




# JUST HOW MUCH PHOSPHORUS DOES A BACTERIUM NEED?

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# What we will discuss...

- How much P is in a (real and not so real) bacterium and how little can they get by on, i.e., how low can they go?  

- Homeostasis: How variable is bacterial C and P content? How does a bacterium and a bacterial community respond to changes in its their environment?  

- The future of Phosphorus?  




# Why are we interested in P?

- It's part of the basic composition of organisms (RNA, DNA, P-lipids)
- It is often a limiting nutrient
- We are releasing too much of it into the environment
- We are running out of it!

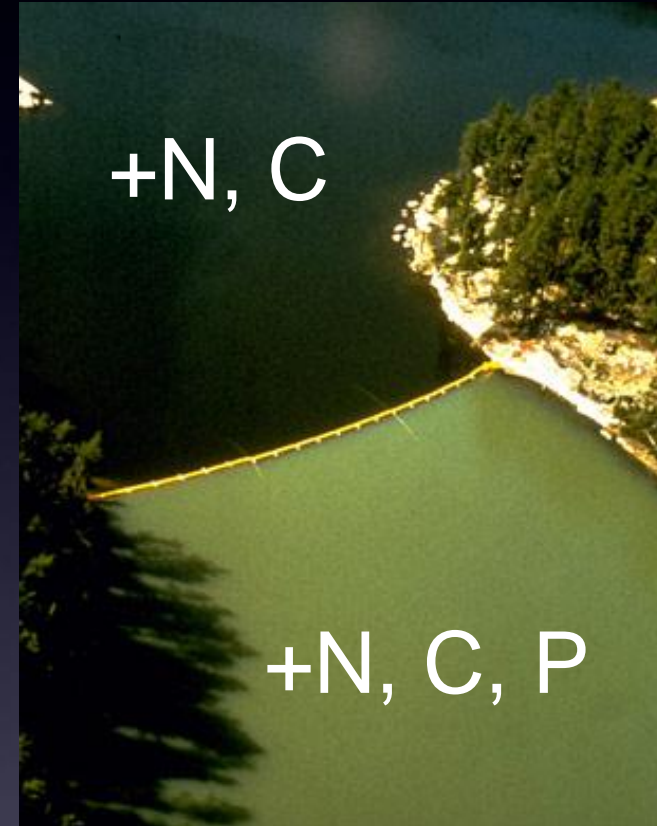
08/05/2011



# Human perturbations to different biogeochemical cycles

**Table 2.** Examples of human intervention in the global biogeochemical cycles of carbon, nitrogen, phosphorus, sulfur, water, and sediments. Data are for the mid-1900s.

Element	Flux	Magnitude of flux (millions of metric tons per year)		% change due to human activities
		Natural	Anthropogenic	
C	Terrestrial respiration and decay CO <sub>2</sub>	61,000		
	Fossil fuel and land use CO <sub>2</sub>		8,000	+13
N	Natural biological fixation	130		
	Fixation owing to rice cultivation, combustion of fossil fuels, and production of fertilizer		140	+108
P	Chemical weathering	3		
	Mining		12	+400
S	Natural emissions to atmosphere at Earth's surface	80		
	Fossil fuel and biomass burning emissions		90	+113
O and H (as H <sub>2</sub> O)	Precipitation over land	111 × 10 <sup>12</sup>		
	Global water usage		18 × 10 <sup>12</sup>	+16
Sediments	Long-term preindustrial river suspended load	1 × 10 <sup>10</sup>		
	Modern river suspended load		2 × 10 <sup>10</sup>	+200

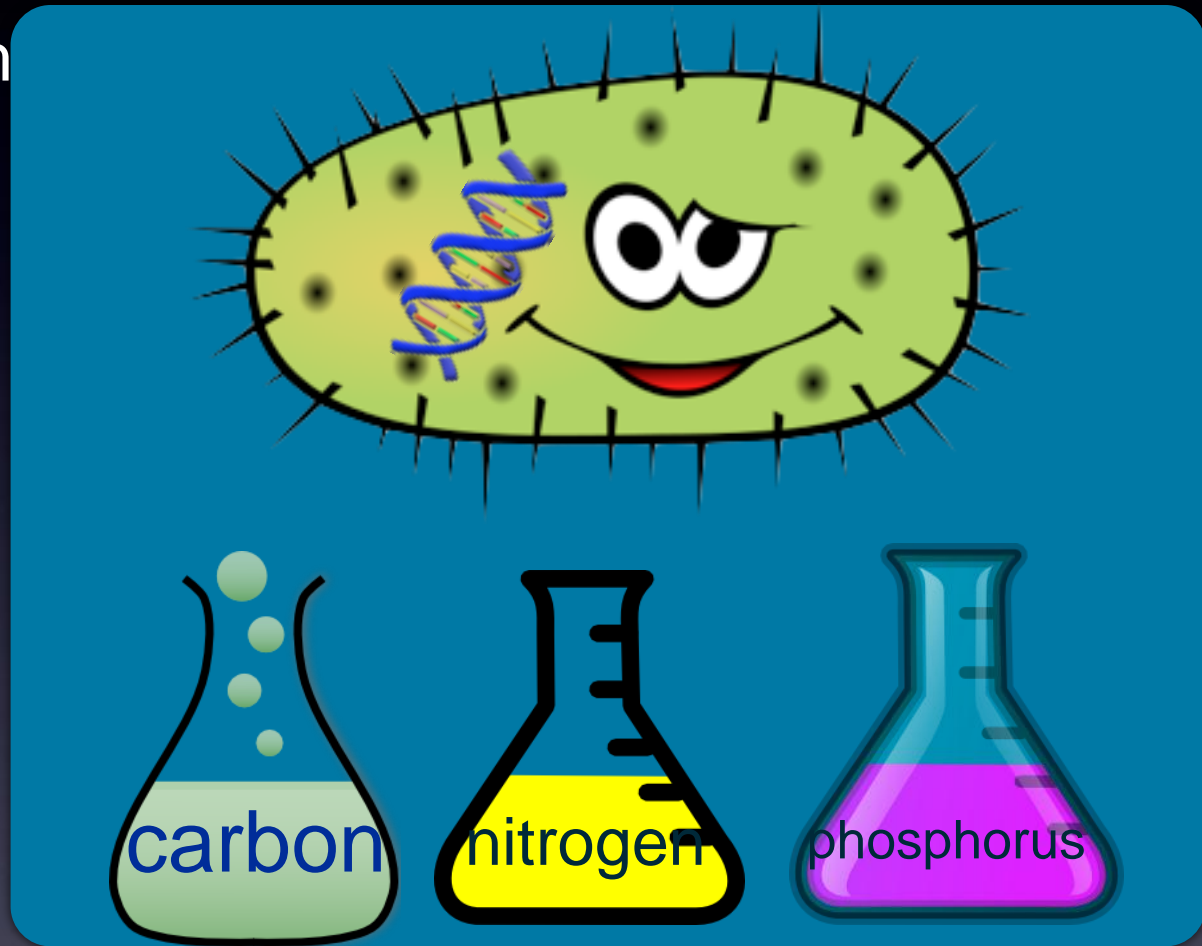
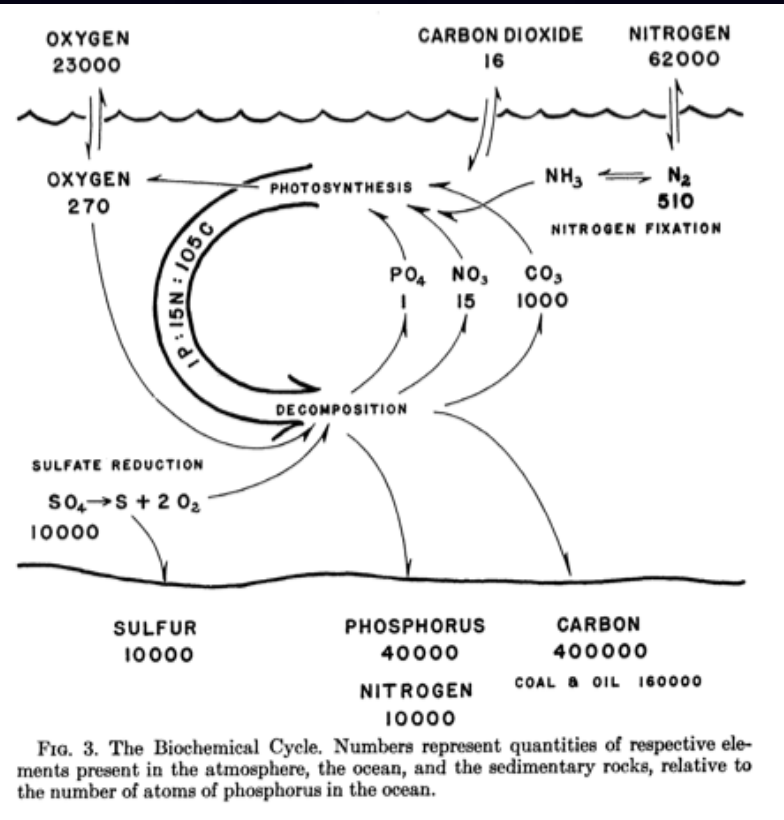


Falkowski, P. G., Scholes, R. J., Boyle, E., Canadell, J., Canfield, D., Elser, J., Gruber, N., Hibbard, K., Högberg, P., Linder, S., Mackenzie, F. T., Moore, B. I., Pedersen, T., Rosenthal, Y., Seitzinger, S., Smetacek, V. & Steffen, W. (2000). The global carbon cycle: a test of our knowledge of Earth as a system. *Science* **290**, 291-296.

# Ecological stoichiometry



How organisms deal with variability in resource



osmotrophs vs. phagotrophs,  
 heterotrophs vs. autotrophs

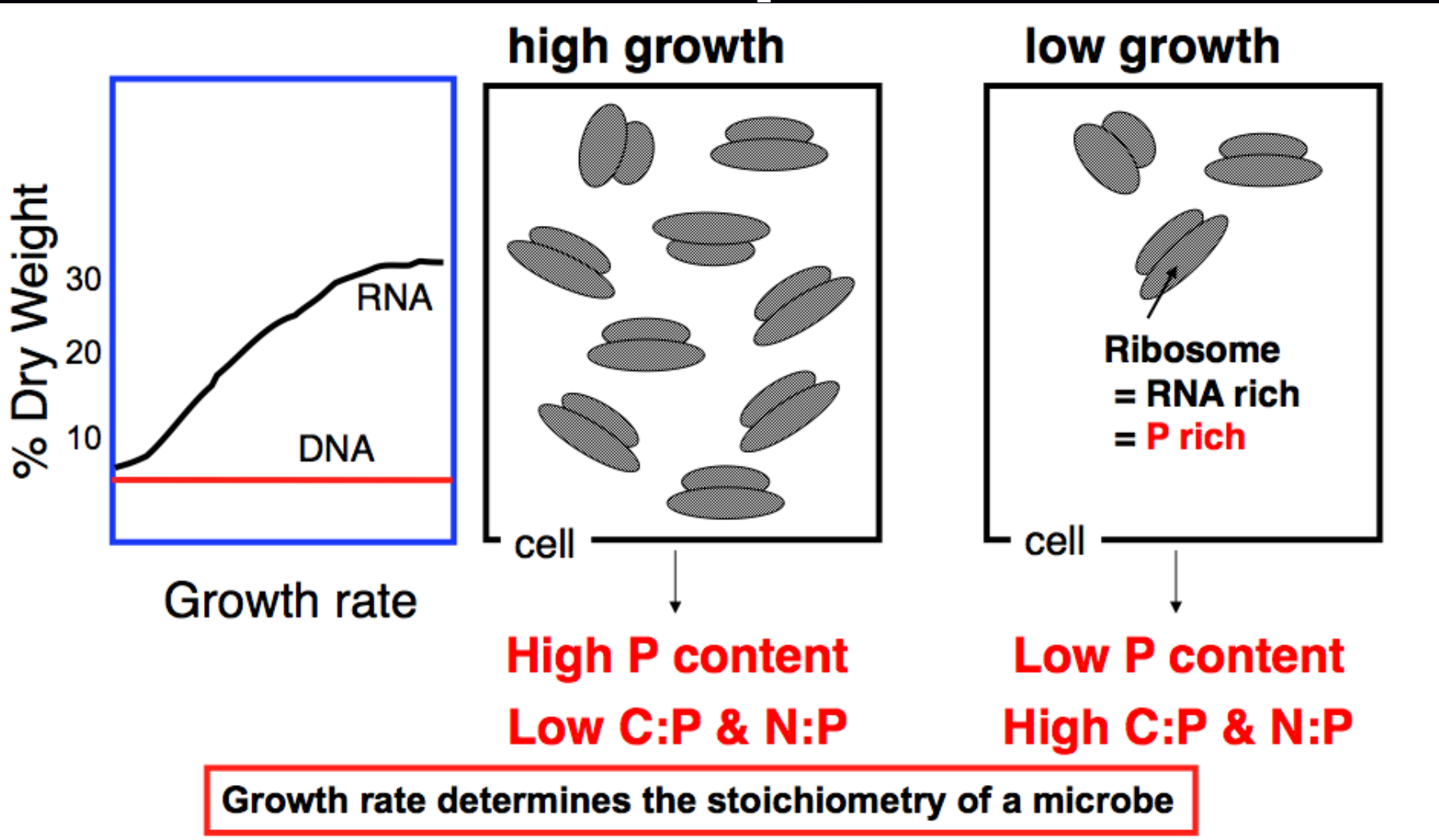
Redfield 1958

# What determines the biomass composition of microbial communities?

- Growth rate (the 'growth rate hypothesis')
- Substrate stoichiometry
- Temperature
- Community composition (prokaryotic vs. eukaryotic; unicellular vs. multi-cellular, autotrophs vs. heterotrophs)

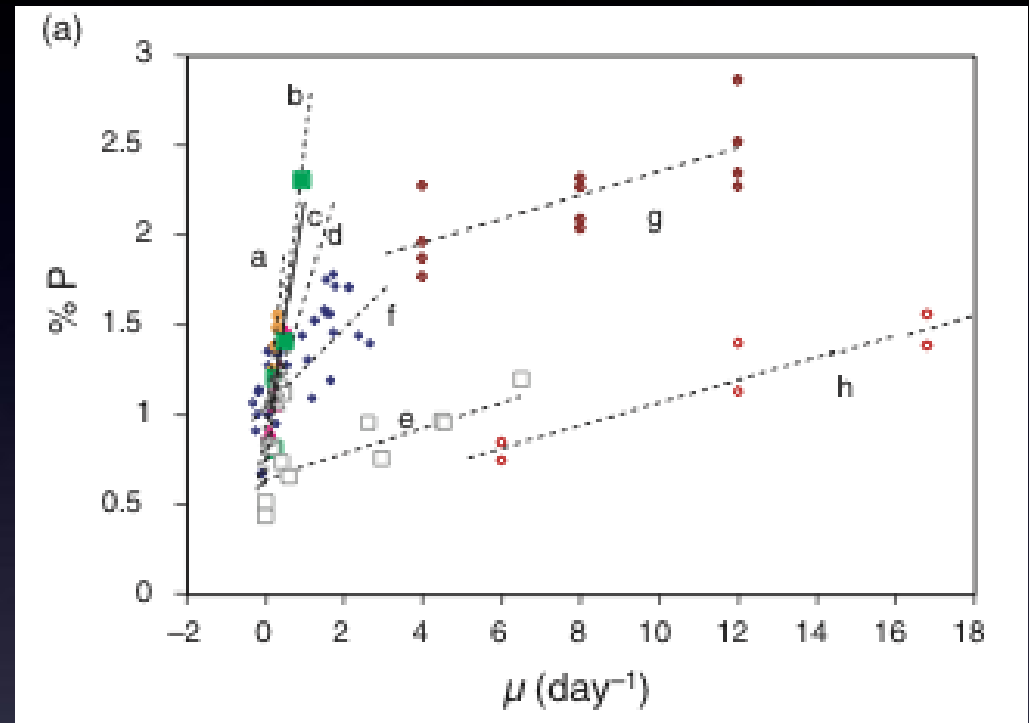
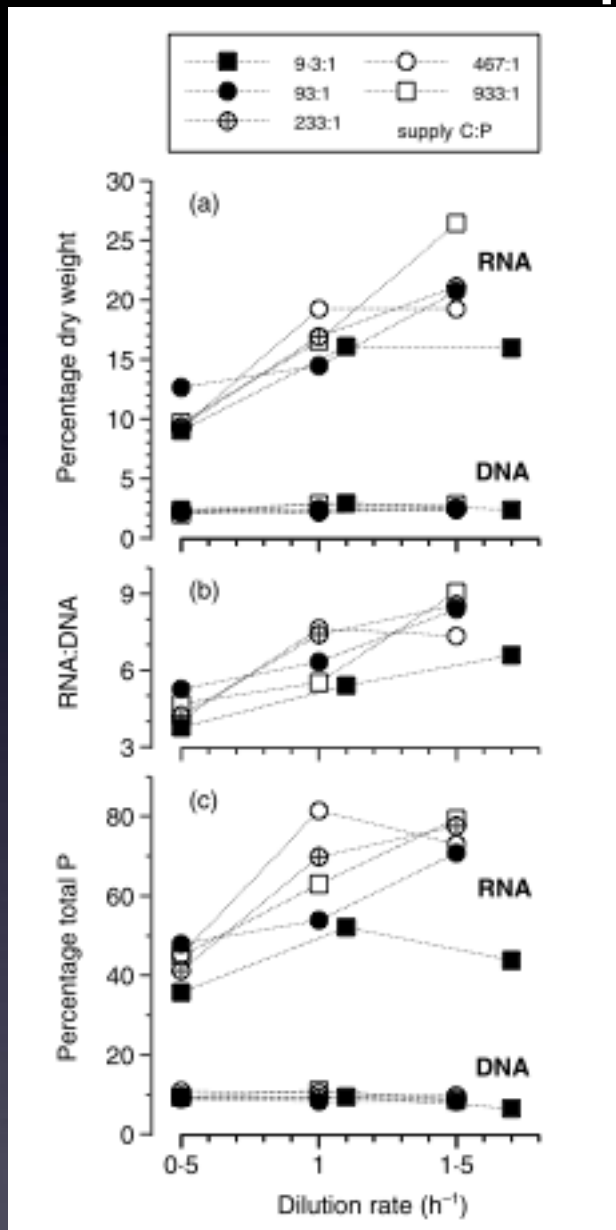
P

# Growth rate, RNA and P



# P and growth: The growth rate hypothesis

P

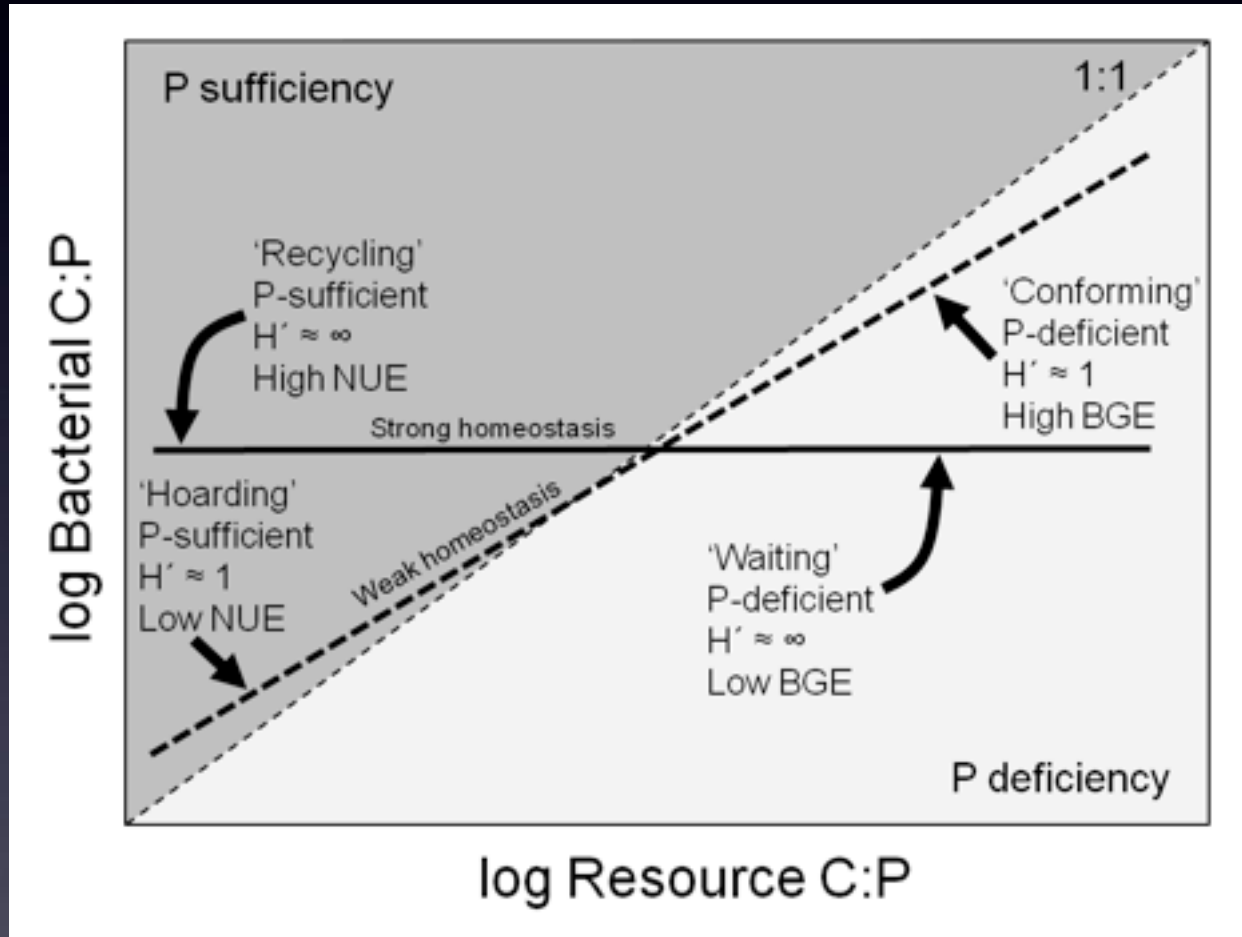


...where's the rest of the P?



# Substrate stoichiometry and homeostasis

P



How much P is there  
in a bacterium?.....

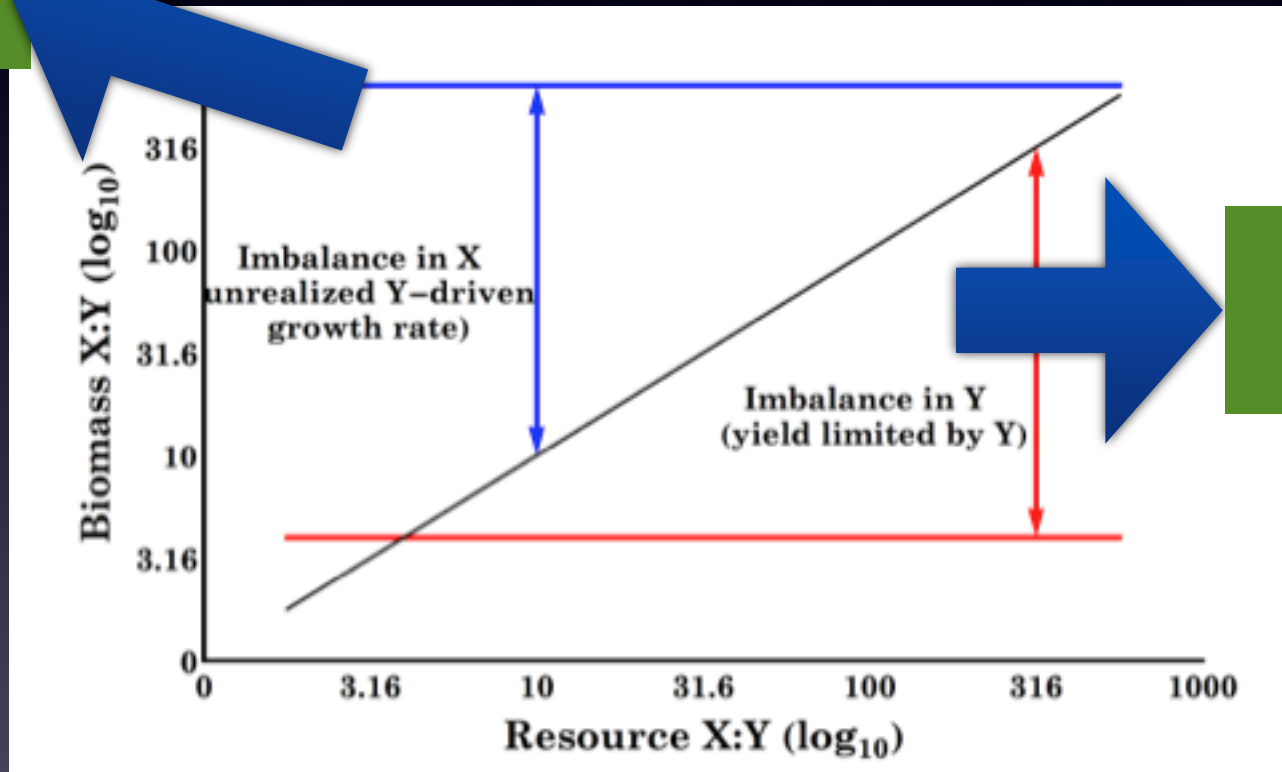


...and how low can they go?

# ...and why should we care

P

Positive feedback  
S



Unrealized production

..How much P does a bacterium have? We used to think a lot...

Redfield ratio 106C: 16N: 1P

P

Most studies assume that bacteria are P-rich with C:P ratios about 50:1

But are they really that nutrient rich?

Bratbak 1985

TABLE 1. Comparison of cell composition, carbon per cell, estimates of cell volume obtained with different methods, and carbon per unit of estimated cell volume for six different cultures of bacteria

Inoculum	Limiting nutrient	Cell composition (C:N:P molar ratio)	g of C per cell ( $\times 10^{-13}$ )	Cell vol ( $\mu\text{m}^3$ ) by:				C per unit of cell vol ( $10^{-13}$ g of C $\mu\text{m}^{-3}$ ) <sup>a</sup> by:		
				SEM	Epifluorescence microscopy		Electronic sizing	SEM	Epifluorescence microscopy	
					Eye-piece graticule	Photographs			Eye-piece graticule	Photographs
<i>P. putida</i>	C	100:22:6.2	1.29	0.30	0.28	0.29	ND <sup>b</sup>	4.2	4.6	4.4
<i>P. putida</i>	N	100:19:5.1	1.69	0.39	0.66	0.71	0.74	4.4	2.6	2.4
<i>P. putida</i>	P	100:18:0.2	3.12	0.34	0.57	0.63	0.66	9.3	5.5	5.0
Mixed	C	100:21:13	1.06	0.14	0.11	0.19	ND	7.7	8.0	5.8
Mixed	N	100:15:4.9	2.14	0.24	0.30	0.48	ND	9.0	7.2	4.5
Mixed	P	100:16:1.8	1.91	0.32	0.27	0.55	ND	6.0	7.1	3.5



# Bacterial and seston stoichiometry

Cotner et al. 2010

Mean among lakes: C:N:P

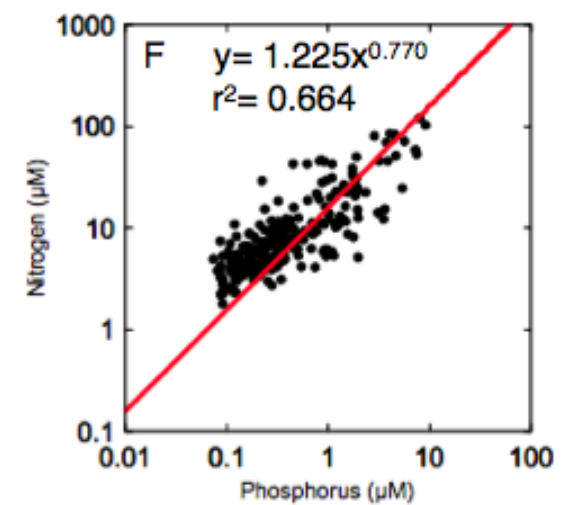
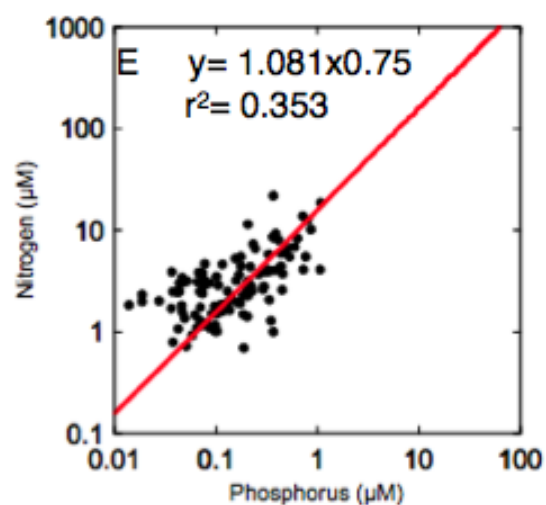
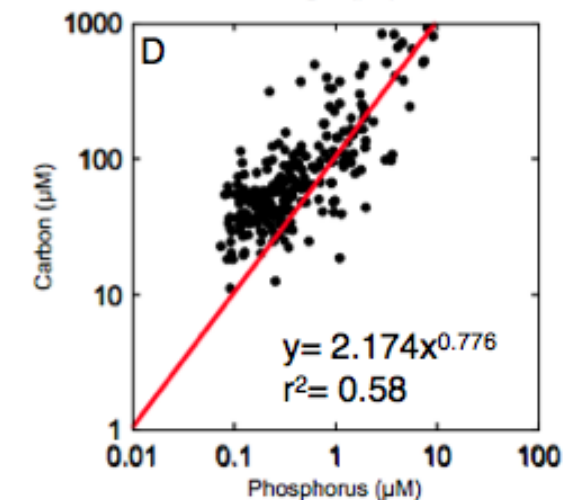
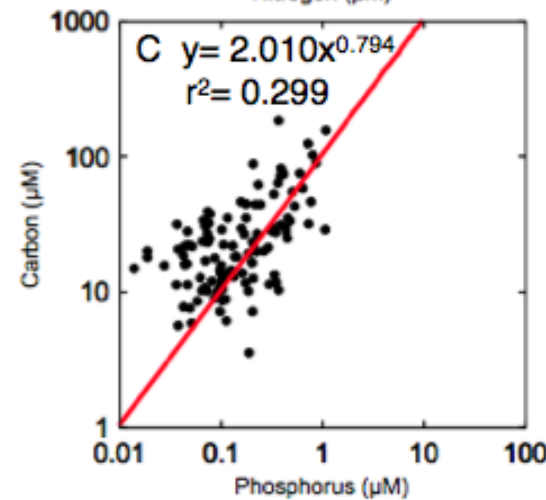
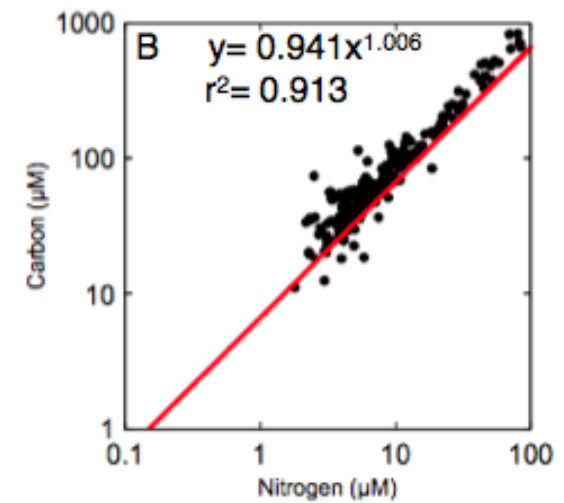
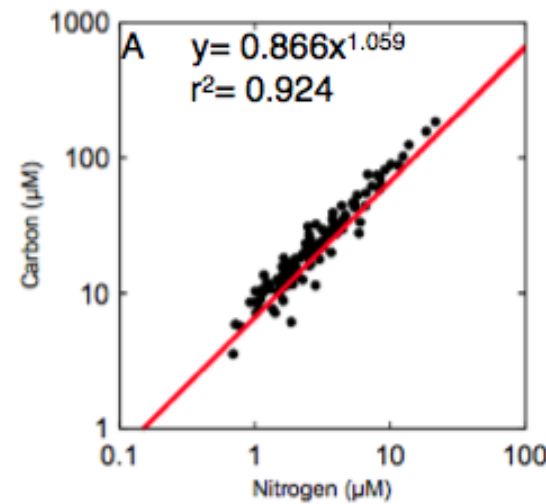
102:12:1

Strains: 875:179:1

Community in a lake:

259:69:1

P



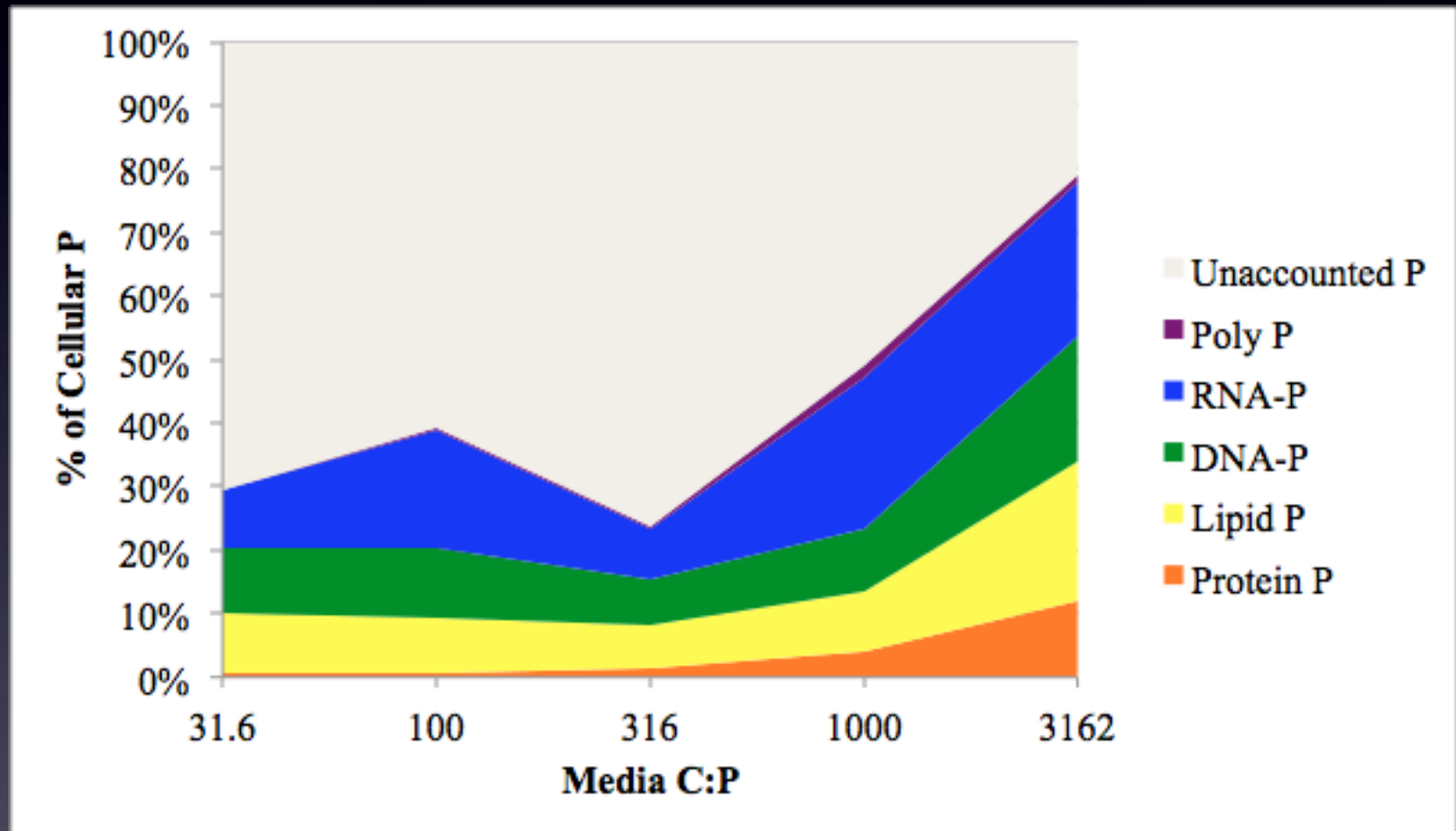
# Chemostats

P



# Where's the P? (lake communities)

P



Growth rates 0.2-0.3 per day

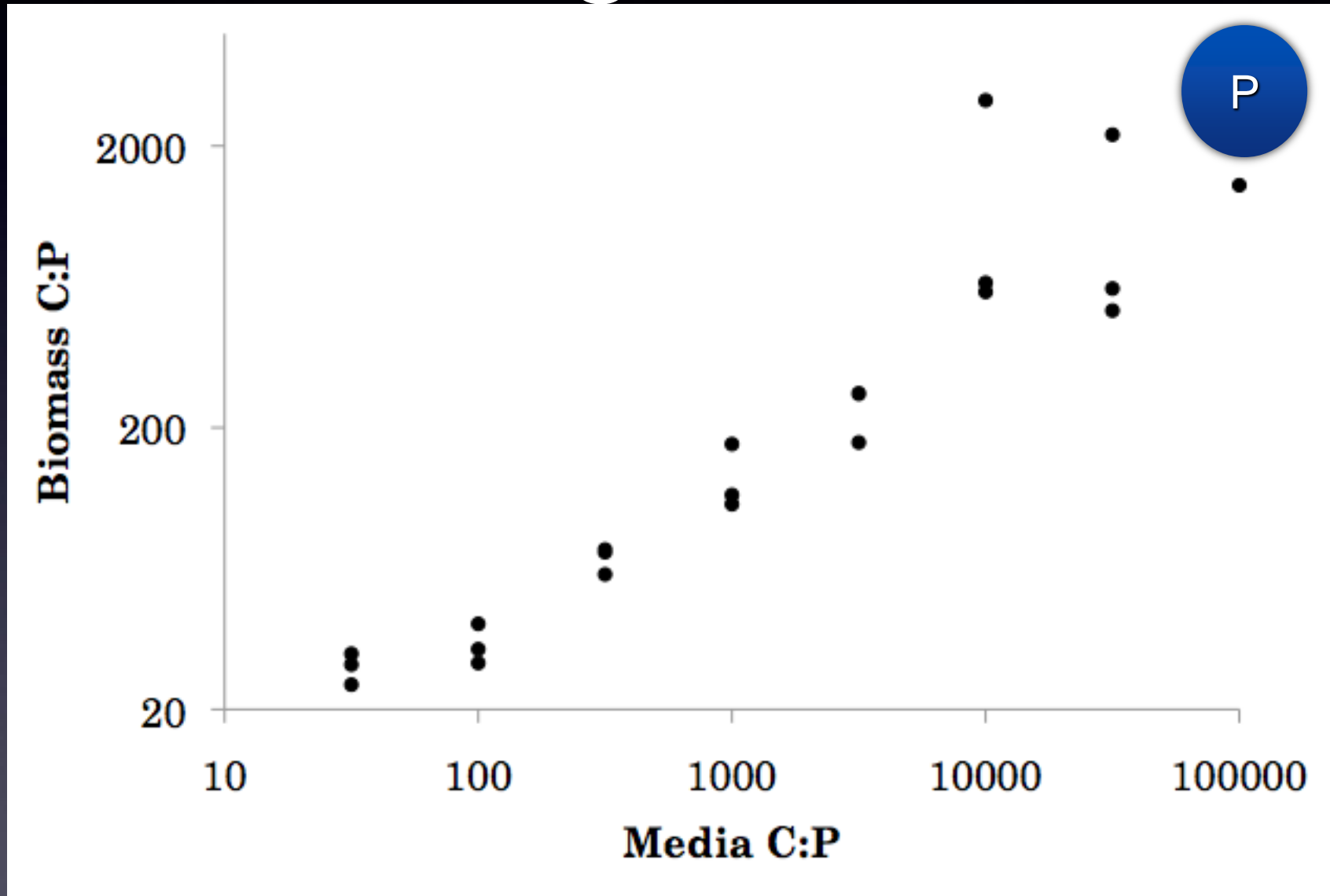
# How low can they go (and how flexible are they)?

P



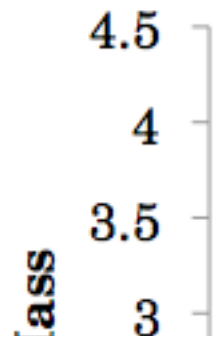


# How high can the C:P go?



# How low can they go? Can a bacterium have P content of 0.02% dw?

P



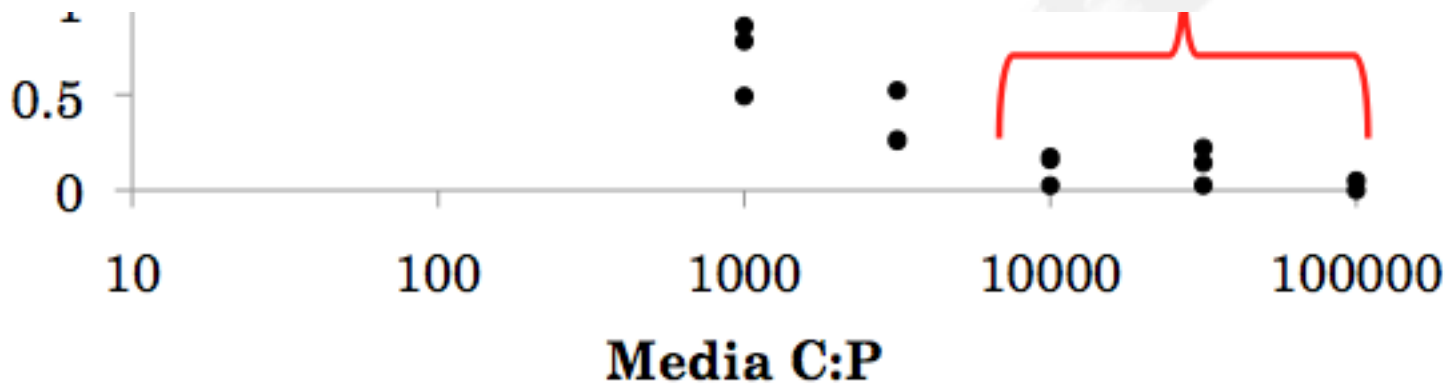
All of these data are above the detection limit of 99% confidence.

**Table 1.** Bulk intracellular elemental profile of strain GFAJ1.\*

(% dry weight)

Condition (n)	As	P	As:P
+As/-P (8)	0.19 ± 0.25	0.019 ± 0.0009	7.3
-As/+P (4)	0.001 ± 0.0005	0.54 ± 0.21	0.002

\*Cells grown and prepared with trace metal clean techniques (11). Number in parentheses indicates replicate samples analyzed.



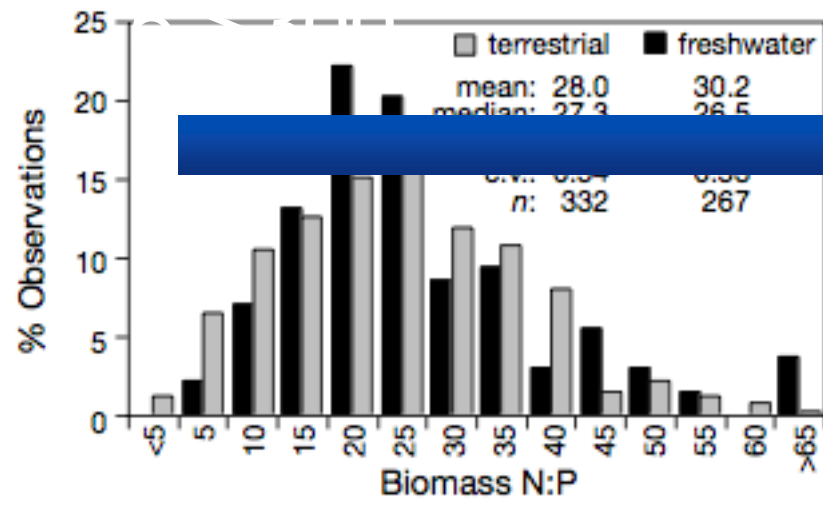
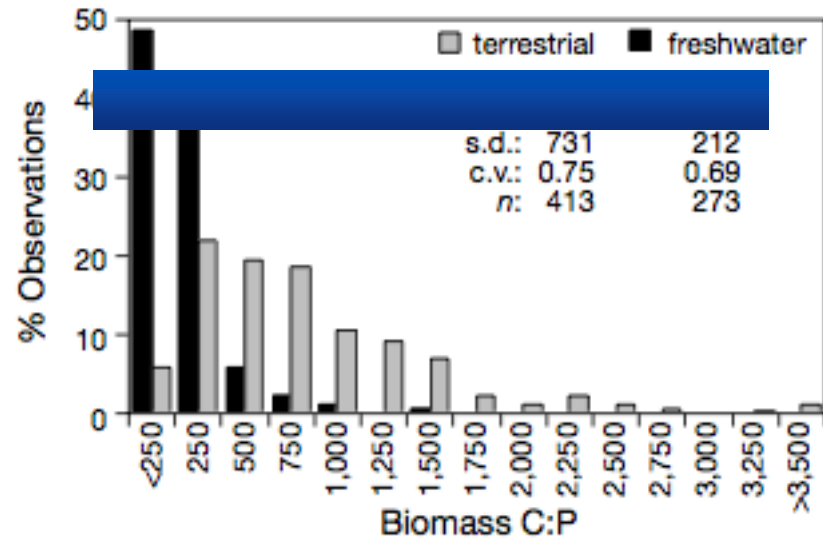
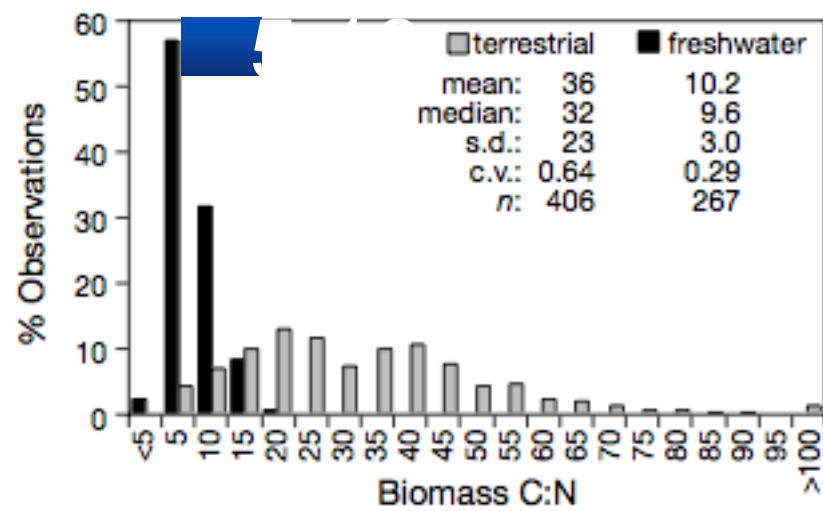
# Homeostasis

How flexible are  
bacteria?



# How flexible? Comparison with autotrophs

H

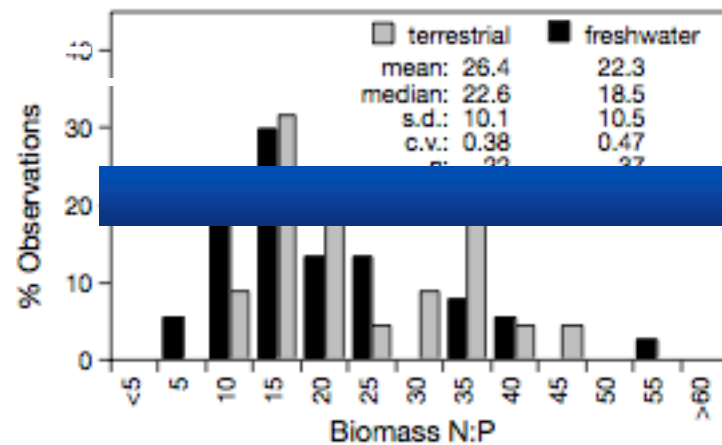
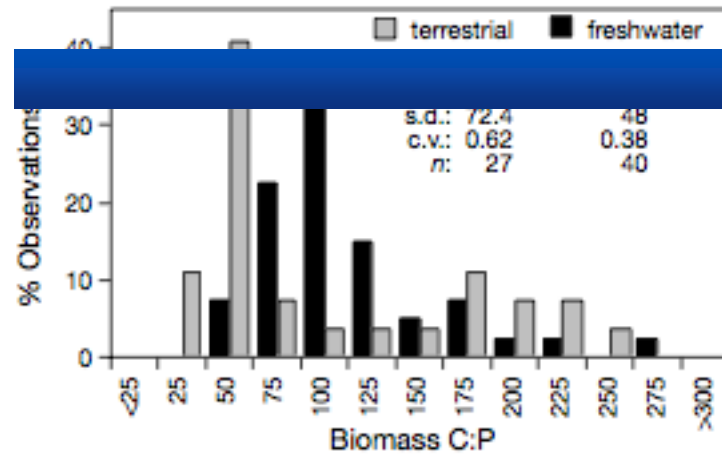
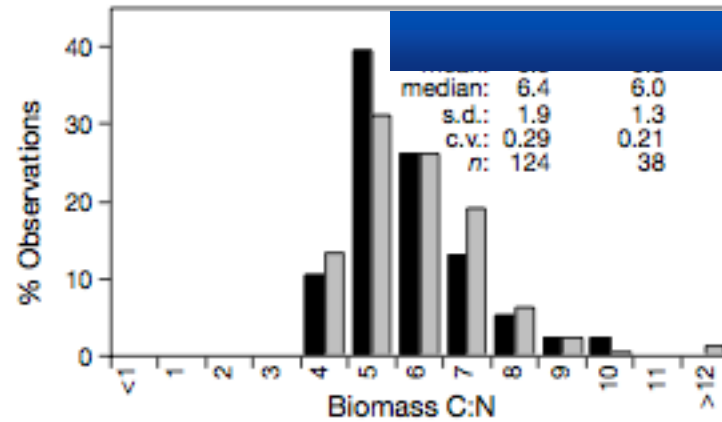


Elser et al. 2007



# Comparison with heterotrophs

Heterotrophic bacteria are the most stoichiometrically diverse organisms on the planet!



# Homeostasis and ecological theory

H

	r-Selected <sup>3,4</sup> , Competitive Specialists <sup>2</sup> , Velocity Strategy <sup>1,5</sup> , <u>Strong Homeostasis</u> , 'Homeostochs' <sup>6</sup>	K-Selected <sup>3,4</sup> , Stress-Tolerant <sup>2</sup> , Affinity-Adapted <sup>1,5</sup> , <u>Non-Homeostasis</u> , 'Heterostochs' <sup>6</sup>
$\mu$ max	high	low
'Storage capacity'	small	large
Nutrient content	high	low / variable
Nutrient requirement	high	low
Strength of Regulation (H)	high	low
Biomass C:X	low / less variable	high / variable
TER	low	high

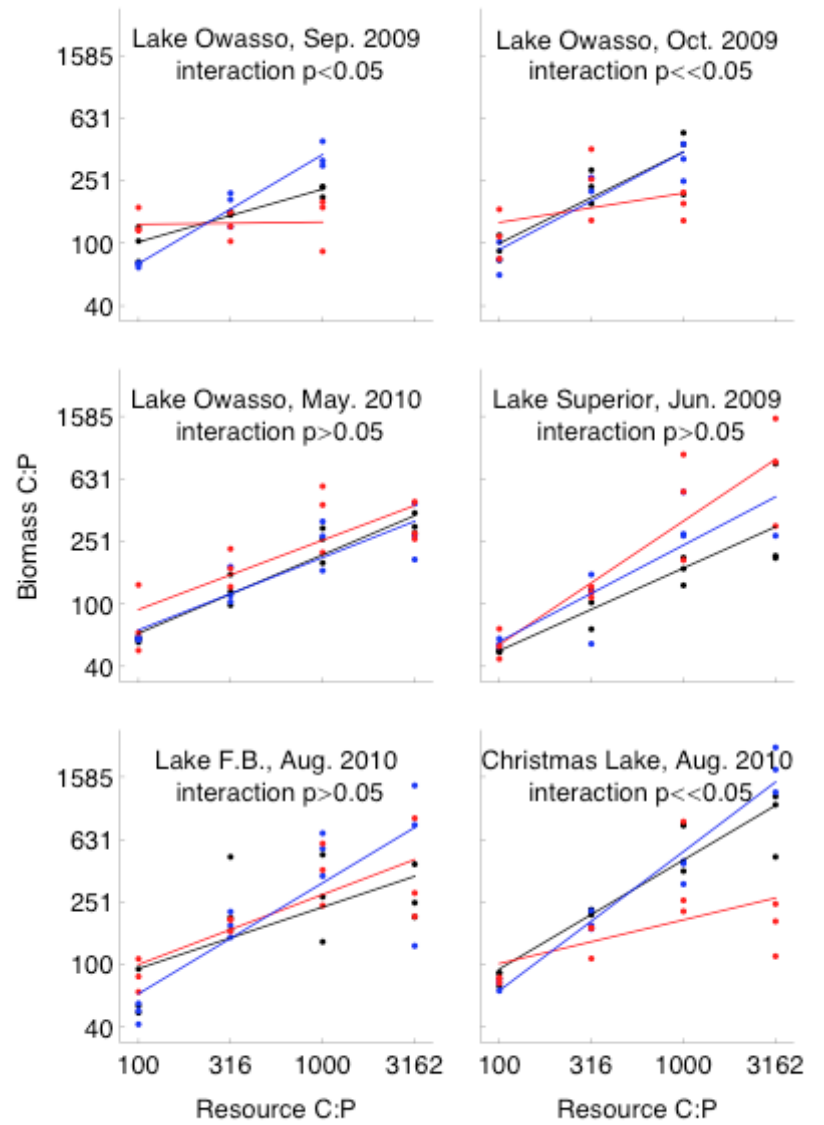
<sup>1</sup> Crowley 1975; <sup>2</sup> Grime 1977; <sup>3</sup> Jannasch 1974; <sup>4</sup> MacArthur and Wilson 1967;

<sup>5</sup> Sommer 1985; <sup>6</sup> Jim Cotner

# Homeostasis and communities: Do P rich conditions select for homeostasis?



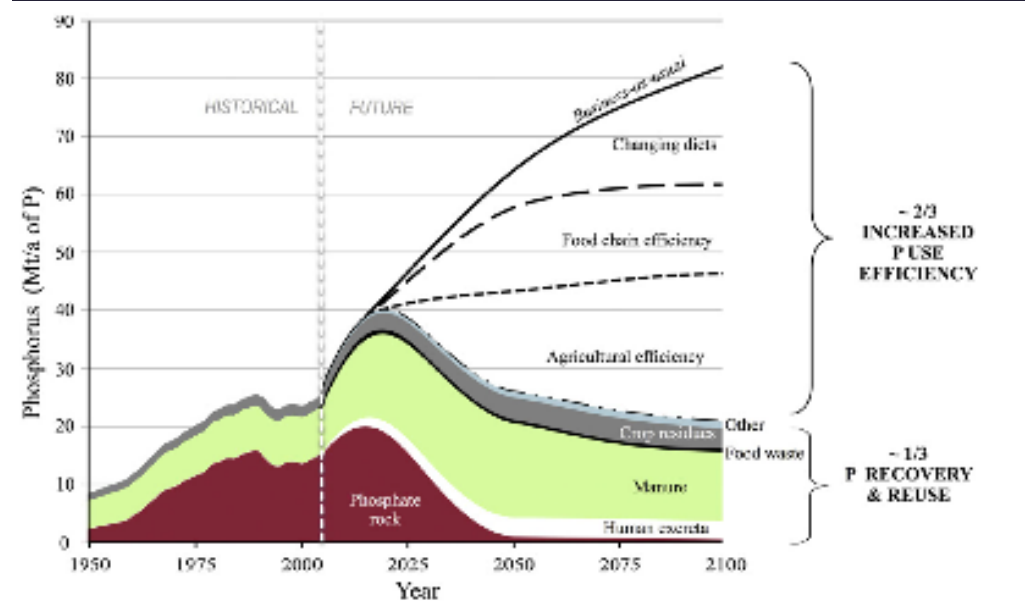
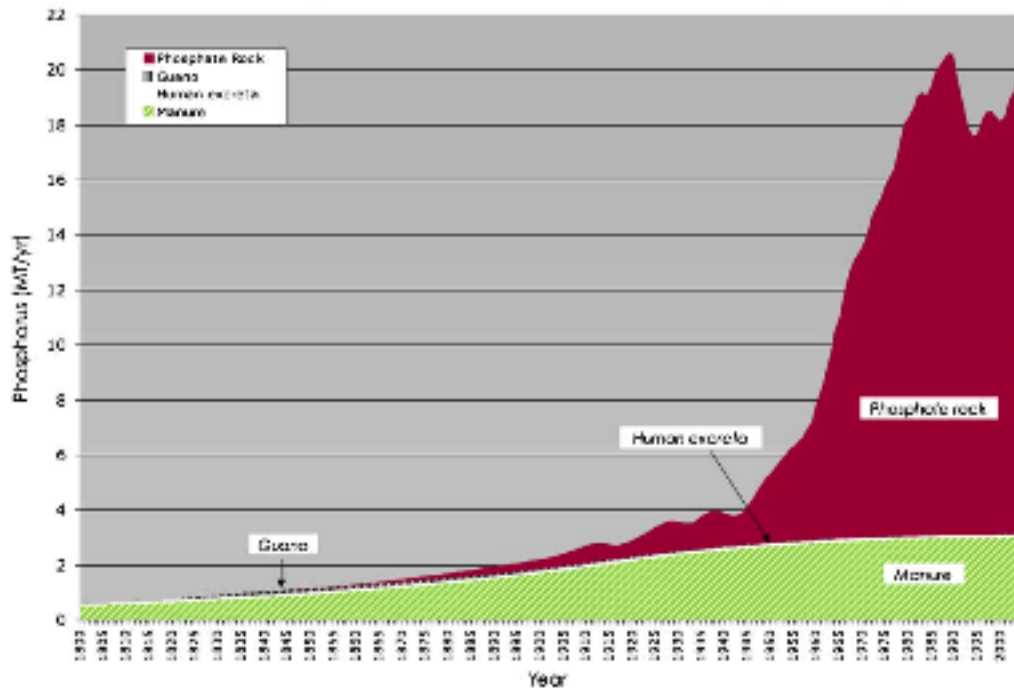
Black-Initial assemblage  
Red-High P  
Blue-Low P





# Running out of P

Historical global sources of phosphorus fertilizers (1800-2000)



Cordell et al.  
2010; 2011

# Conclusions

- bacteria are extremely stoichiometrically flexible with respect to P and they don't need a lot of it
- there are two main stoichiometric 'behaviors' that parallel r and K-selected species and our evidence suggests that 'K' selected species rule the day
- we're running out of P but we also have too much, i.e., eutrophication

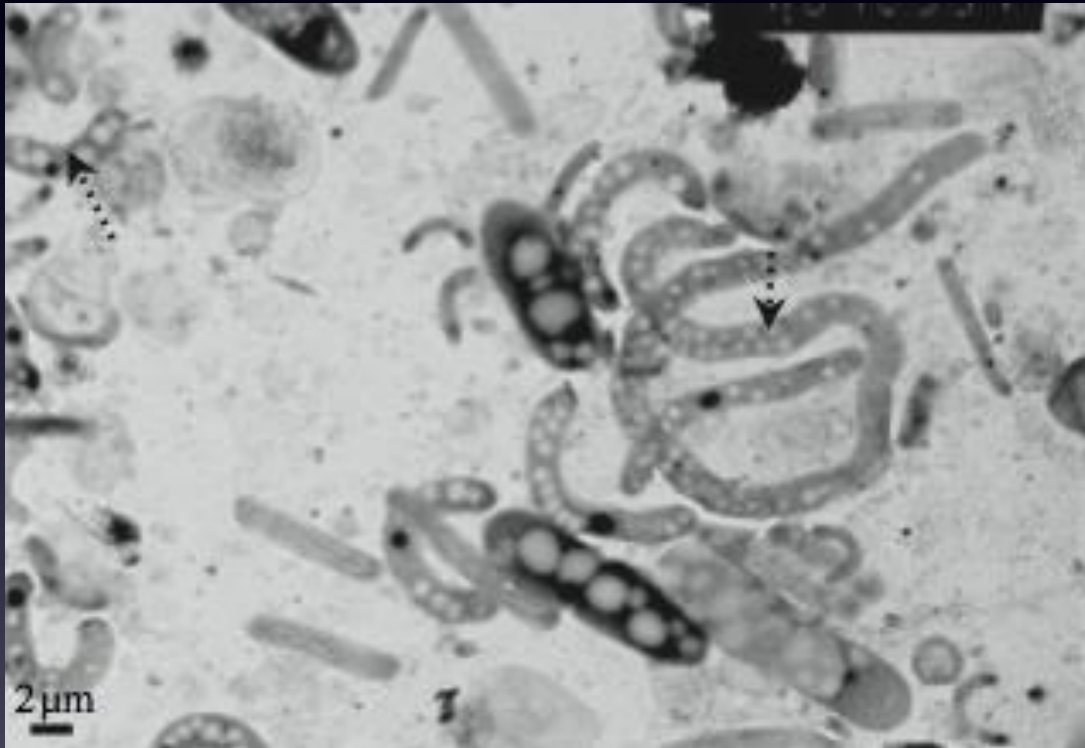


# Acknowledgments

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- Mikal Heldal and Frede Thingstad
- Funding: NSF, University of Minnesota (IonE/IREE)

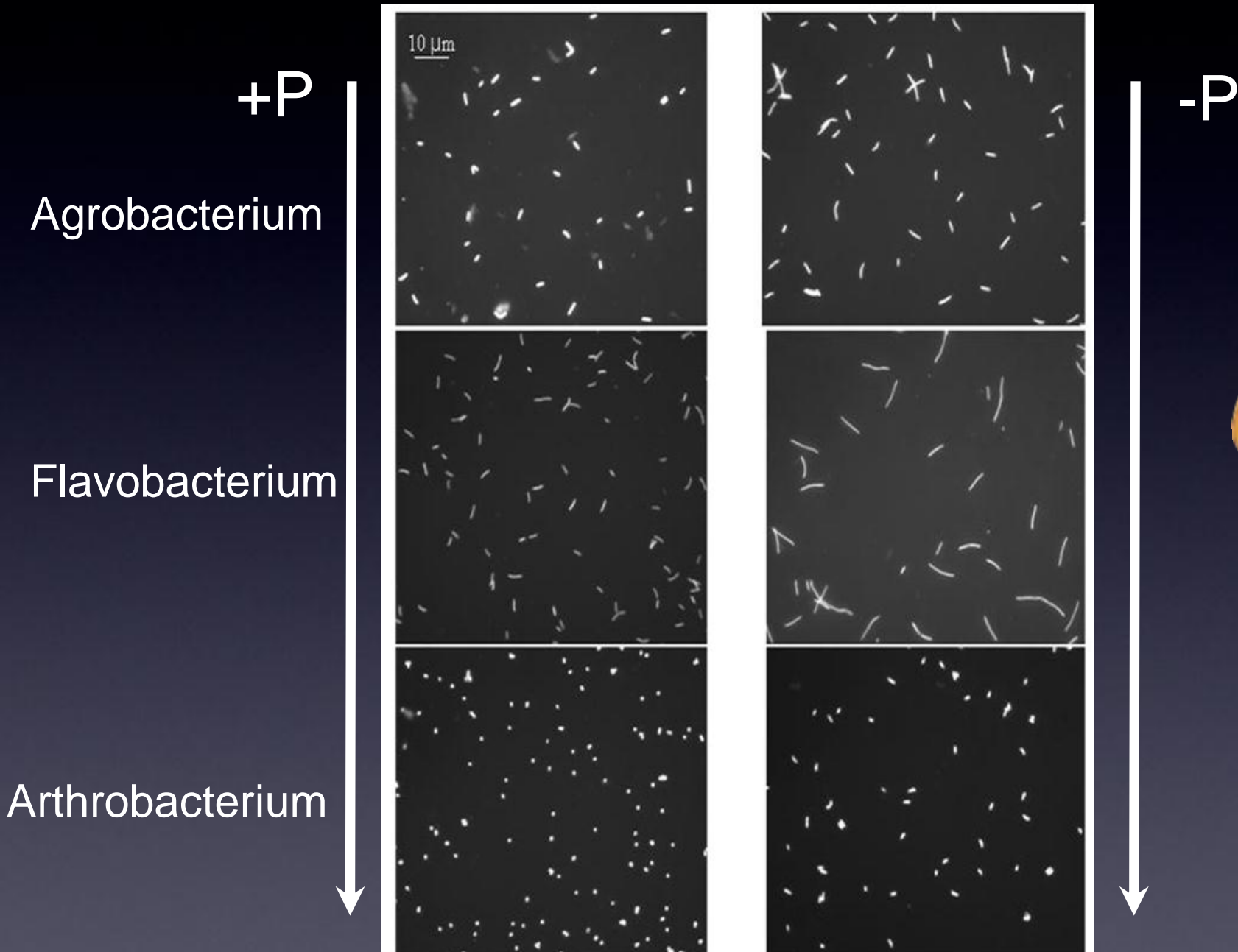


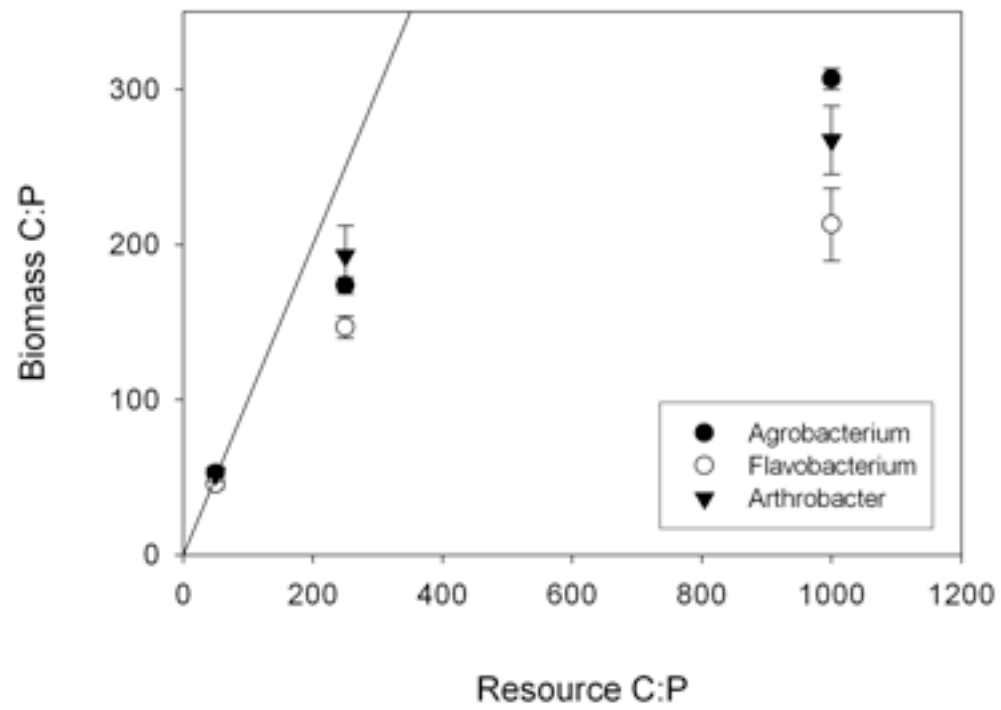
# Non-homoestasis: Using carbon to get phosphorus



Thingstad et al. 2005

# Morphometric changes under P limitation





# More info on the As:P controversy

<http://www.sciencemag.org/content/332/6034/1163>