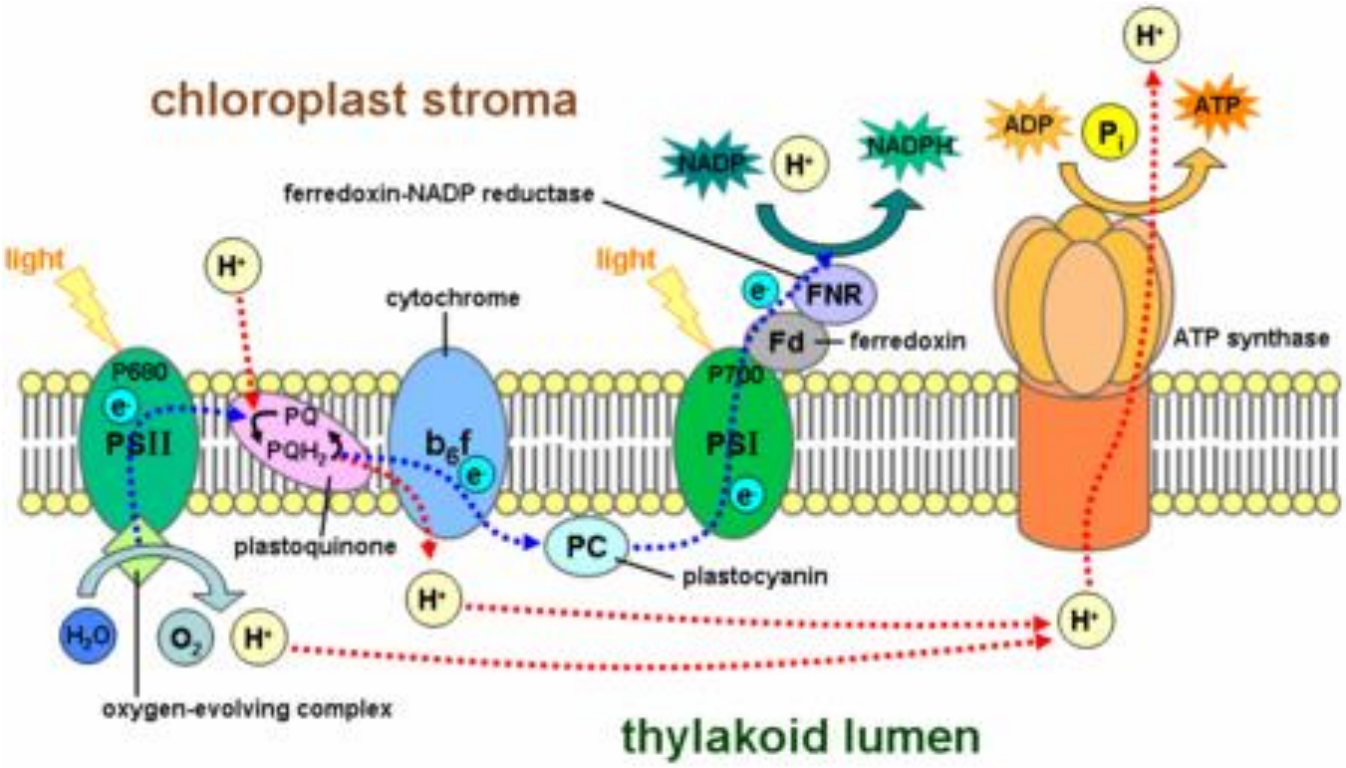


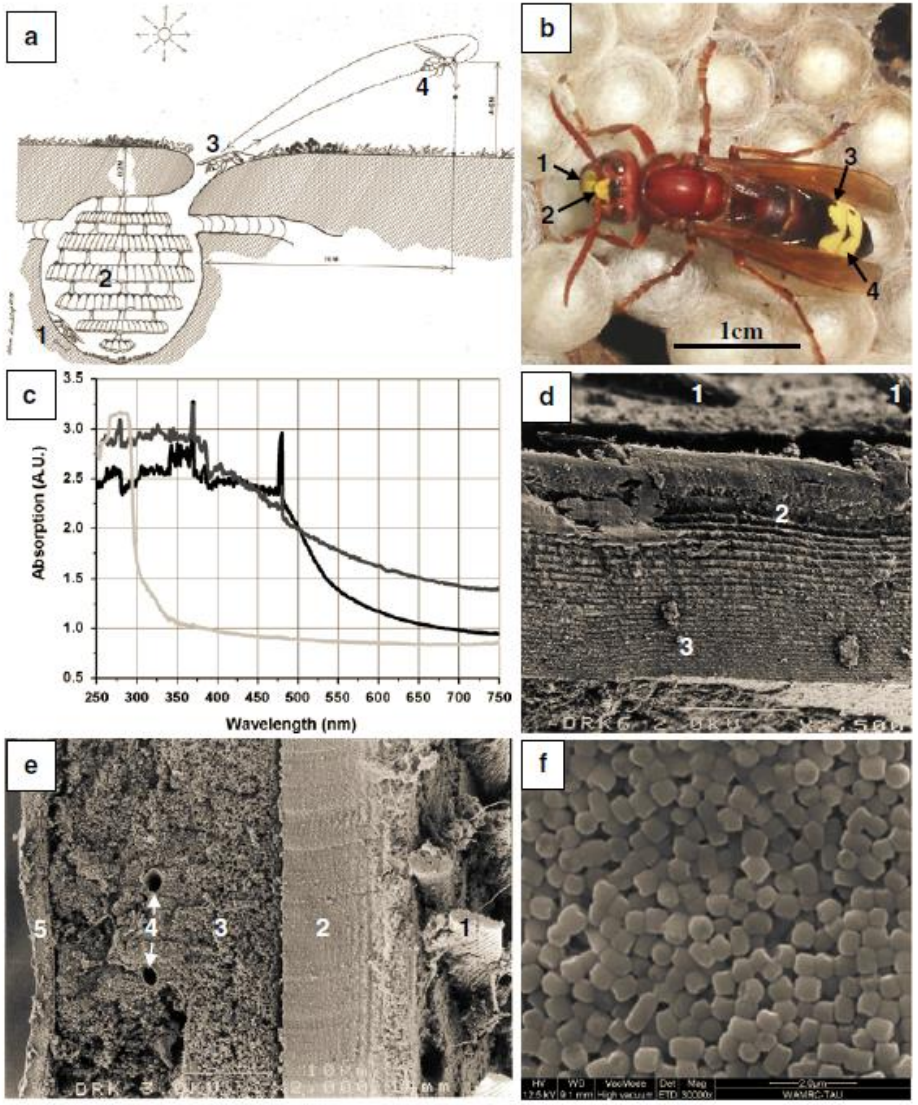

*Figure 2. The photosynthetic apparatus associated with the light-dependent reactions of photosynthesis. Th transfer pathways involved in photosynthesis are depicted as red arrows, electron transfer pathways as blue the proton transfer pathways as black arrows. For further details, refer to Jon Nield's Web site* (http://macro ac.uk)*, where the original figure can be found. The thylakoid membrane-bound pigment–protein complexes and photosystem II, use the energy of an absorbed photon to drive electron transfer reactions. Light-harvest molecules act to absorb sunlight and transfer this energy to the reaction center, where the photochemistry ta photosystem II, the electron transfer reaction is linked to the splitting of water ($H_2O$), creating a proton gra eventually drives the formation of adenosine triphosphate (ATP). Photosystem I drives a transmembrane el*



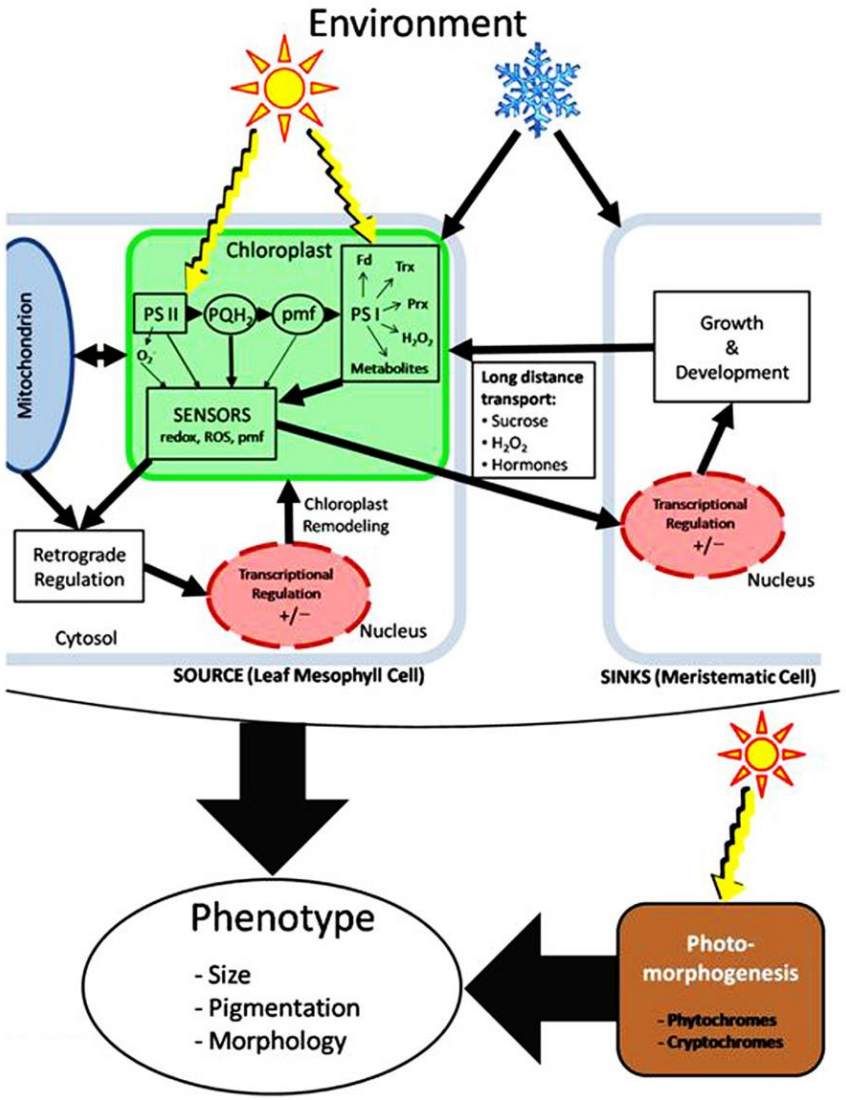

http://en.wikipedia.org/wiki/Photosynthesis

# Solar energy harvesting in the epicuticle of the oriental hornet (*Vespa orientalis*)

Plotkin et al 2011




Yellow pigment granule
(` 500 nm)




Huner et al 2012

Of the approximately three-thousand proteins found in chloroplasts, some 95% of them are encoded by nuclear genes. Many of the chloroplast's protein complexes consist of subunits from both the chloroplast genome and the host's nuclear genome. As a result, protein synthesis must be coordinated between the chloroplast and the nucleus.

# Spatial Movement of Chloroplasts in Response to Light Conditions

The chloroplasts of plant and algal cells can orient themselves to best suit the available light. In low-light conditions, they will spread out in a sheet—maximizing the surface area to absorb light. Under intense light, they will seek shelter by aligning in vertical columns along the plant cell's cell wall or turning sideways so that light strikes them edge-on. This reduces exposure and protects them from photooxidative damage.[107] This ability to distribute chloroplasts so that they can take shelter behind each other or spread out may be the reason why land plants evolved to have many small chloroplasts instead of a few big ones.[108] Chloroplast movement is considered one of the most closely regulated stimulus-response systems that can be found in plants.[109]

http://en.wikipedia.org/wiki/Chloroplast

Chloroplast Inheritance is generally maternal (seed),
But can be variable.
Even in photosynthetic organisms without pollen and ova, but with separate mating types can show uniparental inheritance.

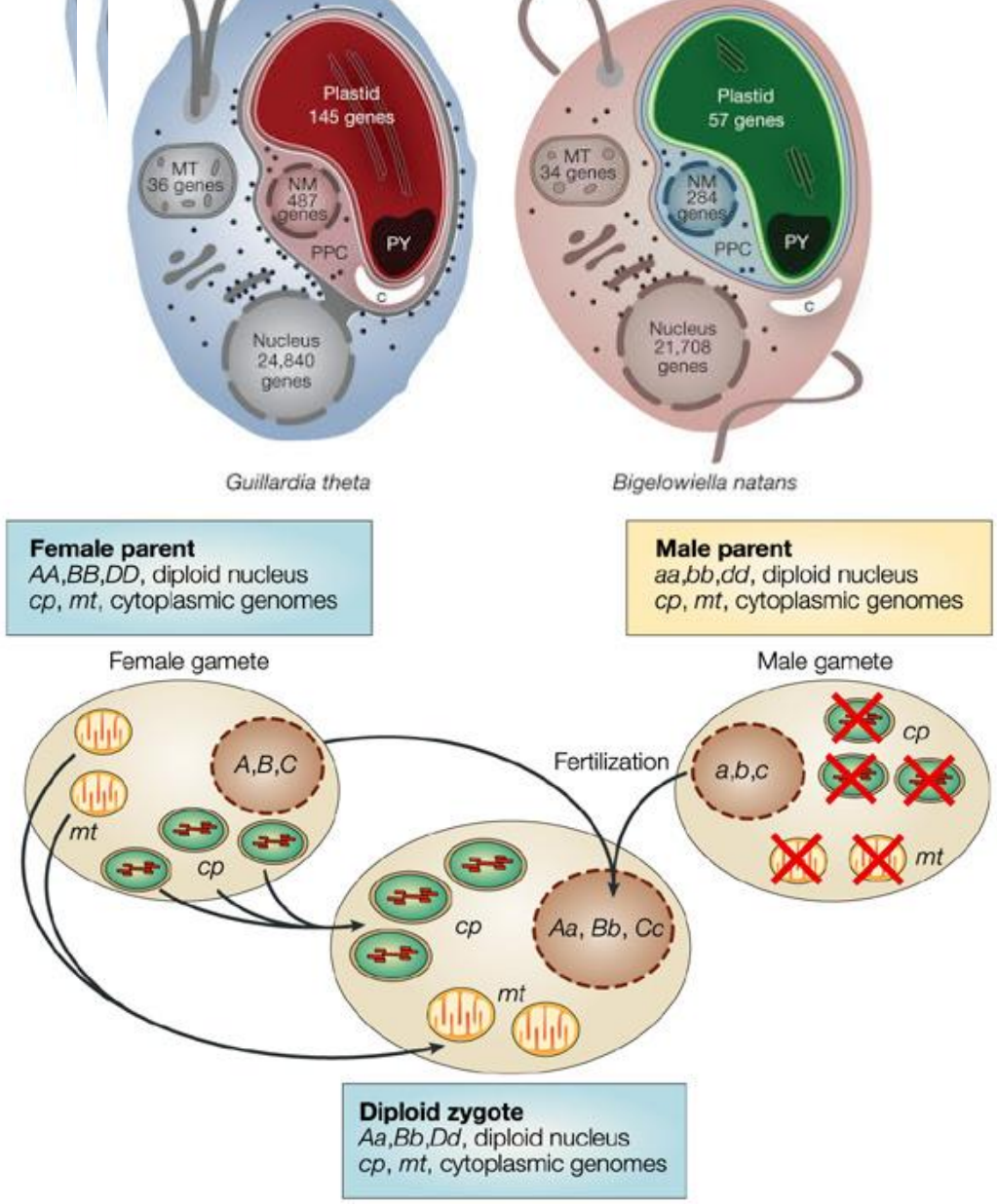
Active mechanisms to ensure uniparental inheritance of chloroplasts (e.g. active elimination of paternal chloroplasts. Why?

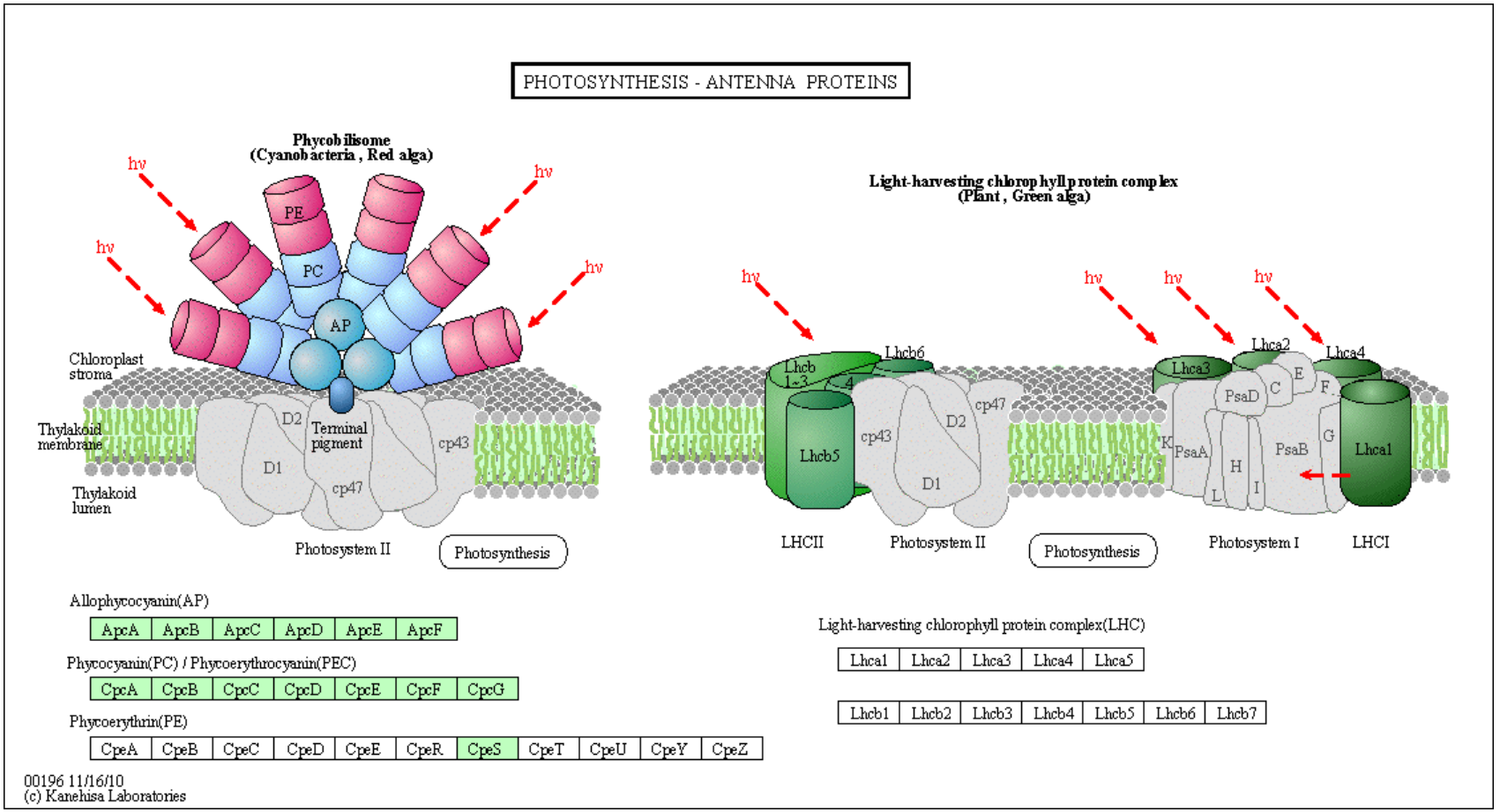
Gymnosperms (e.g. pines and firs) pass chloroplasts paternally.

Some angiosperms are now know to do this as well.

Chloroplast inheritance often disrupted in hybrids (showing genetic control of inhertiance).

Many mechanisms prevent biparental chloroplast DNA inheritance including selective destruction of chloroplasts or their genes within the gamete or zygote, and chloroplasts from one parent being excluded from the embryo. Parental chloroplasts can be sorted so that only one type is present in each offspring.[137]
Gymnosperms, such as pine trees, mostly pass on chloroplasts paternally,[138] while flowering plants often inherit chloroplasts maternally.[139][140] Flowering plants were once thought to only inherit chloroplasts maternally. However, there are now many documented cases of angiosperms inheriting chloroplasts paternally.[ From wiki

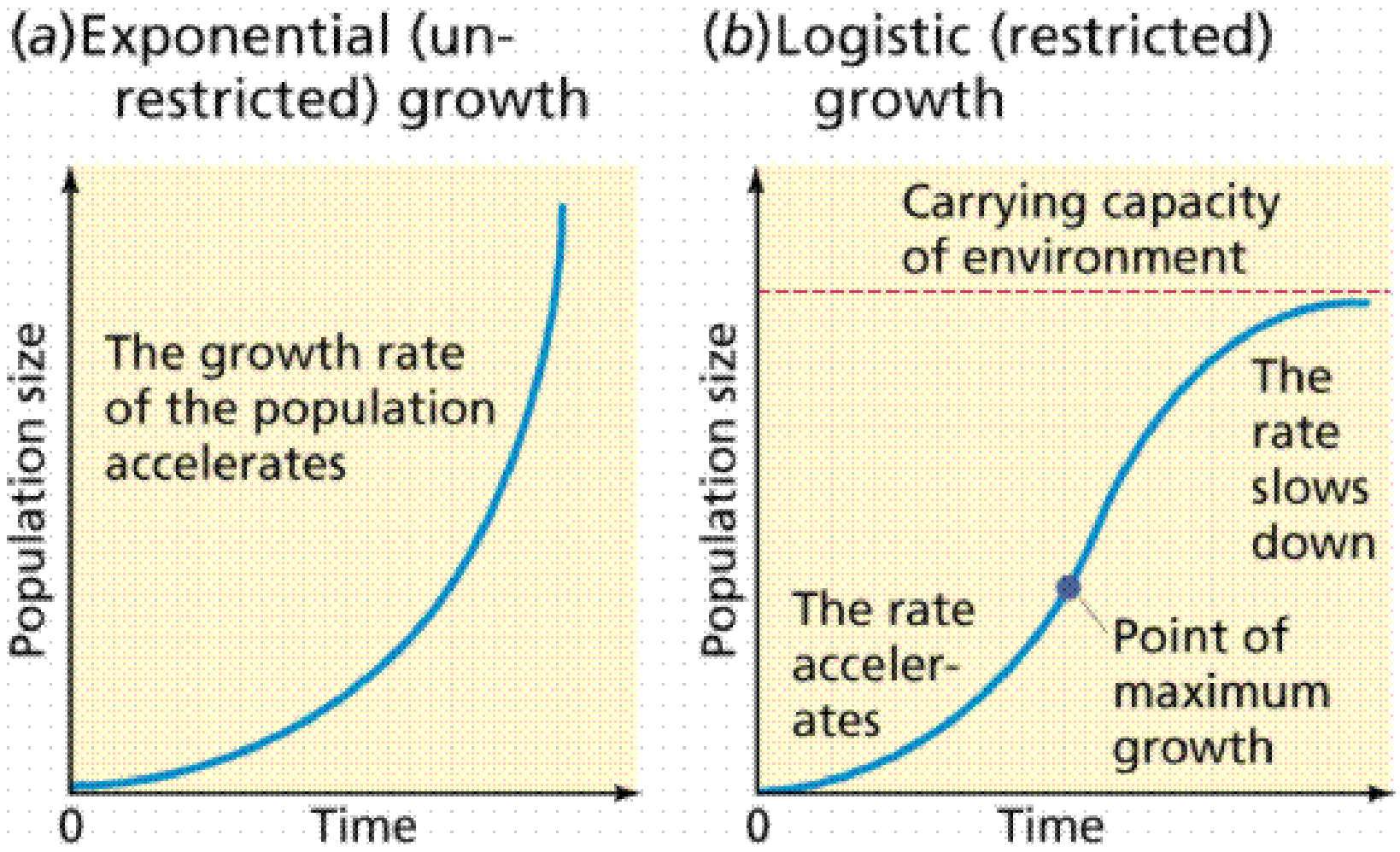

Plastid
145 genes
MT
36 genes
NM
487
genes
PPC
PY
C
Nucleus
24,840
genes
Guillardia theta
Plastid
57 genes
MT
34 genes
NM
284
genes
PPC
PY
C
Nucleus
21,708
genes
Bigelowiella natans
Female parent
AA,BB,DD, diploid nucleus
cp, mt, cytoplasmic genomes
Male parent
aa,bb,dd, diploid nucleus
cp, mt, cytoplasmic genomes
Female gamete
Male gamete
A,B,C
mt
cp
Fertilization
a,b,c
cp
mt
cp
Aa, Bb, Cc
mt
Diploid zygote
Aa,Bb,Dd, diploid nucleus
cp, mt, cytoplasmic genomes




PSII – 20 protein subunits & ~50 cofactors

PSI – 13 protein subunits & ~190 cofactors

Antennae – chlorophyl-protein matrix


(a) Exponential (unrestricted) growth
Population size
The growth rate of the population accelerates
0
Time
(b) Logistic (restricted) growth
Carrying capacity of environment
Population size
The rate slows down
The rate accelerates
Point of maximum growth
0
Time

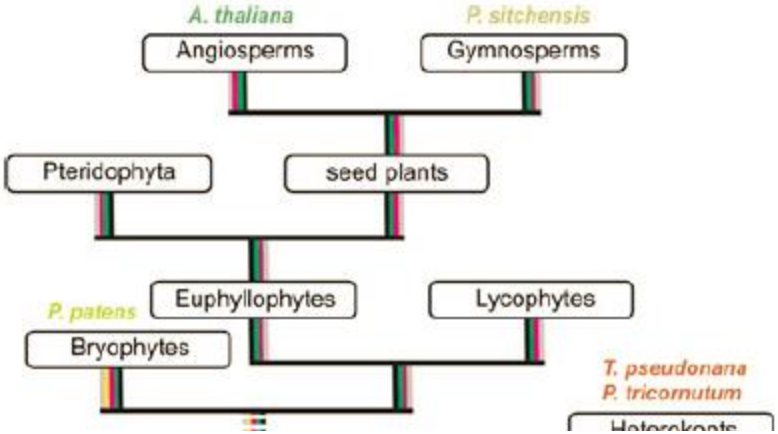
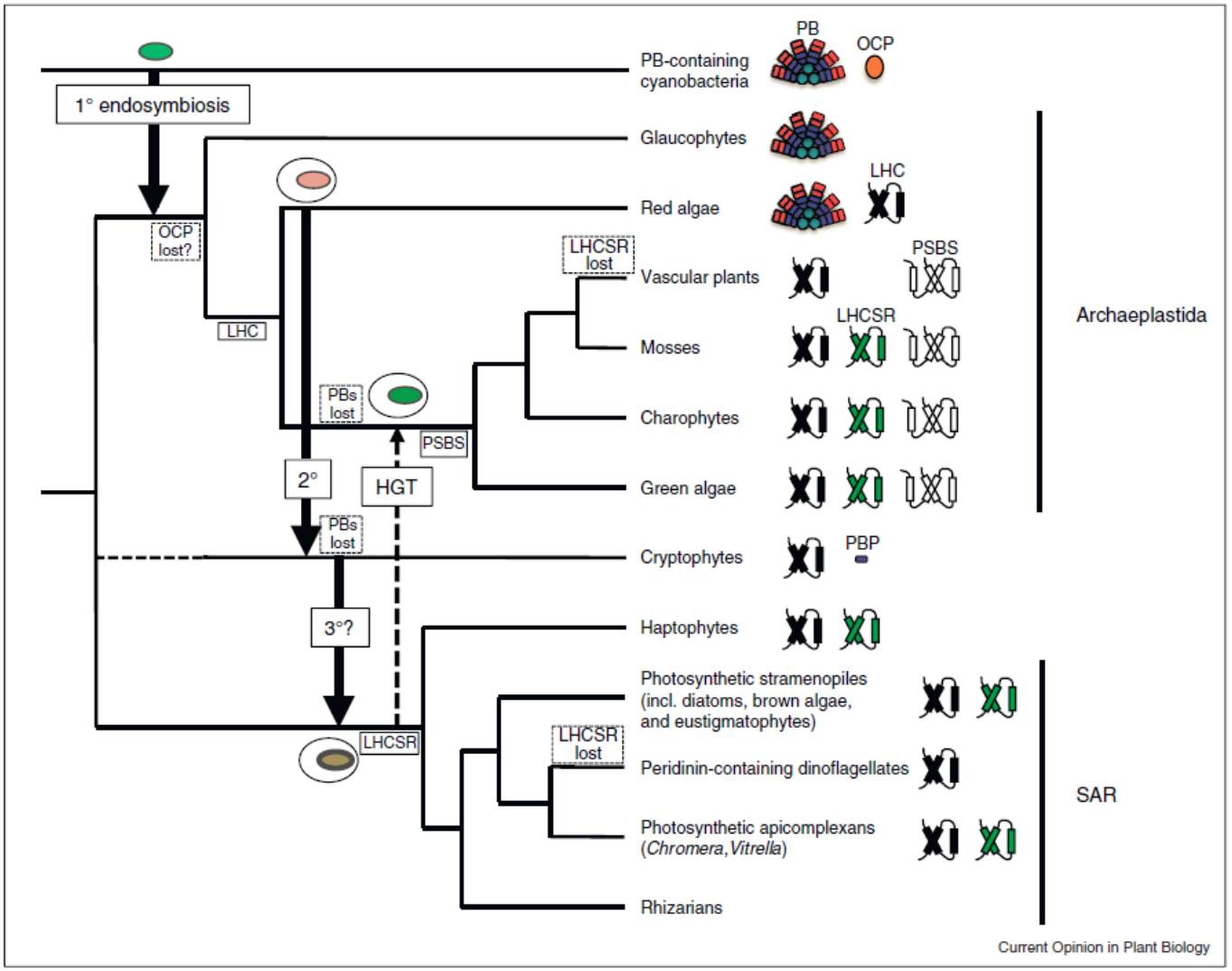



**Fig. 2** Simplified phylogenetic relationships between main photosynthetic eukaryotic organism groups and the distribution of LHC proteins. The species listed are the ones used in Table 1. Rhodophyta and Heterokonts belong to what is referred to as the "*red* lineage" in the text. Heterokonts, Cryptophytes and Haptophytes contain Chl *a*/*c* and together comprise the group of the Chromophytes. LHC are colour-coded as follows: RedCAP *red*; LHC *green*; PsbS *pink*; LHCSR *yellow*; ELIP *grey*; OHP *black*

Grouneva et al 2012 LHC1 = PS1, etc




Schematic depiction of the relationships between major groups of oxygenic photosynthetic organisms and the possible evolutionary steps relevant to flexible NPQ. Branch lengths are drawn for convenience and are not meant to imply specific lengths of time. Hypothetical endosymbioses, horizontal gene transfer (HGT) events, and acquisition events are shown in solid boxes; loss events are shown in dashed boxes. Not shown are algae derived from secondary endosymbiosis of green algae; one of these groups (Chlorarachniophytes) is part of the Rhizarian taxon. Cryptophytes have an unusual phycobiliprotein (PBP) antenna that is not part of a phycobilisome (PB) complex. Other abbreviations are defined in Box 1.

Nyogi & Truong 2013

In addition to the harvesting of sunlight, the chloroplasts also function as "receptors" of environmental signals. We aim at system biology view on the chloroplast-derived regulation of nuclear gene expression by environmental cues, including redox and metabolite signaling. Redox signalling from chloroplasts to the nucleus is likely to be an important component in various stress responses and acclimation of plants but also metabolites derived from CO2 fixation are important regulators of nuclear gene expression (Piippo et al, 2006).
Information on global redox regulation of nuclear genes by chloroplast signals is obtained by transcript profiling and proteomics approaches.

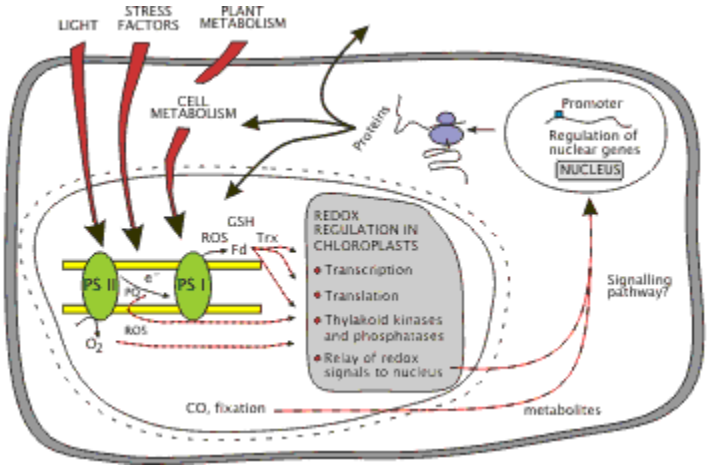
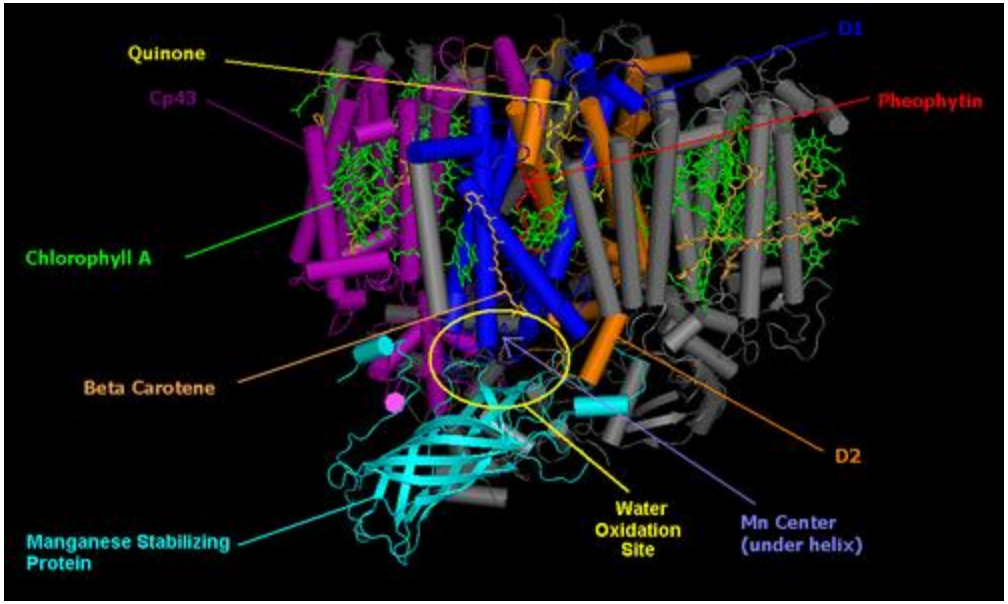


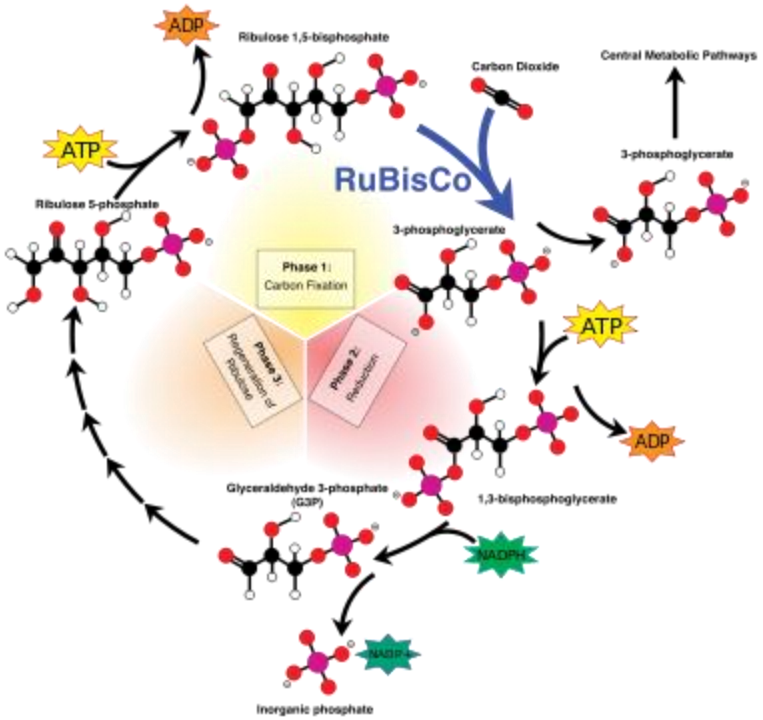

**Fig 2.** *Redox and metabolite control of nuclear gene expression in photosynthetic cells. Both environmental and metabolic cues modulate the function of chloroplasts, which in turn is likely to be involved in the relay of information to the nuclear compartment, finally leading to plant acclimation to prevailing conditions.*

Plastids are semiautonomous organelles found, in one form or another, in practically all plant and algal cells, several taxa of marine mollusks and at least one phylum of parasitic protists. The members of the plastid family play pivotal roles in photosynthesis, amino acid and lipid synthesis, starch and oil storage, fruit and flower coloration, gravity sensing, stomatal functioning, and environmental perception. Plastids arose via an endosym biotic event in which a protoeukaryotic cell engulfed and retained a photosynthetic bacterium. This polyphyletic event occurred multiple times between roughly 1.5 to 1.6 billion years ago. Although most of the algal genes were transferred to the nuclear genome, plastids have retained a complete protein synthesizing machinery and enough information to code for about 100 of their approximately 2,500 proteins; all other plastid proteins are coded for by the nuclear genome and imported from the cytoplasm. Plastids divide via fission prior to cytokinesis and are equally apportioned between the two daughter cells, along with the rest of the cytoplasmic contents.

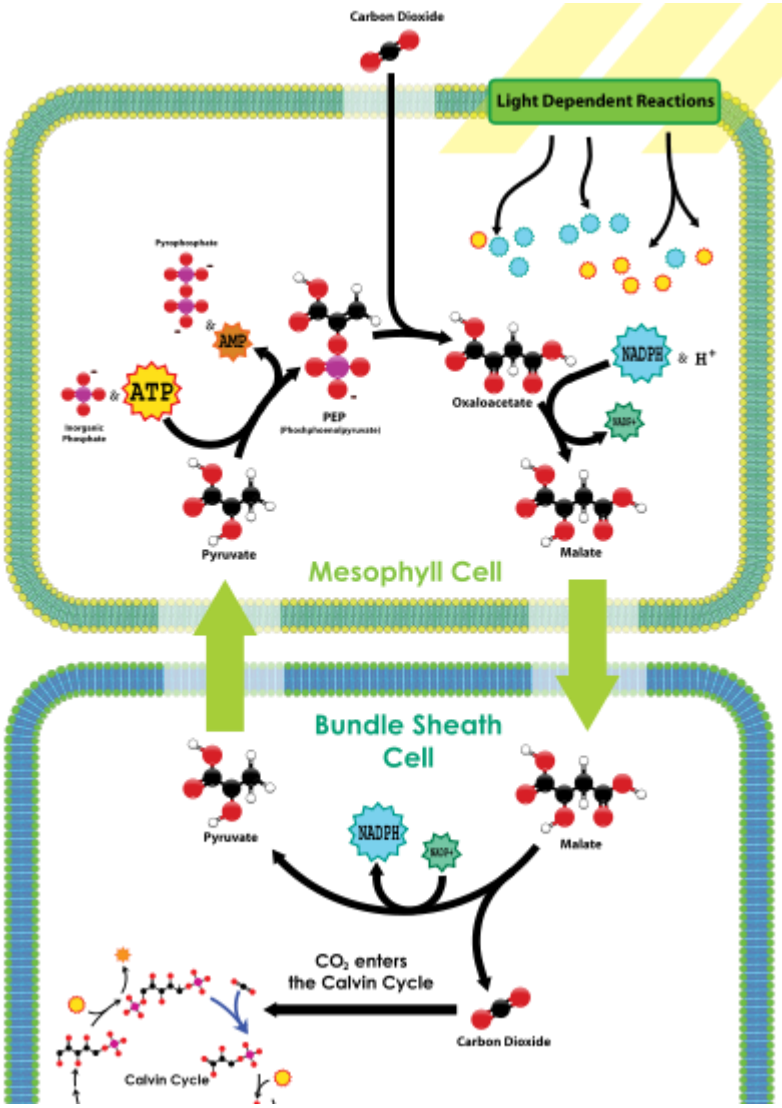
Wise 2006




Cyanobacteria photosystem II, Monomer, PDB 2AXT.




Overview of the Calvin cycle




C4 Carbon Fixation

A phenomena known as quantum walk increases the efficiency of the energy transport of light significantly. In the photosynthetic cell of an algae, bacteria or plant, there are light-sensitive molecules called chromophores arranged in an antenna shaped structure named a photocomplex. When a photon is absorbed by a chromophore, it is converted into a quasiparticle referred to as an exciton, which jumps from chromophore to chromophore towards the reaction center of the photocomplex, a collection of molecules who traps its energy in a chemical form that makes it accessible for the cell's metabolism. The particle's wave properties enables it to cover a wider area and try out several possible paths simultaneously, allowing it to instantaneously "choose" the most efficient route where it will have the highest probability of arriving its destination at the minimum possible time. Because it takes place at temperatures far higher than quantum phenomena usually occurs in, quantum walking is only possible over very short distances due to obstacles in the form of destructive interference that will come into play, causing the particle to lose its wave properties for an instant before they are regained once again after it has been freed from its locked position through a classic "hop". The distance towards the center is therefore covered in a series of conventional hops and quantum walks.[33][34][35]

http://en.wikipedia.org/wiki/Photosynthesis

# A Little Coherence in Photosynthetic Light Harvesting

JESSICA M. ANNA, GREGORY D. SCHOLES, AND RIENK VAN GRONDELLE

14 BioScience • *January 2014 / Vol. 64 No. 1*

Anna et al. 2014. BioScience

Anna et al. 2014. BioScience

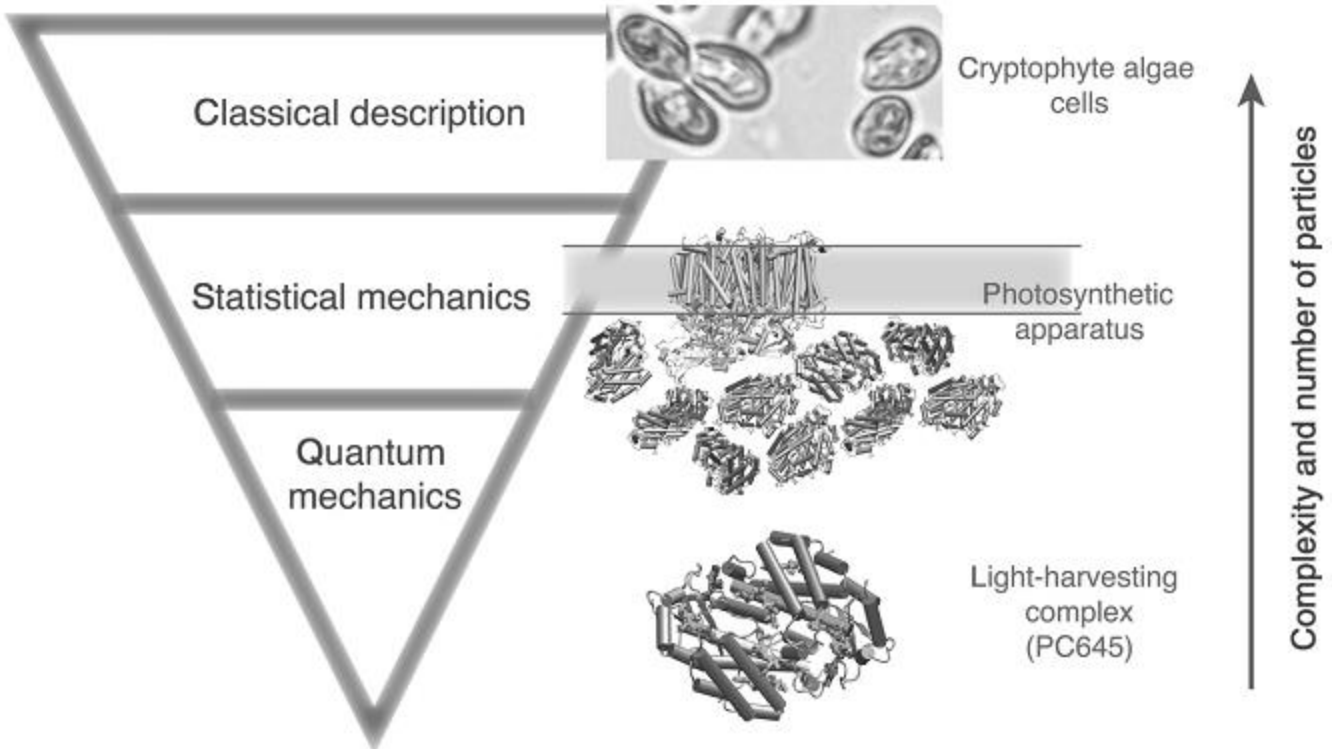



*Figure 1. A depiction of the scales of biological length and complexity, as described in the text. Atomic-scale and, possibly, quantum mechanical effects govern the function of a protein. These details are lost as the system becomes more complex. In that case, certain emergent phenomena or functions are the primary observables.*

Anna et al. 2014. BioScience

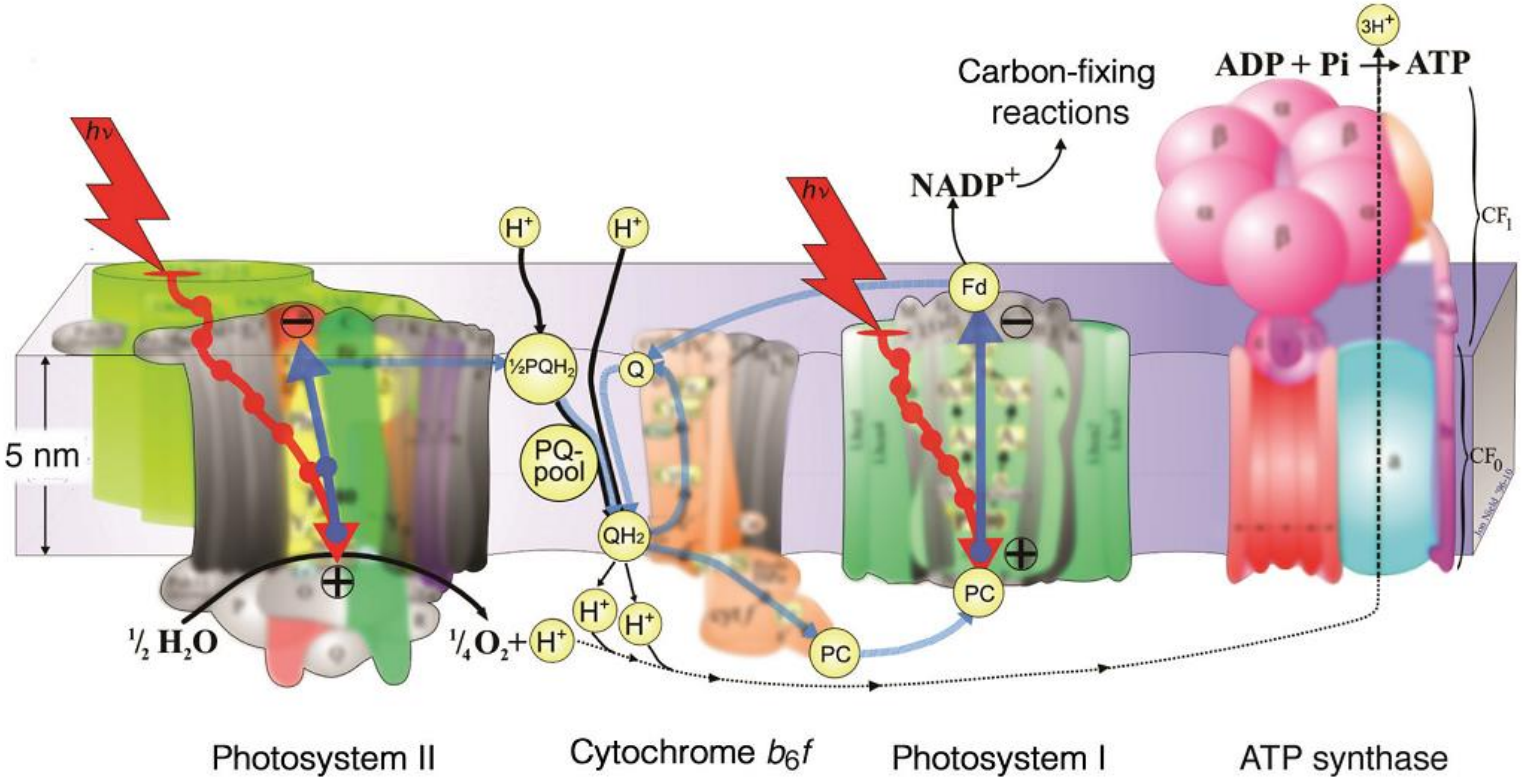



*Figure 2. The photosynthetic apparatus associated with the light-dependent reactions of photosynthesis. The energy transfer pathways involved in photosynthesis are depicted as red arrows, electron transfer pathways as blue arrows, and the proton transfer pathways as black arrows. For further details, refer to Jon Nield's Web site (*http://macromol.sbcs.qmul.ac.uk*), where the original figure can be found. The thylakoid membrane-bound pigment–protein complexes, photosystem I and photosystem II, use the energy of an absorbed photon to drive electron transfer reactions. Light-harvesting chlorophyll molecules act to absorb sunlight and transfer this energy to the reaction center, where the photochemistry takes place. In photosystem II, the electron transfer reaction is linked to the splitting of water ($H_2O$), creating a proton gradient, which eventually drives the formation of adenosine triphosphate (ATP). Photosystem I drives a transmembrane electron transfer reaction, which leads to the reduction of nicotinamide adenine dinucleotide phosphate ($NADP^+$) to NADPH, which is subsequently linked to carbon fixation. Source: Reprinted from Boeker and van Grondell (2011) with permission from John Wiley and Sons, copyright (2011). Abbreviations: ADP, adenine dinucleotide phosphate; CF, photosynthetic coupling factor; Fd, ferredoxin; H, hydrogen; hv, energy from the sun; nm, nanometers; O, oxygen; PC, plastocyanin; Pi, phosphate; $PQH_2$, dihydroplastoquinone; PQ, plastoquinone; Q, quinone; $QH_2$, plastoquinol.*

Anna et al. 2014. BioScience

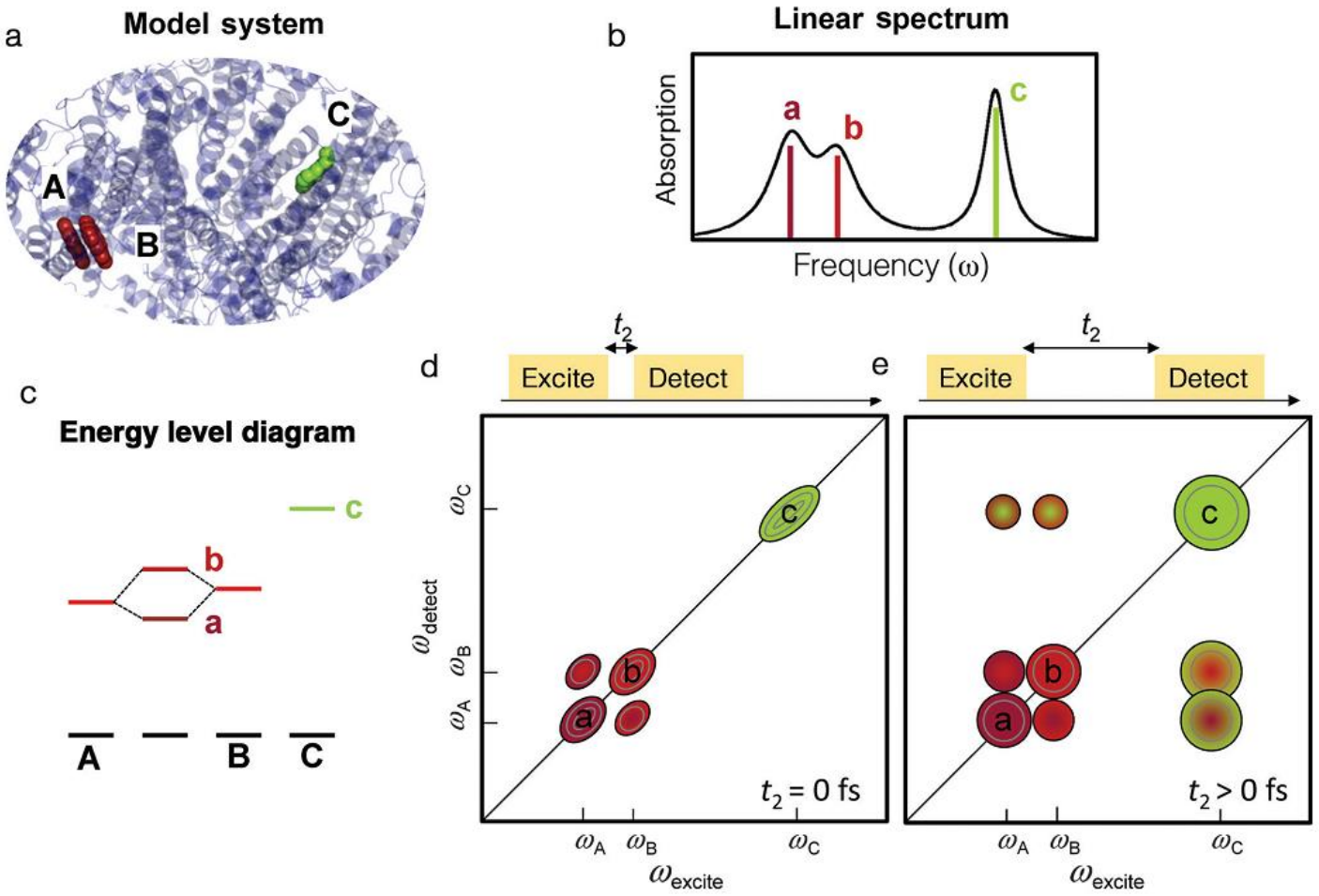



*Figure 3. A model system consisting of three identical chromophores in a protein scaffold (a) along with the corresponding linear spectrum (b) and energy level diagram (c). Schematic two-dimensional spectra at $t_2$ = 0 femtoseconds (fs) (d) and a later waiting time (e). At early waiting times, cross-peaks indicate that the corresponding diagonal peaks are electronic transitions involving common electronic orbitals. At later waiting times, the appearance of cross-peaks indicates energy transfer between the different electronic transitions.*

a et al. 2014. BioScience

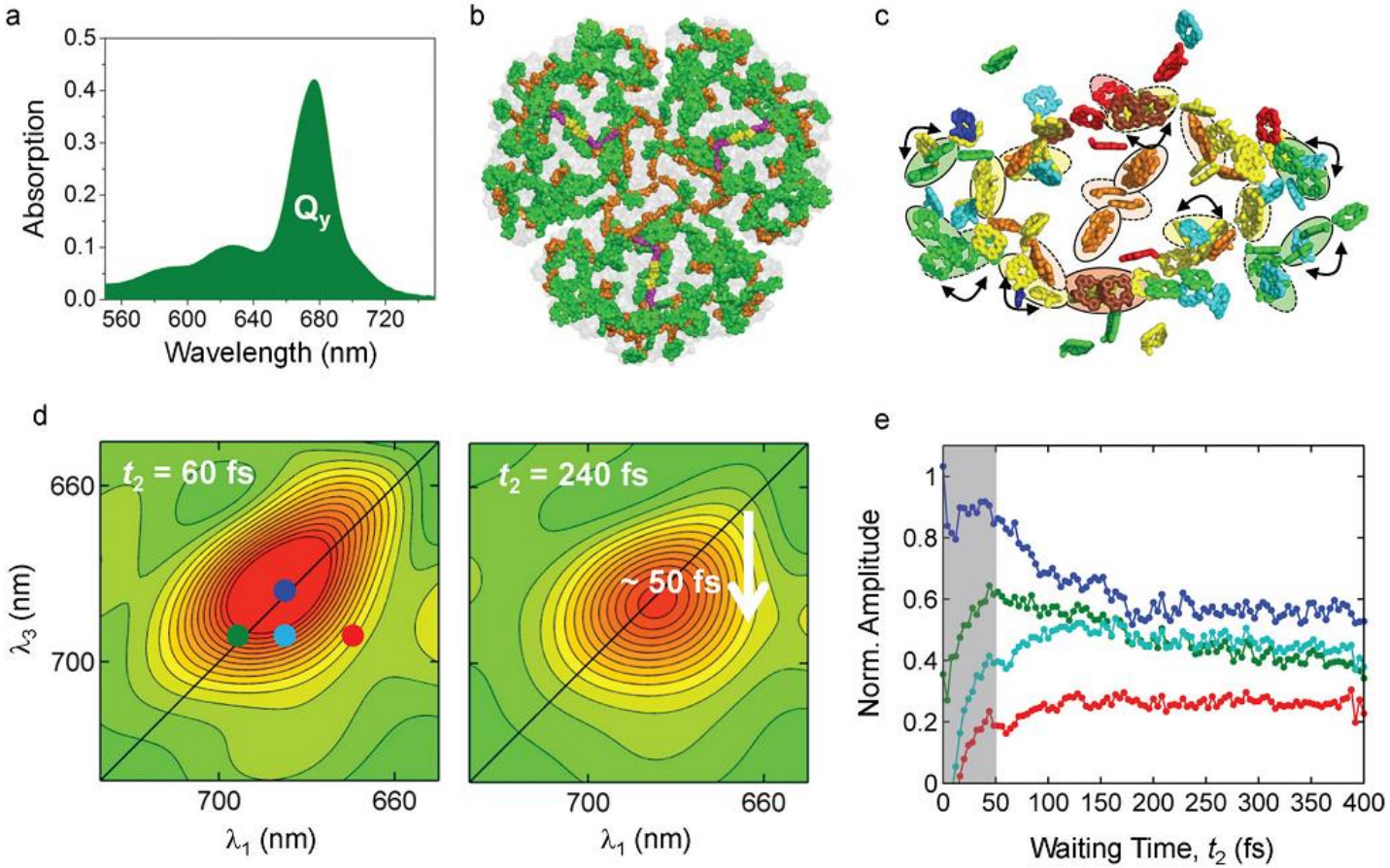



*Figure 4. The linear absorption spectrum of photosystem I trimers from* Thermosynechococcus elongatus *in the (a) $Q_y$ spectral region along with (b) the 2.5-angstrom resolution crystal structure (Jordan et al. 2001). (c) The chlorophyll molecules for the monomer are shown and colored according to the site energies from Byrdin and colleagues (2002), which were calculated on the basis of the structure of photosystem I: blue, 660–665 nanometers (nm); cyan, 665–670 nm; green, 670–675 nm; yellow, 675–680 nm; orange, 680–690 nm; brown, 690–700 nm; red, 700–720 nm. The chromophores that have an electronic coupling greater than 120 wavenumbers are indicated with shaded ovals (calculated using the point dipole approximation; see Byrdin et al. 2002 for more details). The ovals with dashed outlines indicated that the chromophores are found near the lumen surface, and the solid outlines indicate that the chromophores are found near the protoplasmic surface. (d) Two representative two-dimensional (2-D) electronic spectra (λ, wavelength) at an early and a later waiting time. (e) The amplitudes for traces taken at the points indicated in the 2-D spectra are plotted as a function of waiting time. The off-diagonal traces grow in with a time scale of 50 femtoseconds (fs). Source: Adapted from Anna and colleagues (2012).*

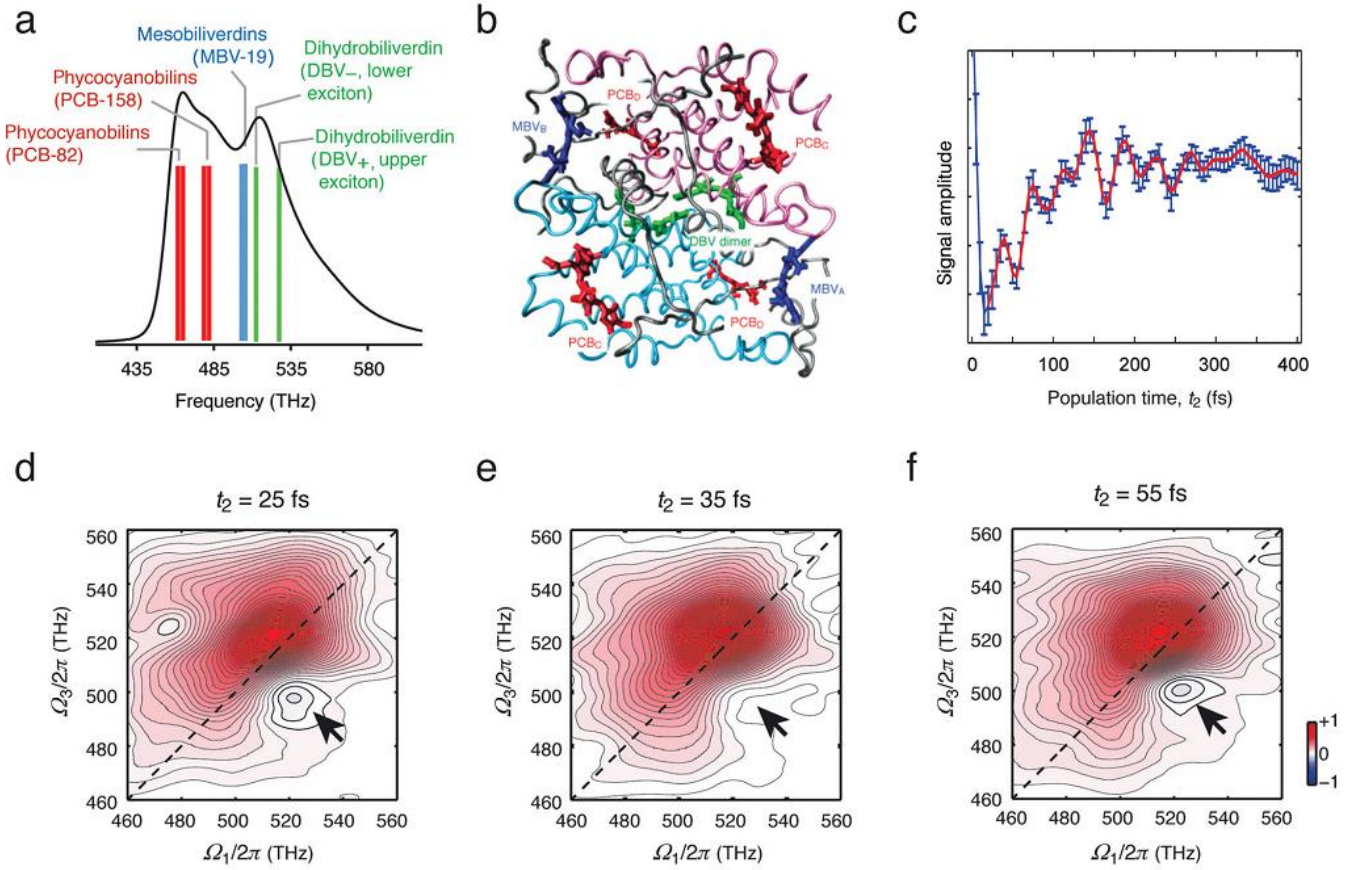



*Figure 5. (a) The linear absorption and (b) the structure of the cryptophyte light-harvesting antenna complex PC645 from* Chroomonas *sp. Strain CCMP270. (c) The waiting-time-dependent amplitude (in arbitrary units) of the cross-peak (indicated with an arrow in the two-dimensional [2-D] electronic spectra). The electronic coherence, determined from analyzing different contributions to the 2-D electronic spectra, was found to dephase with a time constant of 170 femtoseconds (fs). (d–f) 2-D electronic spectra at three different waiting times recorded at ambient temperature. The appearance and disappearance of the cross-peak is indicated with an arrow. Source: Adapted from Collini and colleagues (2010) and Turner and colleagues (2011). Abbreviation: THz, terahertz.*

Caruso, 2013, Quantum_Transport

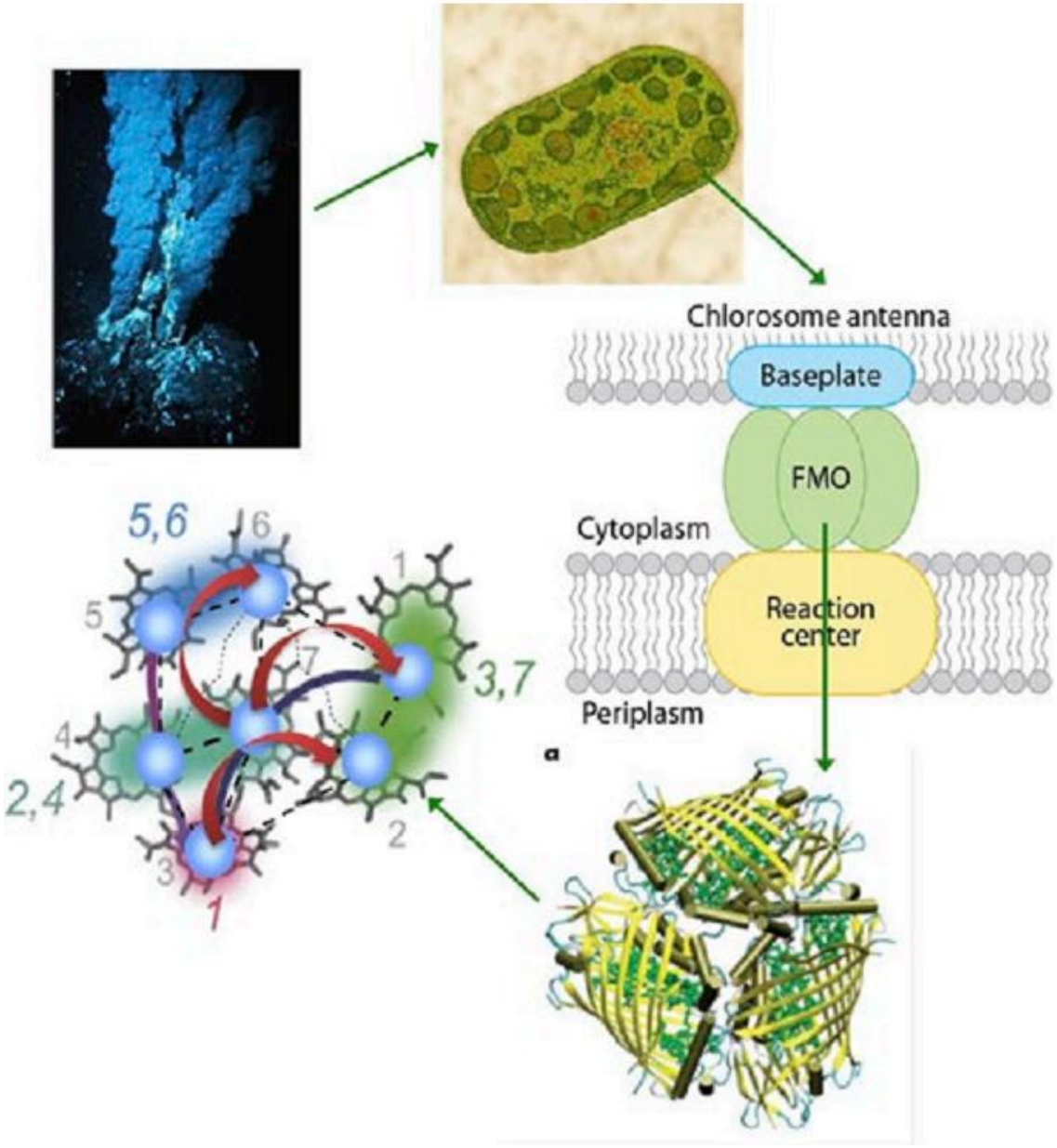



Fig. 1. Green Sulphur Bacteria are prototypes of light-harvesting systems, and probably the progenitors of life on Earth. They are even found living at the bottom of the Pacific Ocean where there is no sunlight and such pigment-protein complexes absorb about one photon every 24 hrs (thermal light), after which the generated electronic excitation is transferred to a reaction center (where the electron energy is converted into chemical energy) with the very remarkable efficiency of 99% in about 5 ps.

# Evolutionary layering and the limits to cellular perfection

Michael Lynch[1]

PNAS | November 13, 2012 | vol. 109 | no. 46 | 18851–18856

Lynch. 2012. PNAS

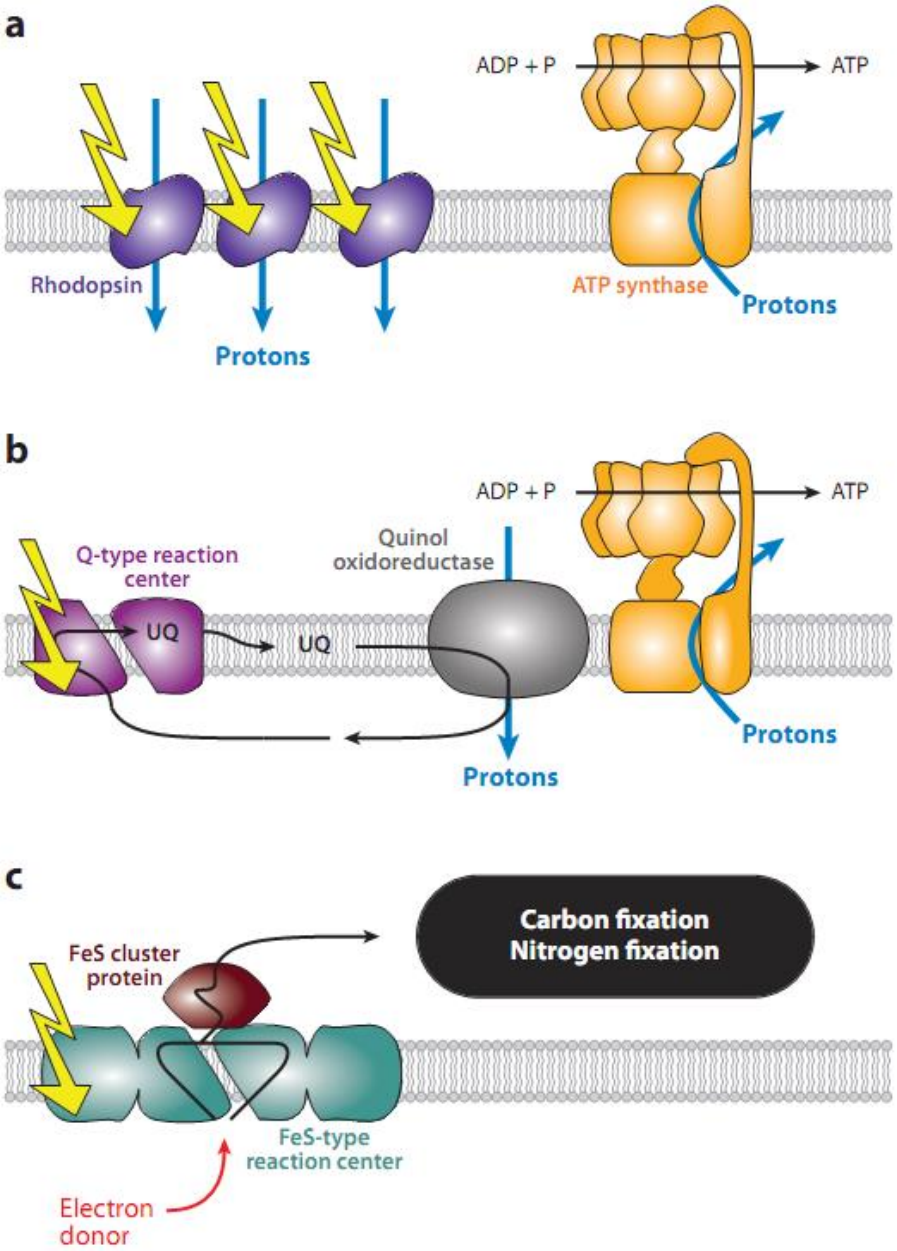



**Figure 1**

Modes of electron transport. Proton translocation and ATP generation by rhodopsin photoconverters (*a*) and a quinone-type reaction center (Q-type RC) participating in cyclic electron transport (*b*). Reductant generation for carbon and nitrogen fixation by FeS-type RCs during linear electron transport (*c*). Proton translocation is indicated by white arrows. Electron transport is indicated by solid lines and arrows. Photon absorption is indicated by yellow lightning bolts.

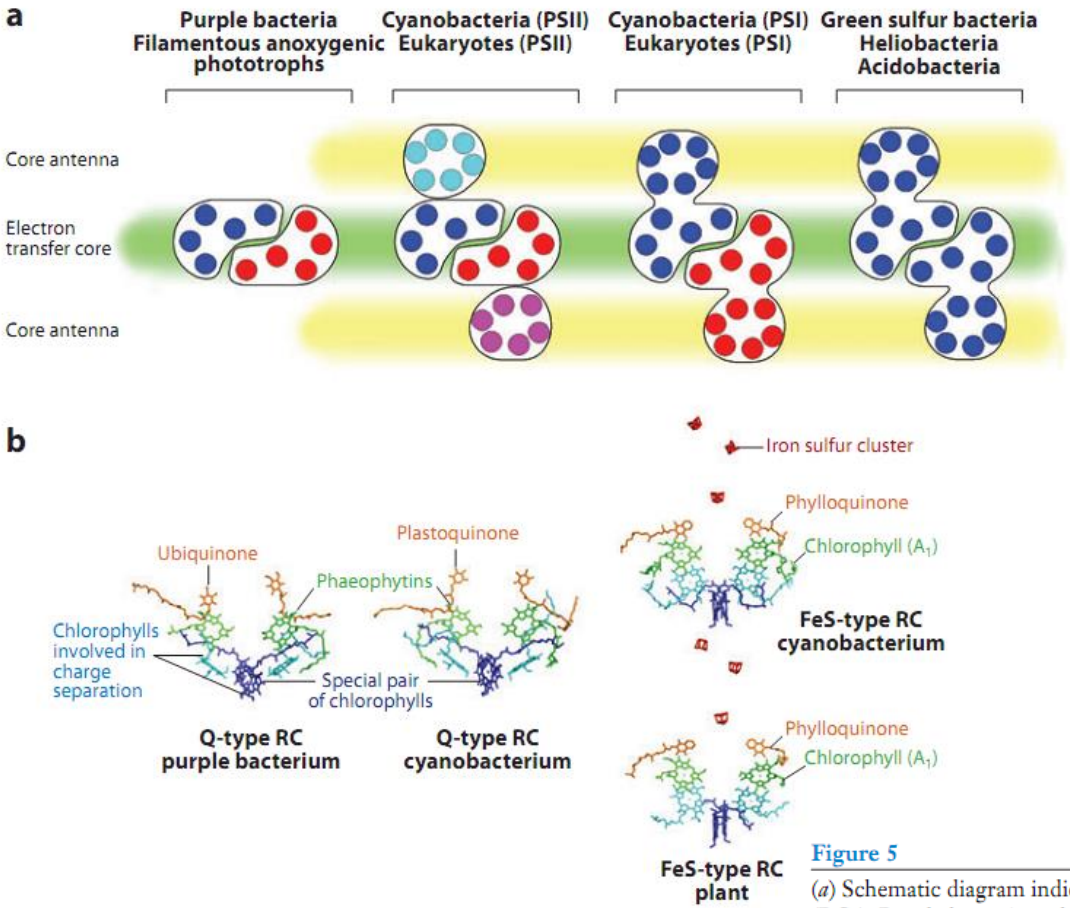
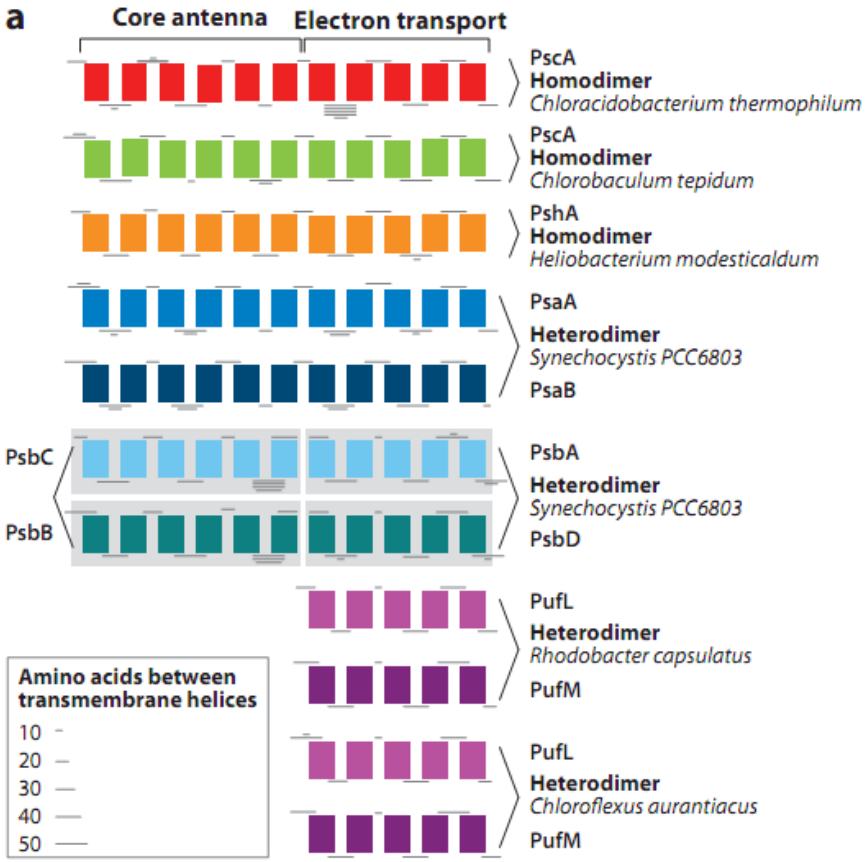
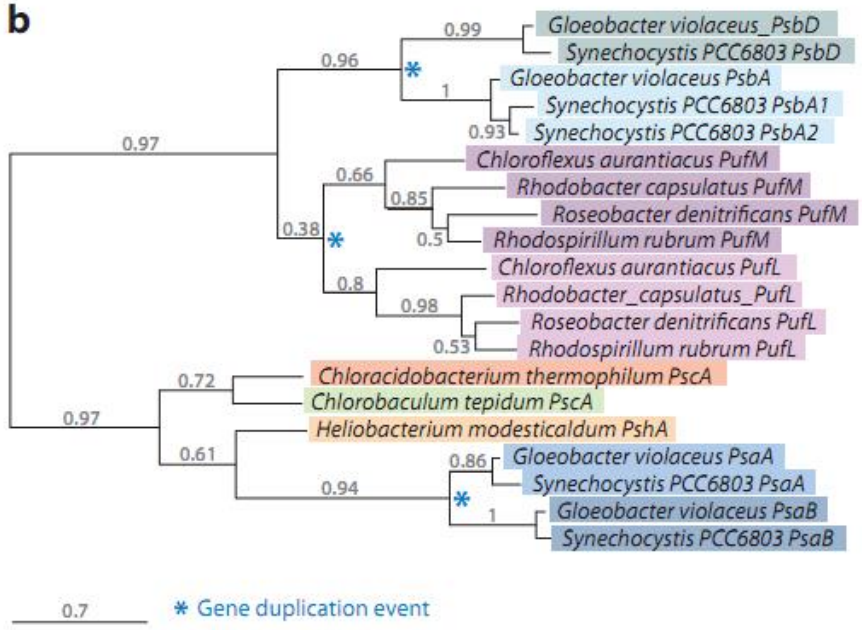



**Figure 5**

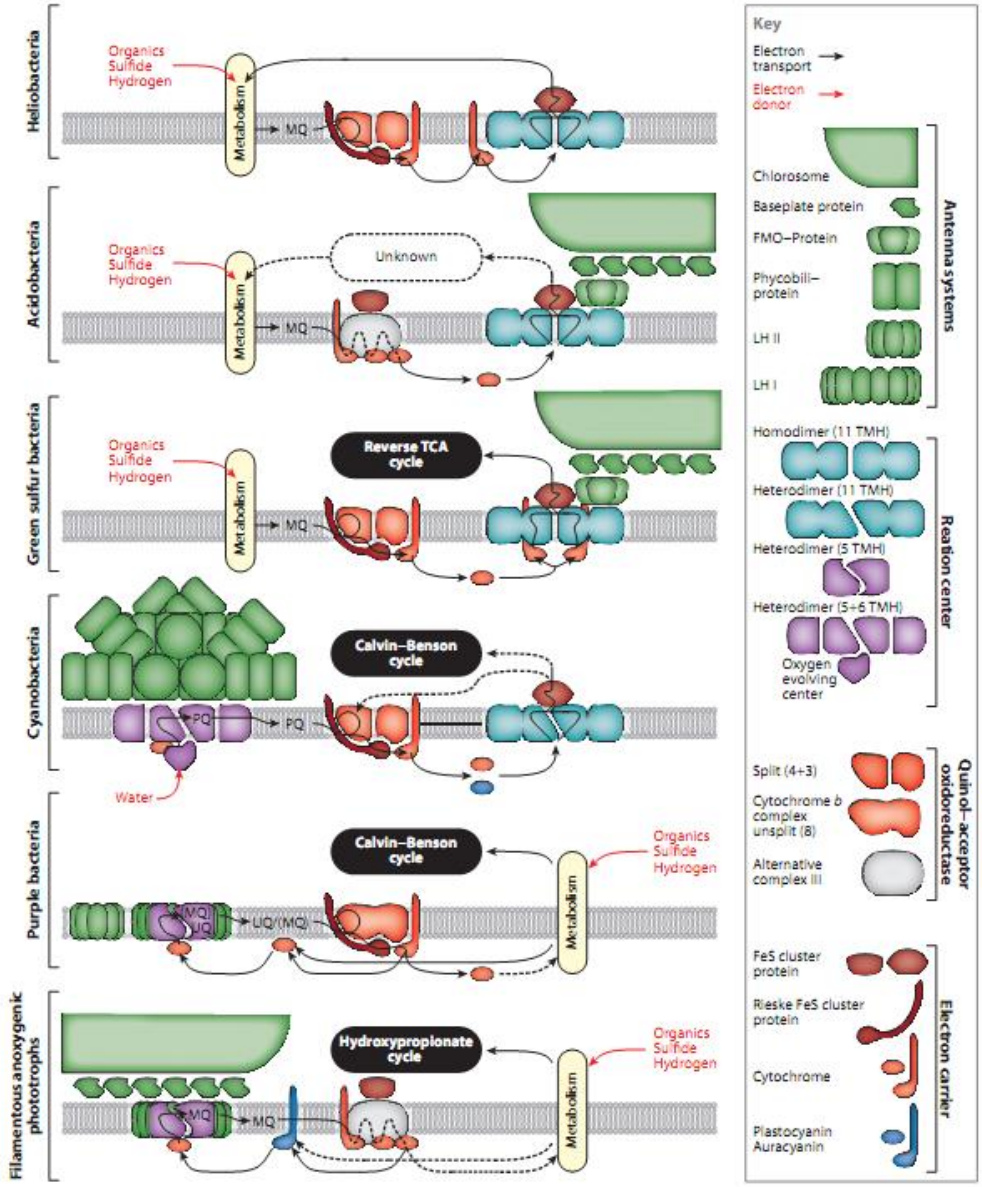
(*a*) Schematic diagram indicating the transmembrane helical composition of photosynthetic reaction centers (RCs). Purple bacteria and filamentous anoxygenic phototrophs possess a heterodimeric (L, M) quinone (Q)-type RC. The Q-type RC (PSII) of cyanobacteria and photosynthetic eukaryotes consists of a heterodimeric electron transfer core (D1, D2) and two homologous subunits (CP47, CP43) that act as a core antenna. The FeS-type RC (PSI) of cyanobacteria and higher plants is heterodimeric. Heliobacteria and green sulfur bacteria possess a homodimeric FeS-type RC. The core antennas of heliobacteria, green sulfur bacteria, and PSI are homologous to the separately encoded core antennas of PSII of oxygenic eukaryotes and cyanobacteria. Transmembrane helices (TMH) (*circles*) are encoded by separate genes shown in different colors. (*b*) Arrangement of electron transport cofactors involved in the charge separation and stabilization of Q-type and FeS-type RCs. The data were obtained from solved crystal structures: Q-type purple bacterium RC (*Rhodobacter sphaeroides*, PDB 1aij), Q-type cyanobacterium RC (*Thermosynechococcus elongatus*, PDB 1s5l), FeS-type cyanobacterium RC (*Thermosynechococcus elongatus*, PDB1jb0), FeS-type plant RC (*Pisum sativum*, PDB 2o01). The special set of chlorophylls involved in charge separation is shown in blue and cyan (special pair). Tetrapyrroles are phaeophytins in Q-type RCs and chlorophylls ($A_1$) in FeS-type RCs and are shown in green. Ubiquinone (UQ) (in purple bacterium), plastoquinones (PQ) (Q-type RC of cyanobacteria), and phylloquinone (FeS-type RC of cyanobacteria and plants) are shown in orange. The FeS clusters of the FeS-type RCs are shown in red. Adapted from Reference 78.




## Figure 6

Topology of transmembrane helices (TMH) in photosynthetic organisms and a phylogenetic tree of electron transport TMH. (*a*) Diagram indicating protein topography of reaction centers (RCs) in selected organisms. (*b*) Phylogenetic tree of the five TMH that constitute the RC electron transfer domain of selected photosynthetic organisms. Colors correspond to organism group representatives in (*a*).




## Figure 9

Photosynthetic machinery and electron transport of photosynthetic bacteria, including a description of photosynthetic complexes. Abbreviations: LH, light harvesting; MQ, menaquinone; PQ, plastoquinone; TCA, tricarboxylic acid; TMH, transmembrane helix(ces); UQ, ubiquinone.

# Two Topics

What forces constrain  how close to the optimum a biological system can evolve?

How might natural genetic variation be exploited to study quantum processes in biology?

# Drift-barrier hypothesis and mutation-rate evolution

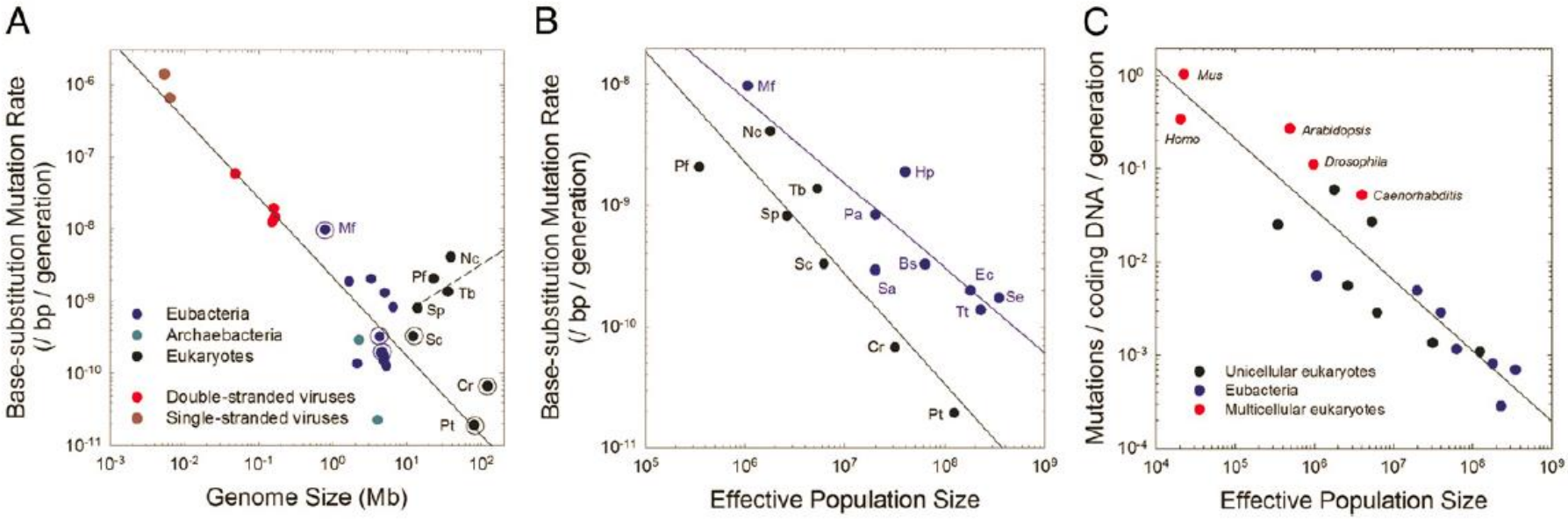
**Way Sung, Matthew S. Ackerman, Samuel F. Miller, Thomas G. Doak, and Michael Lynch[1]**

Department of Biology, Indiana University, Bloomington, IN 47401

Contributed by Michael Lynch, September 21, 2012 (sent for review September 9, 2012)

**18488–18492** | PNAS | **November 6, 2012** | vol. 109 | no. 45

Sung et al. 2012. PNAS




Sung et al 2012

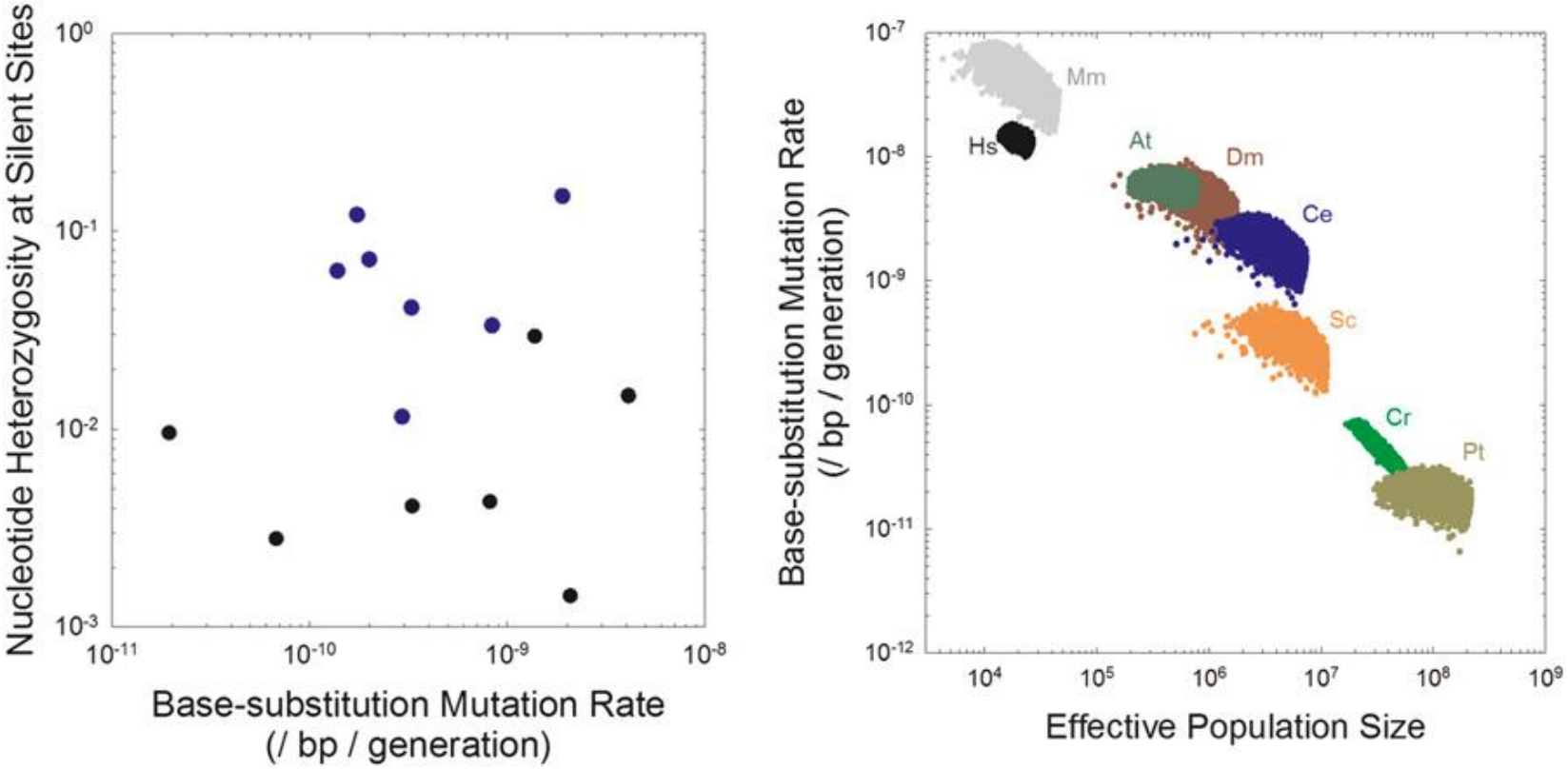
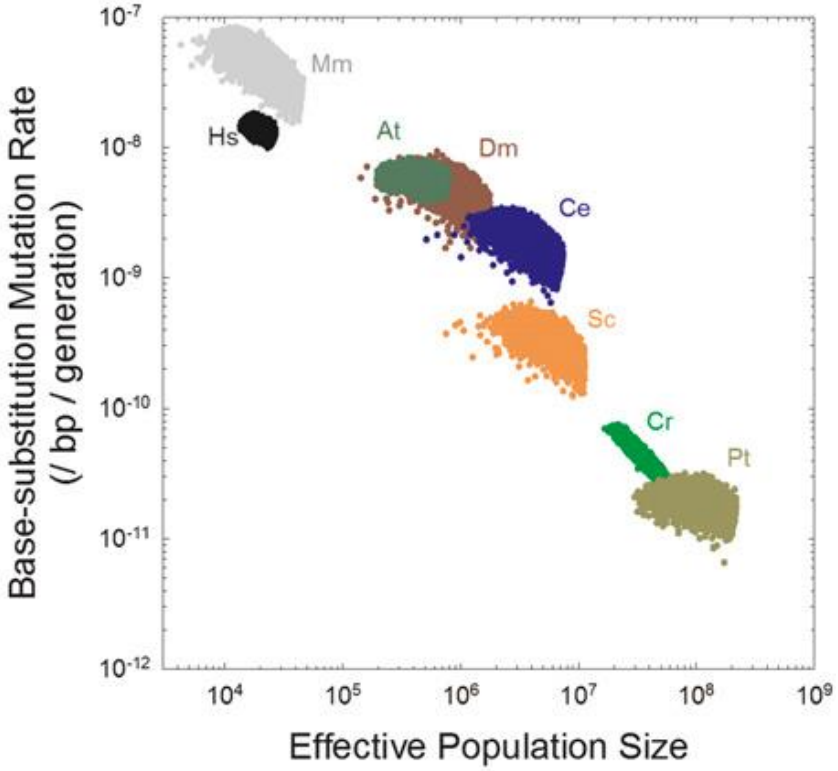



**Fig. S1.** (*Left*) Absence of a relationship between mutation-rate estimates ($u$) and population-genetic estimates of silent-site diversities ($\pi_s$) for unicellular prokaryotes (blue) and eukaryotes (black). (*Right*) The 95% support regions for joint estimates of the mutation rate and the effective population size ($N_e$) for a sampling of taxa. In each case, estimates for both $u$ and $\pi_s$ and their respective SEs were available. The sampling distributions of both parameters were assumed to be Gaussian in form, with no covariance between them; for this, 10,000 random pairs of estimates were drawn, and for each pair an estimate of $N_e$ was derived as $\pi_s/(ku)$, where $k = 2$ or 4 depending on whether the species was haploid or diploid. For each species, the cloud of data represents the set of 9,500 sample pairs with the minimal Euclidean distance to the original point estimates of $u$ and $N_e$. Although a negative sampling covariance exists between estimates of $u$ and $N_e$, because of the acquisition of the latter by dividing $\pi_s$ by the former, such covariance cannot account for the broad patterns seen in Fig. 1 *B* and *C*. At, *Arabidopis thaliana*; Ce, *Caenorhabditis elegans*; Cr, *Chlamydomonas reinhardtii*; Dm, *Drosophila melanogaster*; Hs, *Homo sapiens*; Mm, *Mus musculus*; Pt, *Paramecium tetraurelia*; Sc, *Saccharomyces cerevisiae*.




Sung et al. 2012. PNAS

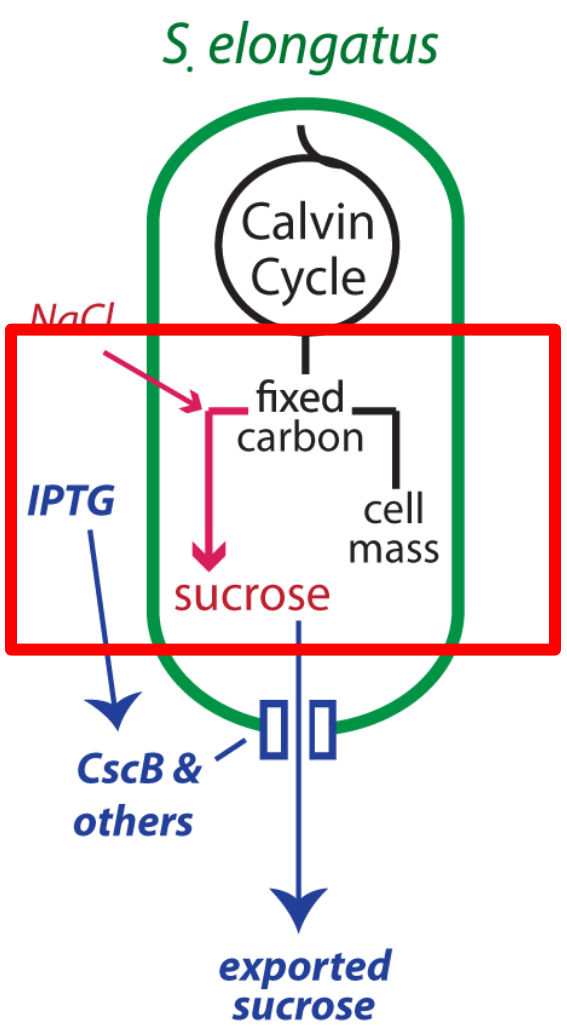
# Microalgae as an efficient alternative to terrestrial plant-based carbohydrate feedstocks?

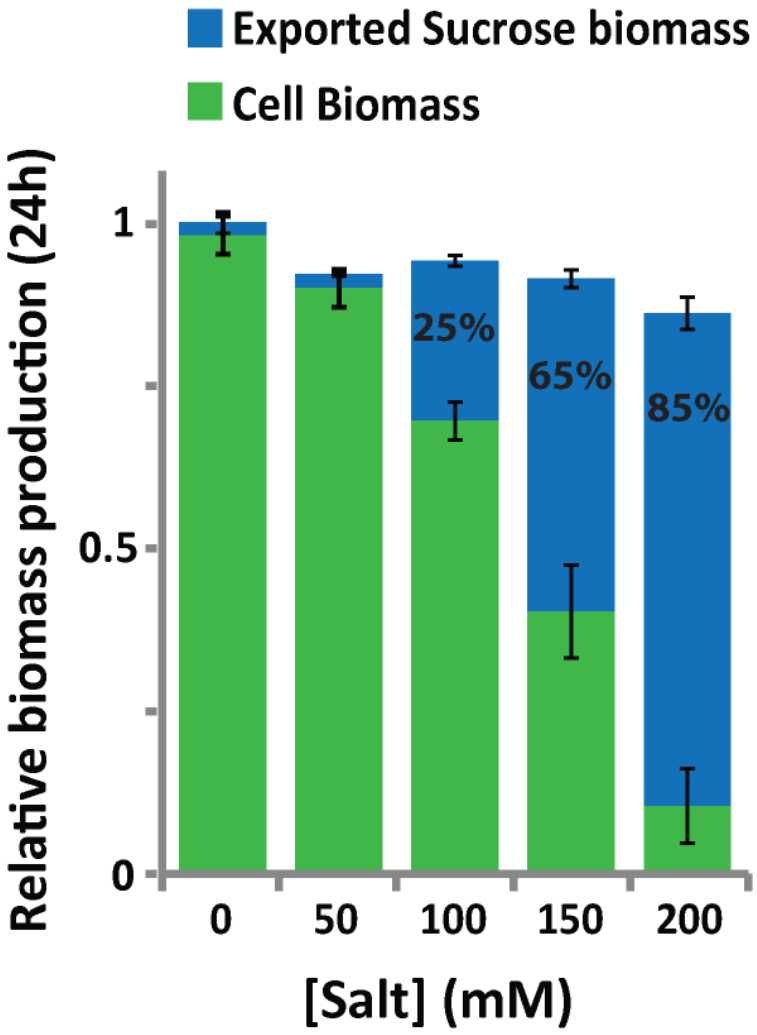
Danny Ducat

05/27/14

Michigan State University – Plant Research Laboratories & Biochemistry Department

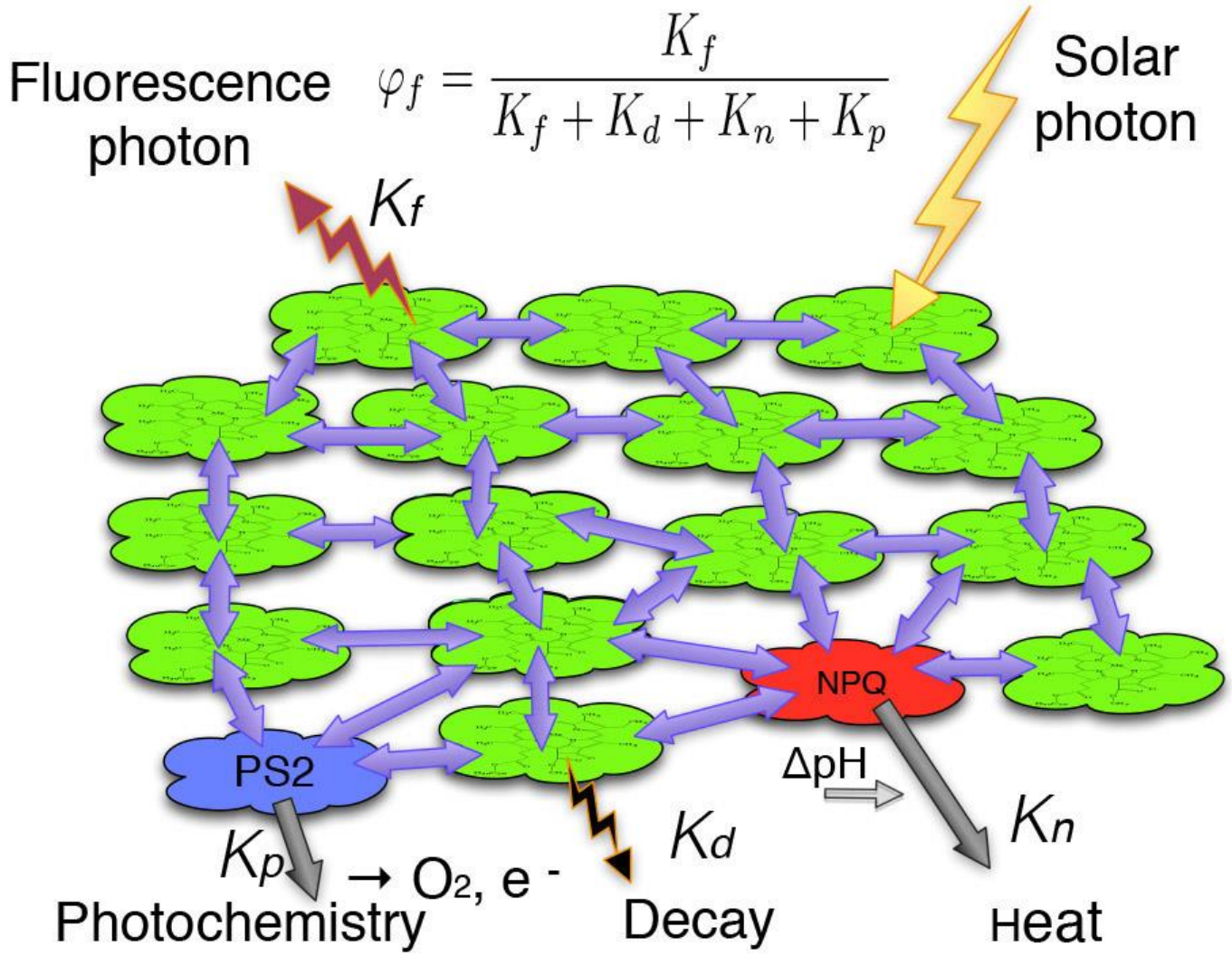
# Expression of Sucrose Transporters Allows Export Over a Tunable Range



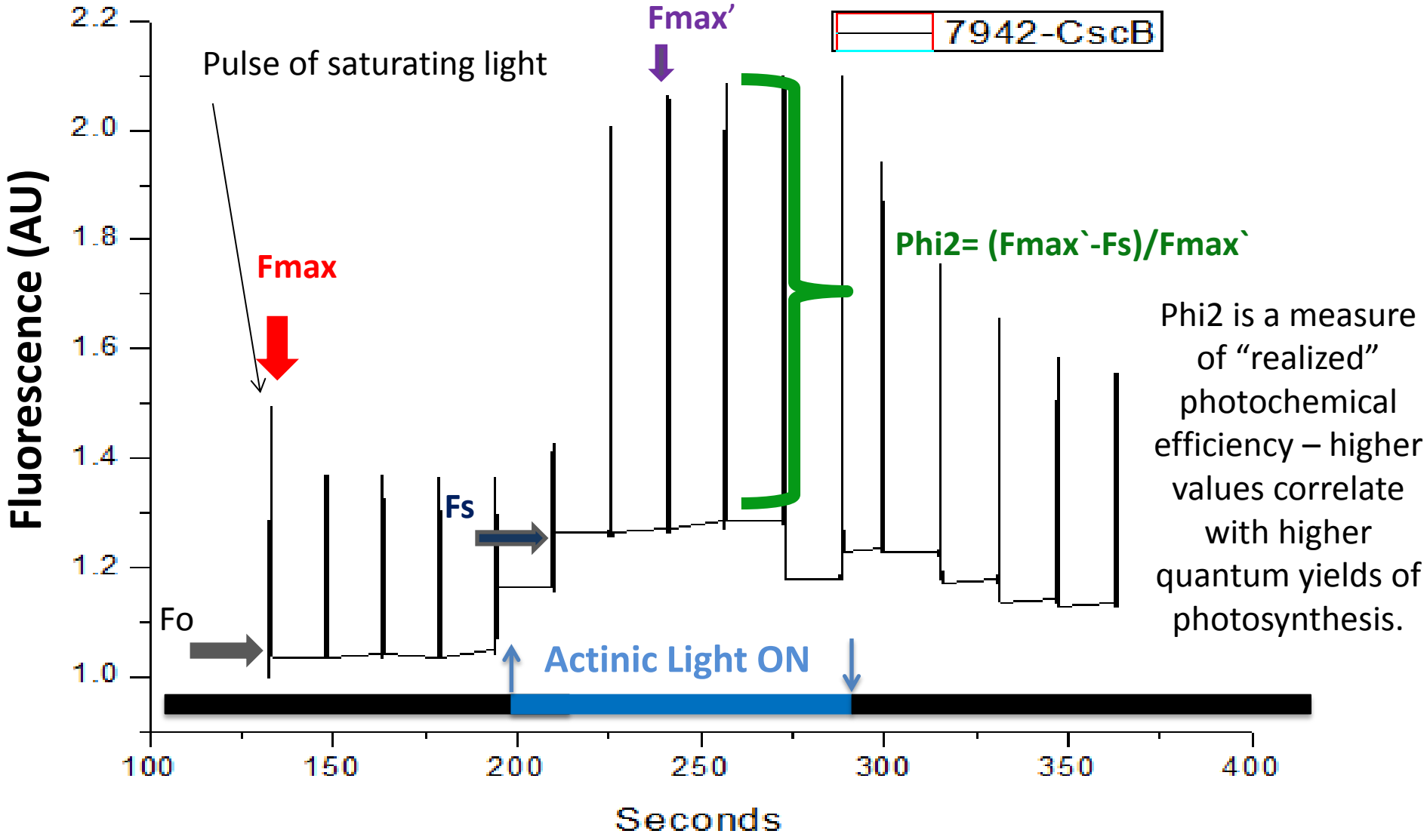

**Over the first 24 hour period, sucrose exported comes at cost of cell biomass at approx. 1 to 1 ratio**

# Chlorophyll a Fluorescence Dynamics Can Provide a Real-Time Measurement of the State of Photochemistry




Frankenberg, Christian, et al. 2013. SPIE

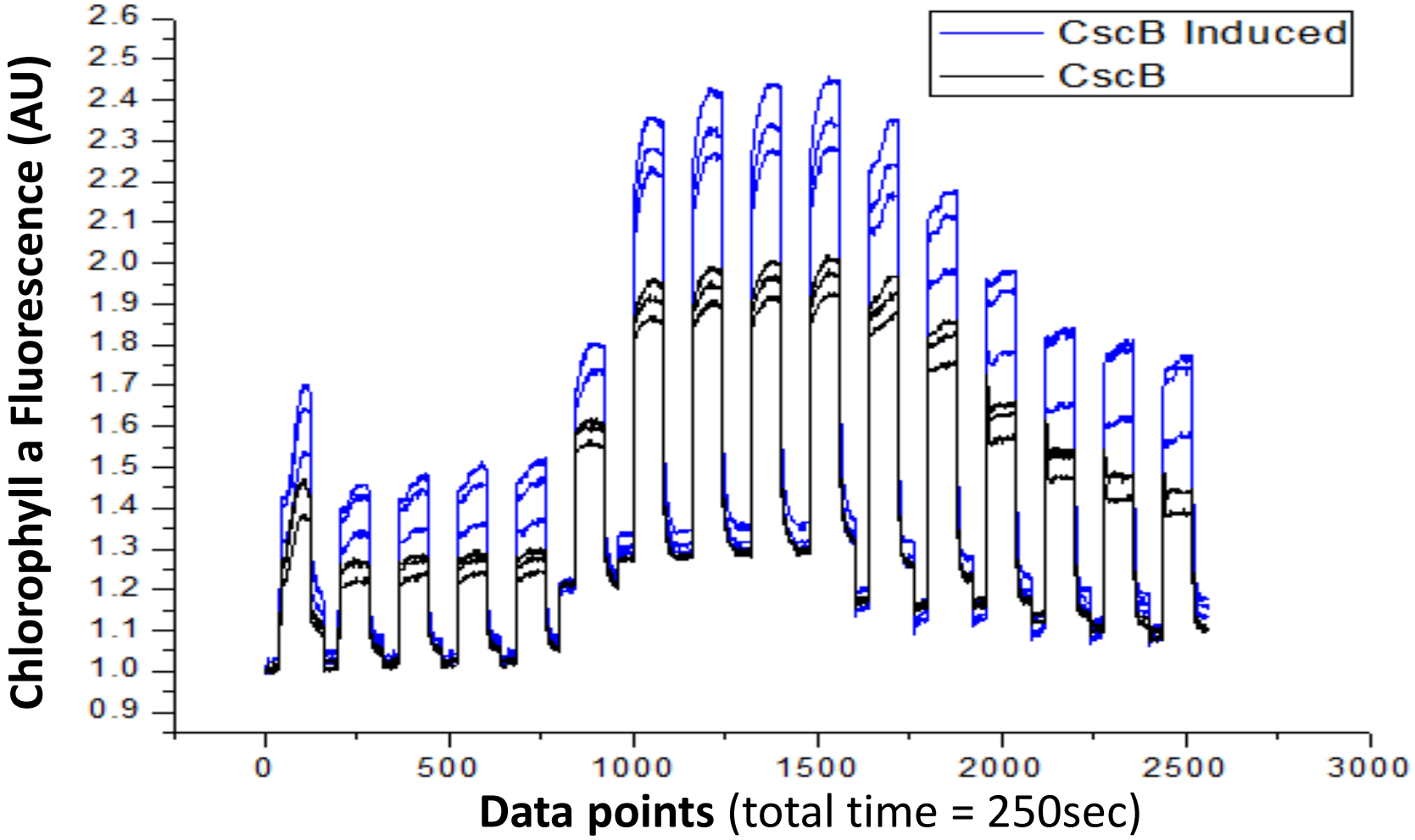
# Analysis of Chlorophyll a Fluorescence Provides a Proxy for Photosynthetic Efficiency




Phi2 is a measure of "realized" photochemical efficiency – higher values correlate with higher quantum yields of photosynthesis.

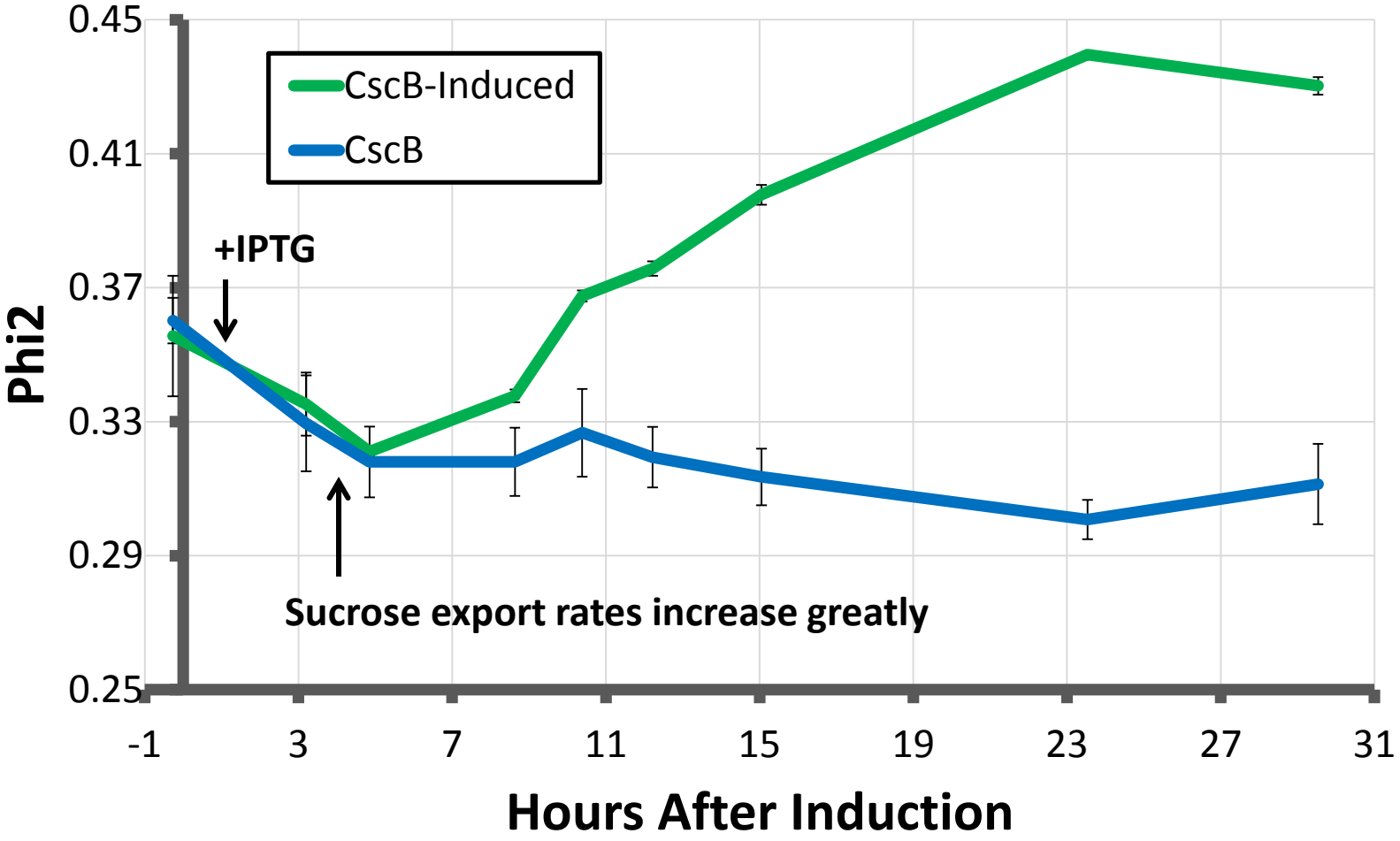
# Induction of Sucrose Export through CscB Leads to a Striking Enhancement of Phi2 Values

(24 hours post induction)




Increased Phi2 is consistent with an enhancement in photosynthetic efficiency in sucrose-secreting cyanobacteria

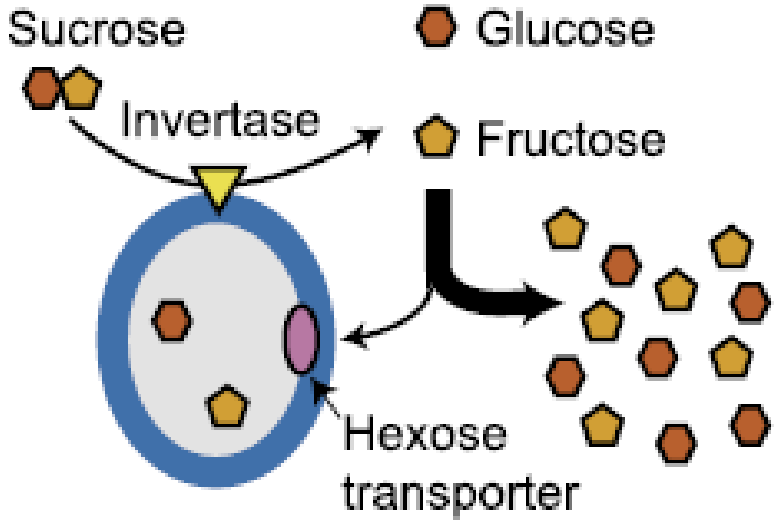
# Sucrose-secreting Cyanobacteria Display Phi2 Increases Shortly Following the Beginning of Sucrose Export




Kinetics of Phi2 rise are consistent with a ‘relaxation’ of metabolic sink limited photosynthesis

# Engineering Heterotroph-Side: Improved Sucrose Utilization

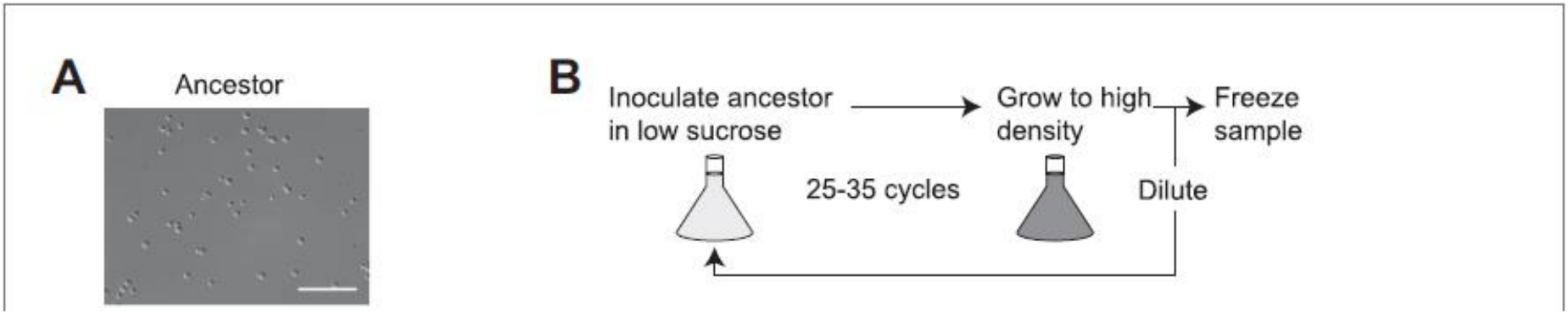
At low cell density in low sucrose concentrations, yeast cells cannot capture enough glucose and fructose to grow.




**External** expression of invertase sets up an interesting biological situation where the yeast must navigate an evolutionary version of the "snowdrift" game theory.

# Engineering Heterotroph-Side: Evolved Tolerance of Environment

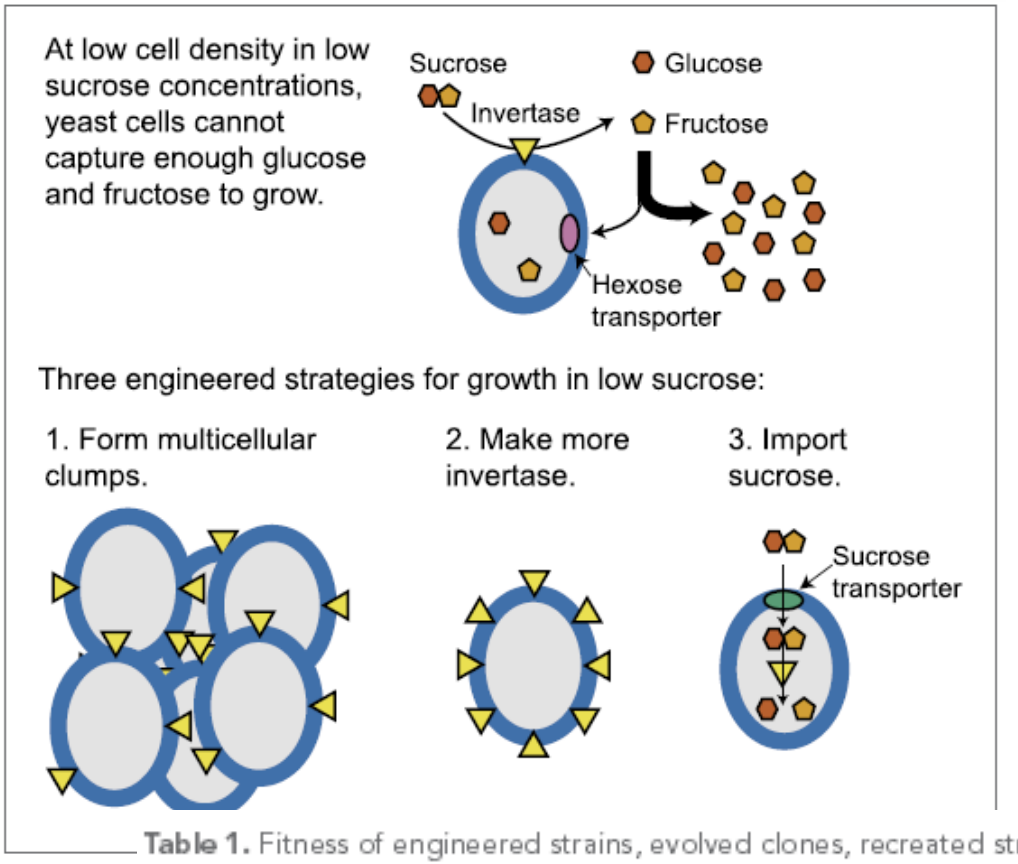
Andrew Murray's Lab: Previously has evolved yeast using multiple rounds of selection on low sucrose media.

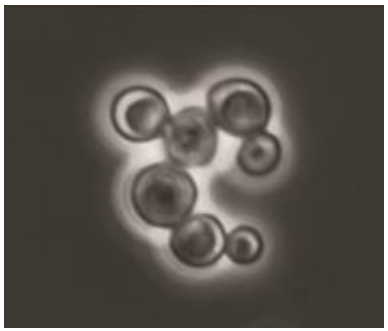



## Improved use of a public good selects for the evolution of undifferentiated multicellularity

John H Koschwanez[1*], Kevin R Foster[2], Andrew W Murray[1]

# Engineering Heterotroph-Side: Evolved Tolerance of Environment



10 Cycles (~100 generations) in BG11 with low sucrose +Ammonium + NaCl

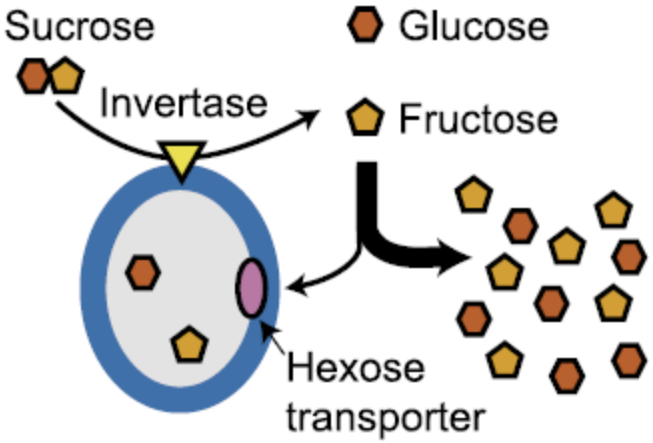
**Table 1.** Fitness of engineered strains, evolved clones, recreated strains, and reverted strains

| Strain 1 | Strain 2 | 1 mM sucrose | 1 mM glucose + 1 mM fructose | 80 mM glucose |
|---|---|---|---|---|
| EngClumpy | Wild-type lab | +++ | 0 | 0 |
| EngHiInvertase | Wild-type lab | + | 0 | 0 |
| EngSucImport | Wild-type lab | +++ | 0 | 0 |
| EvoClone1 | Ancestor | ++++ | --- | ---- |
| EvoClone2 | Ancestor | ++++ | 0 | -- |
| EvoClone3 | Ancestor | ++++ | --- | ---- |

# Some Relevant Population Genetic Principles

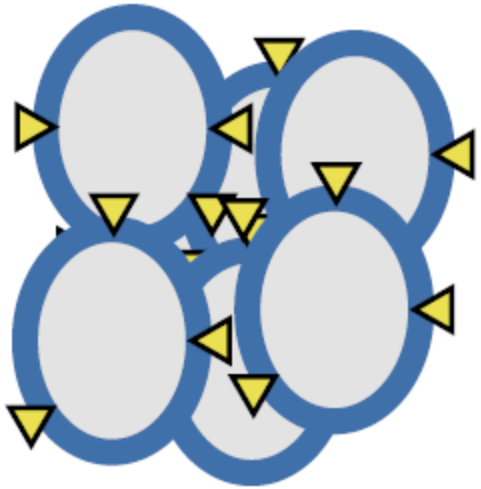
- Mutation-Selection Balance
- Genetic Drift & Population Size
- Pleiotropy
- Epistatis (within and between proteins)
- Clonal Interference
- Functional Trade-offs
- Genetic Hitchhiking, Linkage & Recombination)

At low cell density in low sucrose concentrations, yeast cells cannot capture enough glucose and fructose to grow.

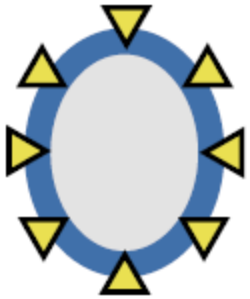



Three engineered strategies for growth in low sucrose:

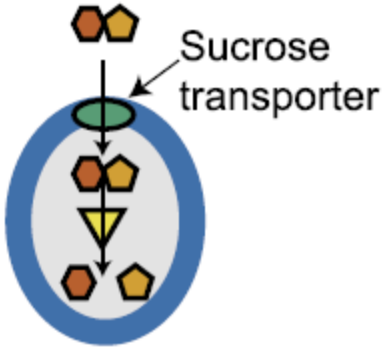
1. Form multicellular clumps.



2. Make more invertase.

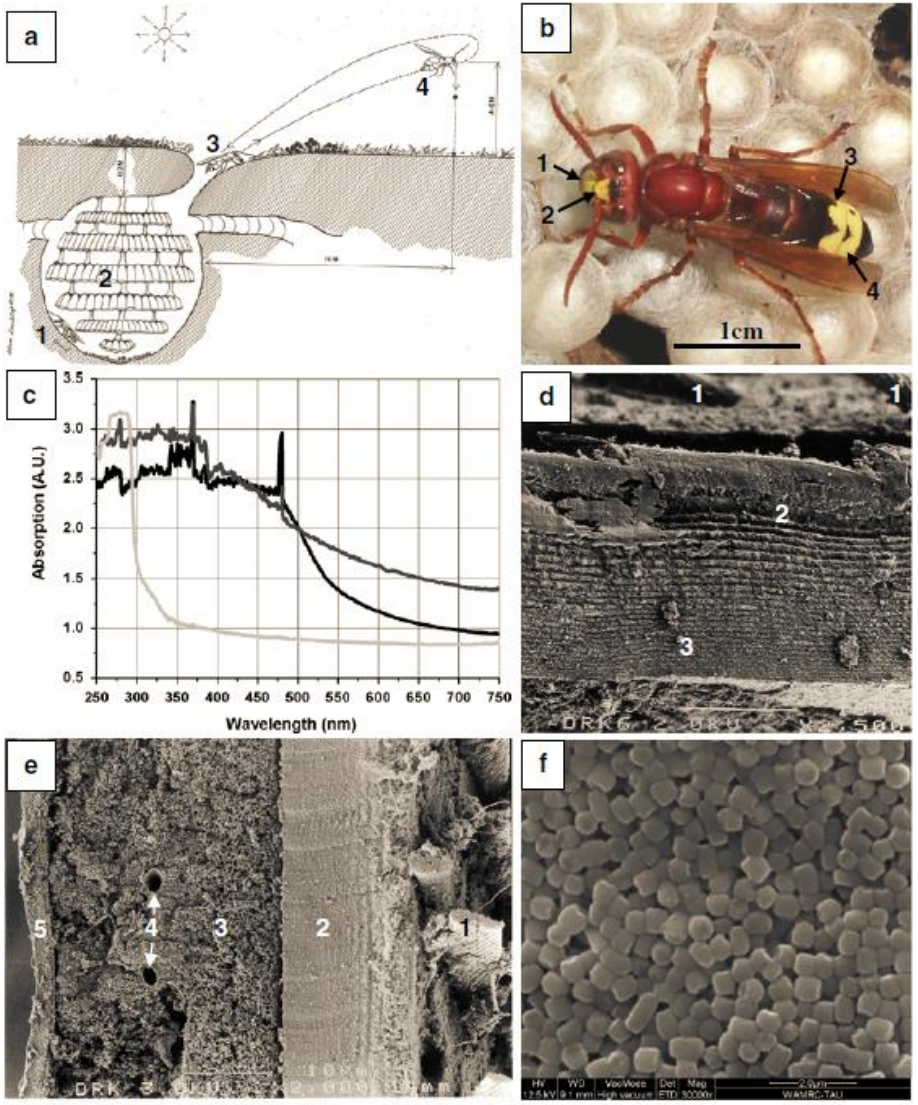


3. Import sucrose.



# Solar energy harvesting in the epicuticle of the oriental hornet (*Vespa orientalis*)

Plotkin et al 2011




Yellow pigment granule
(` 500 nm)