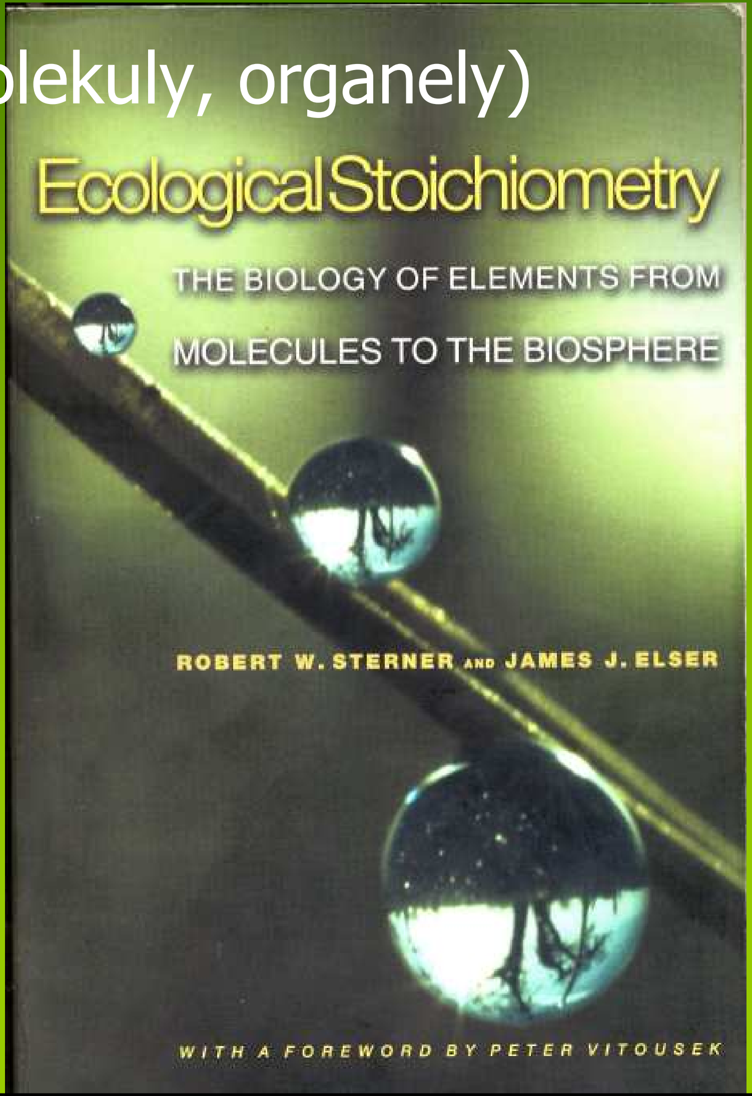
Ekologická stechiometrie

- **Zdroje** (živiny)
- **Fyzika a chemie** (z. zachování hmoty a energie, prvky)
- **Biochemie a buňka** (makromolekuly, organely)
- **Autotrofní růst**
- **Heterotrofní homeostáze**
- **Nerovnováha zdrojů**
- **Regenerace živin**
- **Stechiometrie společenstev**
- **Stechiometrie ekosystémů**



Ecological Stoichiometry

THE BIOLOGY OF ELEMENTS FROM
MOLECULES TO THE BIOSPHERE

ROBERT W. STERNER AND JAMES J. ELSER

WITH A FOREWORD BY PETER VITOUSEK

Ekologická stechiometrie ?

Syntéza produkční ekologie a populační ekologie…

$$\mathbf{10}\ CO_2 + 6\ H_2O + 2802\ kJ \longrightarrow \mathbf{C_6H_{12}O_6} + 6\ O_2$$

$$106\ CO_2 + 16\ NO_3^{-} + HPO_4^{2-} + 122\ H_2O + 18\ H^{+}$$

$$+ \text{ stopové prvky } + \text{ energie}$$

$$\xleftrightarrow[\text{Respirace}]{\text{Produkce}} \boxed{\mathbf{C_{106}H_{263}O_{110}N_{16}P_1}} + 138\ O_2$$

biomasa řas = $\boxed{\mathbf{(CH_2O)_{106}(NH_3)_{16}(H_3PO_4)}}$

člověk = $\boxed{\mathbf{H}_{375000000}\ \mathbf{O}_{1320000000}\ \mathbf{C}_{85700000}\ \mathbf{N}_{6430000}\ \mathbf{Ca}_{1500000}\ \mathbf{P}_{1020000}\ \mathbf{S}_{206000}\ \mathbf{Na}_{183000}\ \mathbf{K}_{177000}\ \mathbf{Cl}_{127000}\ \mathbf{Mg}_{40000}\ \mathbf{Si}_{38600}\ \mathbf{Fe}_{2680}\ \mathbf{Zn}_{2110}\ \mathbf{Cu}_{76}\ \mathbf{I}_{14}\ \mathbf{Mn}_{13}\ \mathbf{F}_{13}\ \mathbf{Cr}_{7}\ \mathbf{Se}_{4}\ \mathbf{Mo}_{3}\ \mathbf{Co}_{1}}$

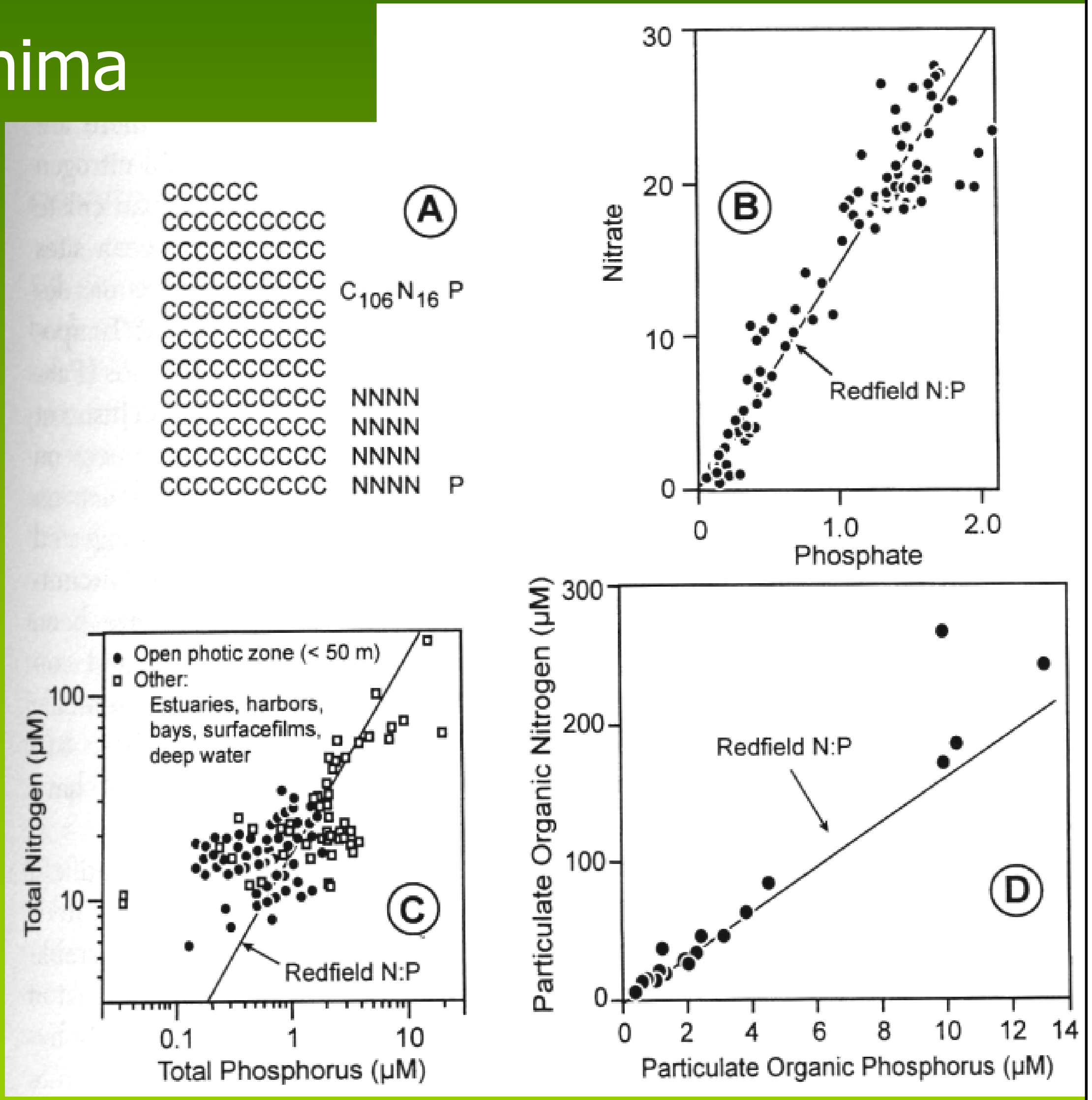
Ekologická stechiometrie – počátky

Stechiometrie zkoumá zákonité („povolené“) poměry prvků

Liebig (1840) – zákon minima

Lotka (1925) – stechiometrie v biologii

Redfield (1934, 1958) – poměr C:N:P = 106:16:1



Ekologická stechiometrie – východiska

Fyzika: zákon zachování hmoty a energie, termodynamika

Chemie: stechiometrie, relativní poměry prvků, biochemie

Biologie: evoluce živých soustav, homeostáze

Ekologie: **produkční biologie** vs. stechiometrie –

uhlík = integrace hmoty a energie

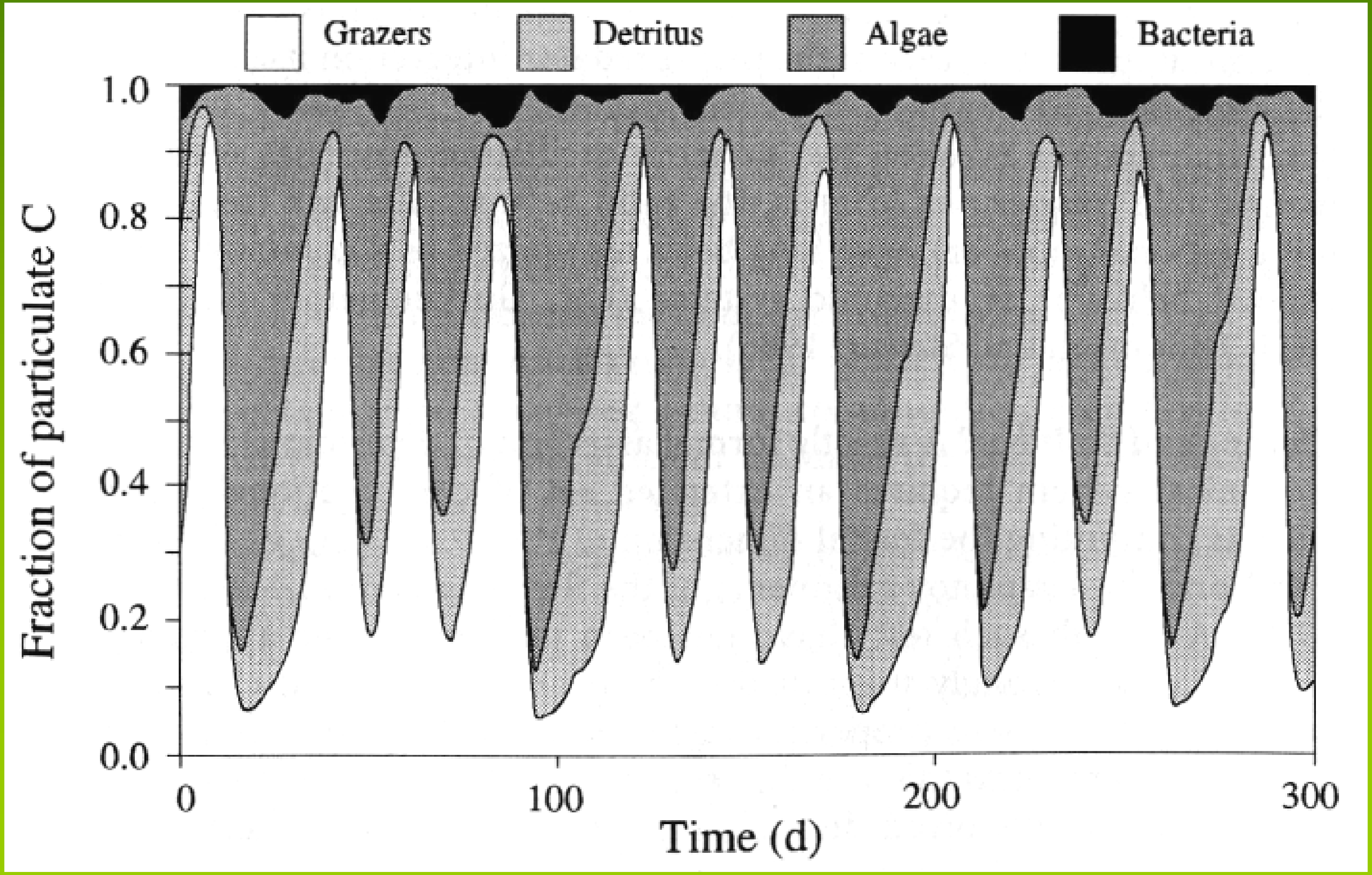
biologická diverzita vs. stechiometrie –

prvky = „nejmenší společné jmenovatele“

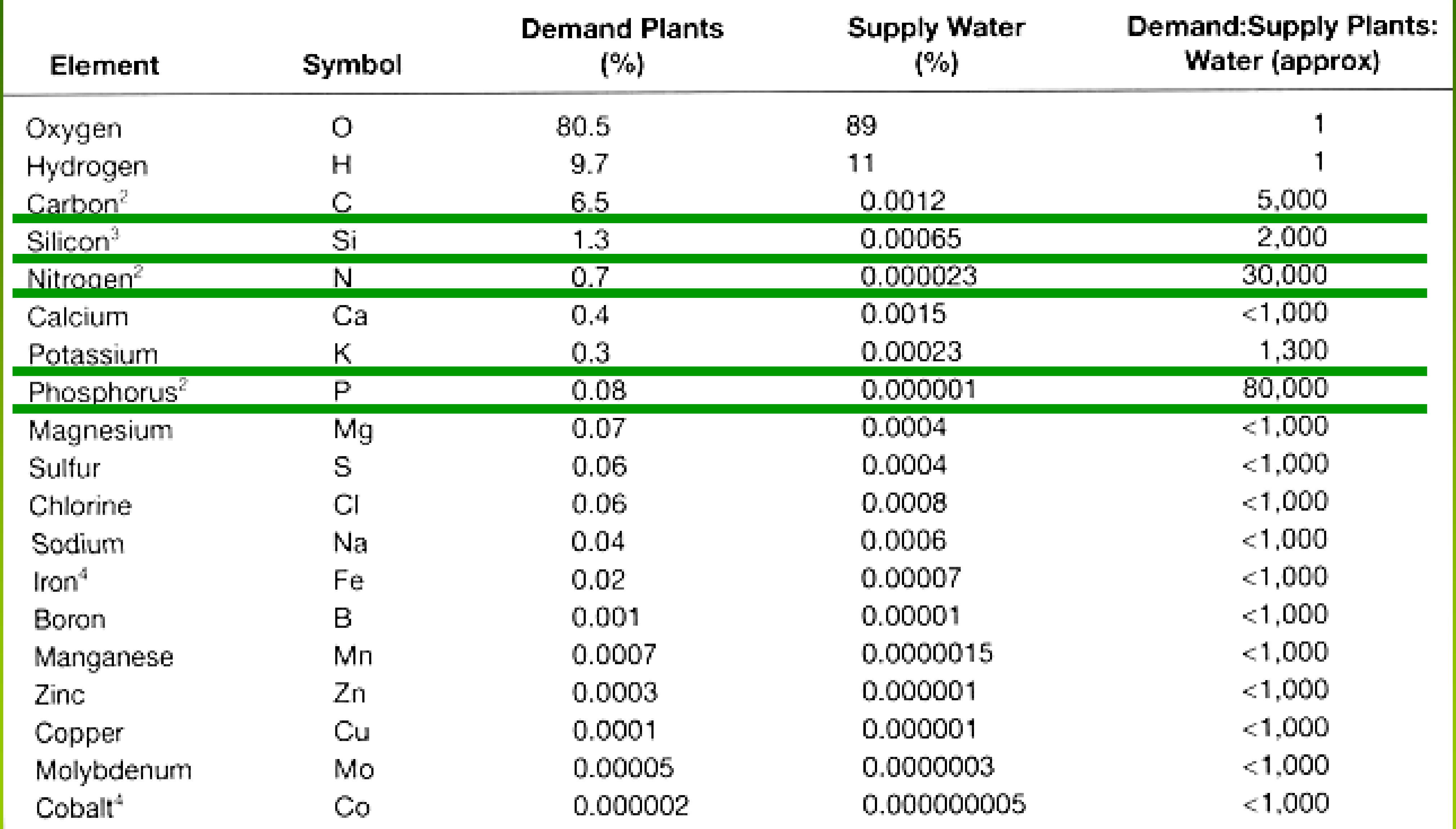
Ekologická stechiometrie – cíle

Realistický popis chování populací a ekosystémů

Prediktivní ekologické modely

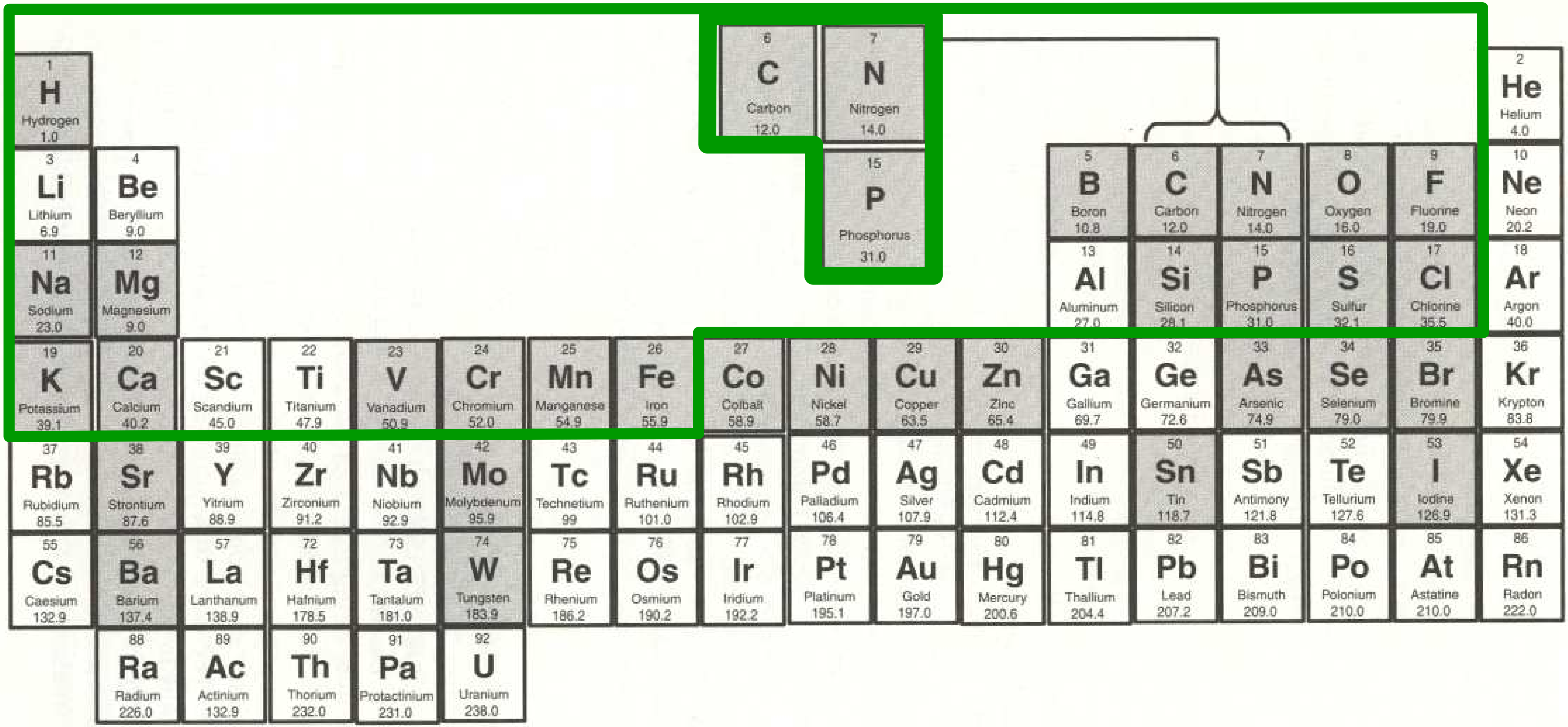


Biogenní prvky: nehomeostatické



Element	Symbol	Demand Plants (%)	Supply Water (%)	Demand:Supply Plants: Water (approx)
Oxygen	O	80.5	89	1
Hydrogen	H	9.7	11	1
Carbon[2]	C	6.5	0.0012	5,000
Silicon[3]	Si	1.3	0.00065	2,000
Nitrogen[2]	N	0.7	0.000023	30,000
Calcium	Ca	0.4	0.0015	<1,000
Potassium	K	0.3	0.00023	1,300
Phosphorus[2]	P	0.08	0.000001	80,000
Magnesium	Mg	0.07	0.0004	<1,000
Sulfur	S	0.06	0.0004	<1,000
Chlorine	Cl	0.06	0.0008	<1,000
Sodium	Na	0.04	0.0006	<1,000
Iron[4]	Fe	0.02	0.00007	<1,000
Boron	B	0.001	0.00001	<1,000
Manganese	Mn	0.0007	0.0000015	<1,000
Zinc	Zn	0.0003	0.000001	<1,000
Copper	Cu	0.0001	0.000001	<1,000
Molybdenum	Mo	0.00005	0.0000003	<1,000
Cobalt[4]	Co	0.000002	0.000000005	<1,000

Biogenní prvky: nehomeostatické / stopové



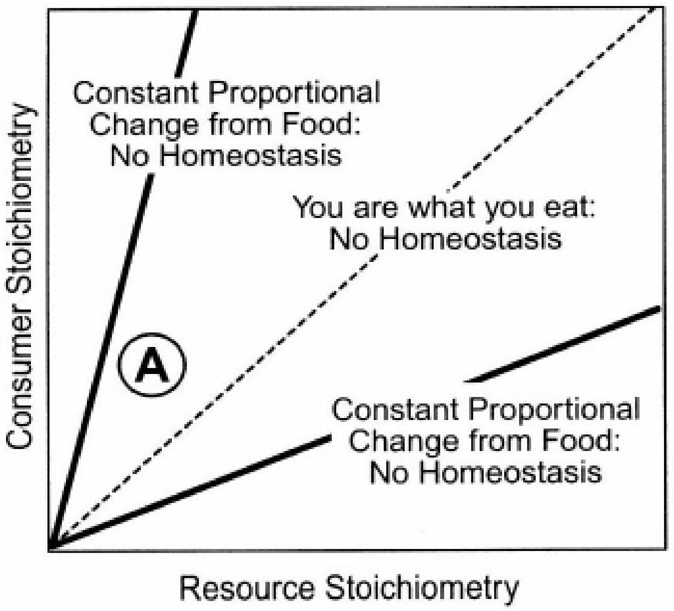
6 **C** Carbon 12.0	7 **N** Nitrogen 14.0	
	15 **P** Phosphorus 31.0	

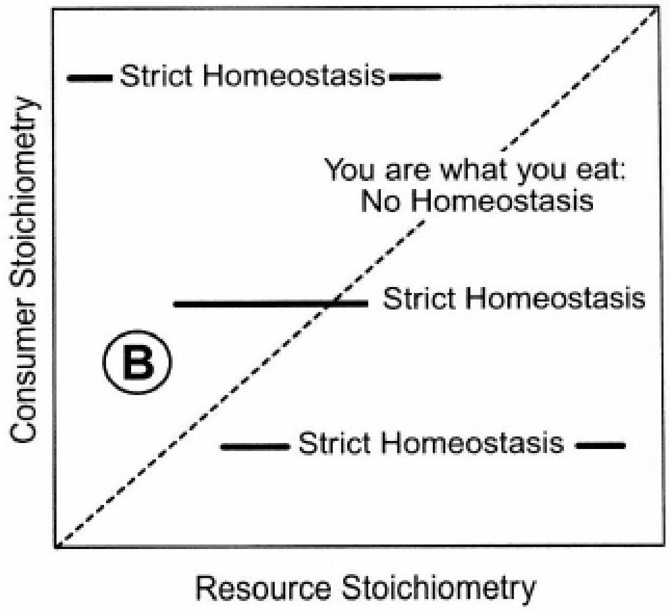
1 **H** Hydrogen 1.0																	2 **He** Helium 4.0
3 **Li** Lithium 6.9	4 **Be** Beryllium 9.0											5 **B** Boron 10.8	6 **C** Carbon 12.0	7 **N** Nitrogen 14.0	8 **O** Oxygen 16.0	9 **F** Fluorine 19.0	10 **Ne** Neon 20.2
11 **Na** Sodium 23.0	12 **Mg** Magnesium 9.0											13 **Al** Aluminum 27.0	14 **Si** Silicon 28.1	15 **P** Phosphorus 31.0	16 **S** Sulfur 32.1	17 **Cl** Chlorine 35.5	18 **Ar** Argon 40.0
19 **K** Potassium 39.1	20 **Ca** Calcium 40.2	21 **Sc** Scandium 45.0	22 **Ti** Titanium 47.9	23 **V** Vanadium 50.9	24 **Cr** Chromium 52.0	25 **Mn** Manganese 54.9	26 **Fe** Iron 55.9	27 **Co** Colbalt 58.9	28 **Ni** Nickel 58.7	29 **Cu** Copper 63.5	30 **Zn** Zinc 65.4	31 **Ga** Gallium 69.7	32 **Ge** Germanium 72.6	33 **As** Arsenic 74.9	34 **Se** Selenium 79.0	35 **Br** Bromine 79.9	36 **Kr** Krypton 83.8
37 **Rb** Rubidium 85.5	38 **Sr** Strontium 87.6	39 **Y** Yitrium 88.9	40 **Zr** Zirconium 91.2	41 **Nb** Niobium 92.9	42 **Mo** Molybdenum 95.9	43 **Tc** Technetium 99	44 **Ru** Ruthenium 101.0	45 **Rh** Rhodium 102.9	46 **Pd** Palladium 106.4	47 **Ag** Silver 107.9	48 **Cd** Cadmium 112.4	49 **In** Indium 114.8	50 **Sn** Tin 118.7	51 **Sb** Antimony 121.8	52 **Te** Tellurium 127.6	53 **I** Iodine 126.9	54 **Xe** Xenon 131.3
55 **Cs** Caesium 132.9	56 **Ba** Barium 137.4	57 **La** Lanthanum 138.9	72 **Hf** Hafnium 178.5	73 **Ta** Tantalum 181.0	74 **W** Tungsten 183.9	75 **Re** Rhenium 186.2	76 **Os** Osmium 190.2	77 **Ir** Iridium 192.2	78 **Pt** Platinum 195.1	79 **Au** Gold 197.0	80 **Hg** Mercury 200.6	81 **Tl** Thallium 204.4	82 **Pb** Lead 207.2	83 **Bi** Bismuth 209.0	84 **Po** Polonium 210.0	85 **At** Astatine 210.0	86 **Rn** Radon 222.0
	88 **Ra** Radium 226.0	89 **Ac** Actinium 132.9	90 **Th** Thorium 232.0	91 **Pa** Protactinium 231.0	92 **U** Uranium 238.0												

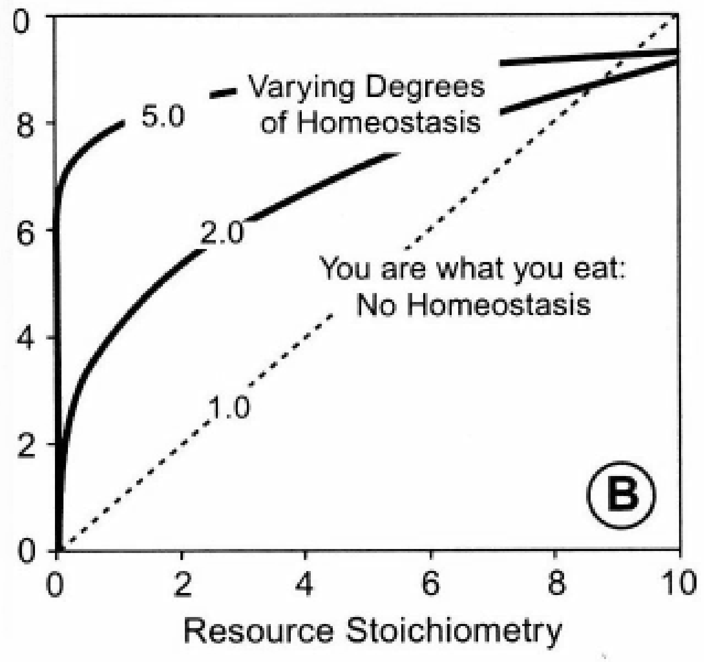
Homeostáze – regulace živých soustav

Negativní zpětná vazba mezi vnitřními podmínkami
a vnějšími podmínkami

Stechiometrie **konzumenta** vs. stechiometrie **zdrojů**





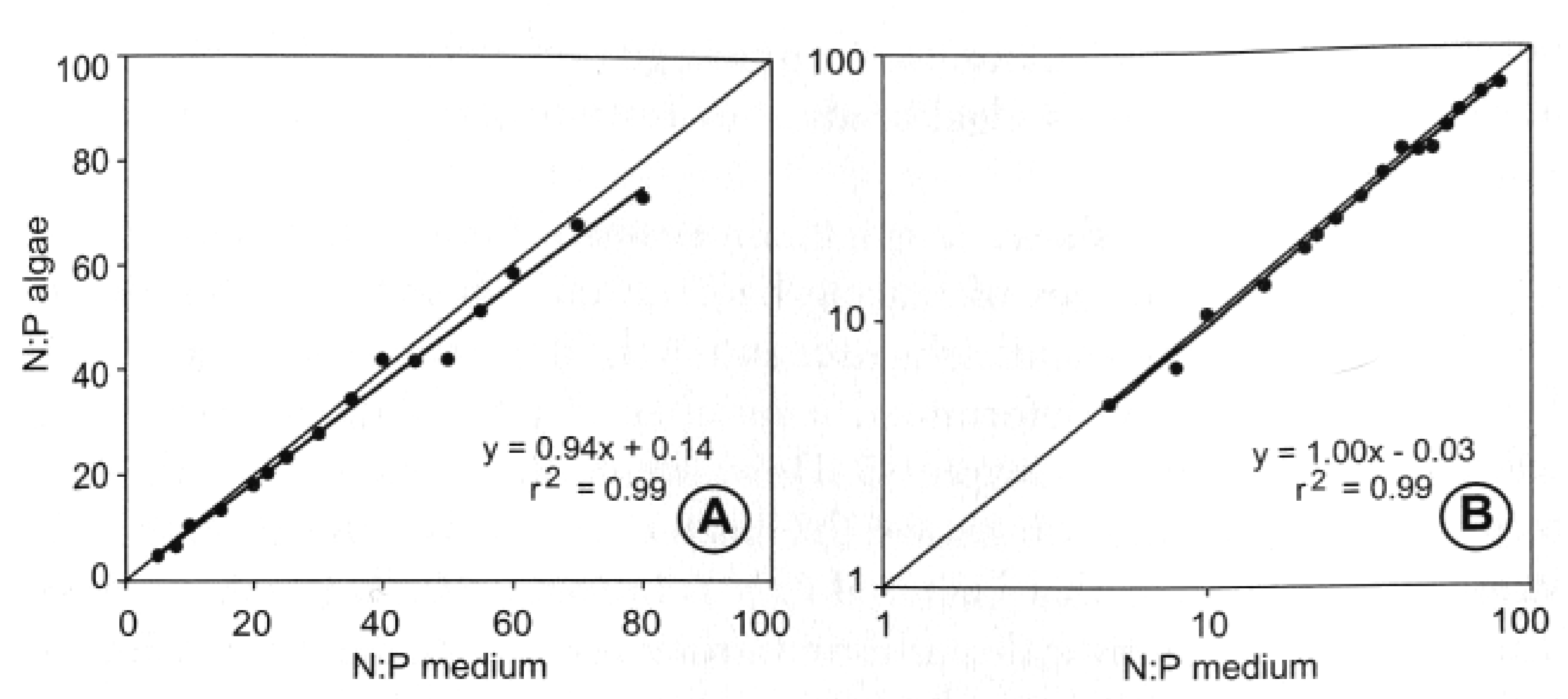


žádná regulace

„striktní homeostáze"

Absence homeostáze – autotrofní růst

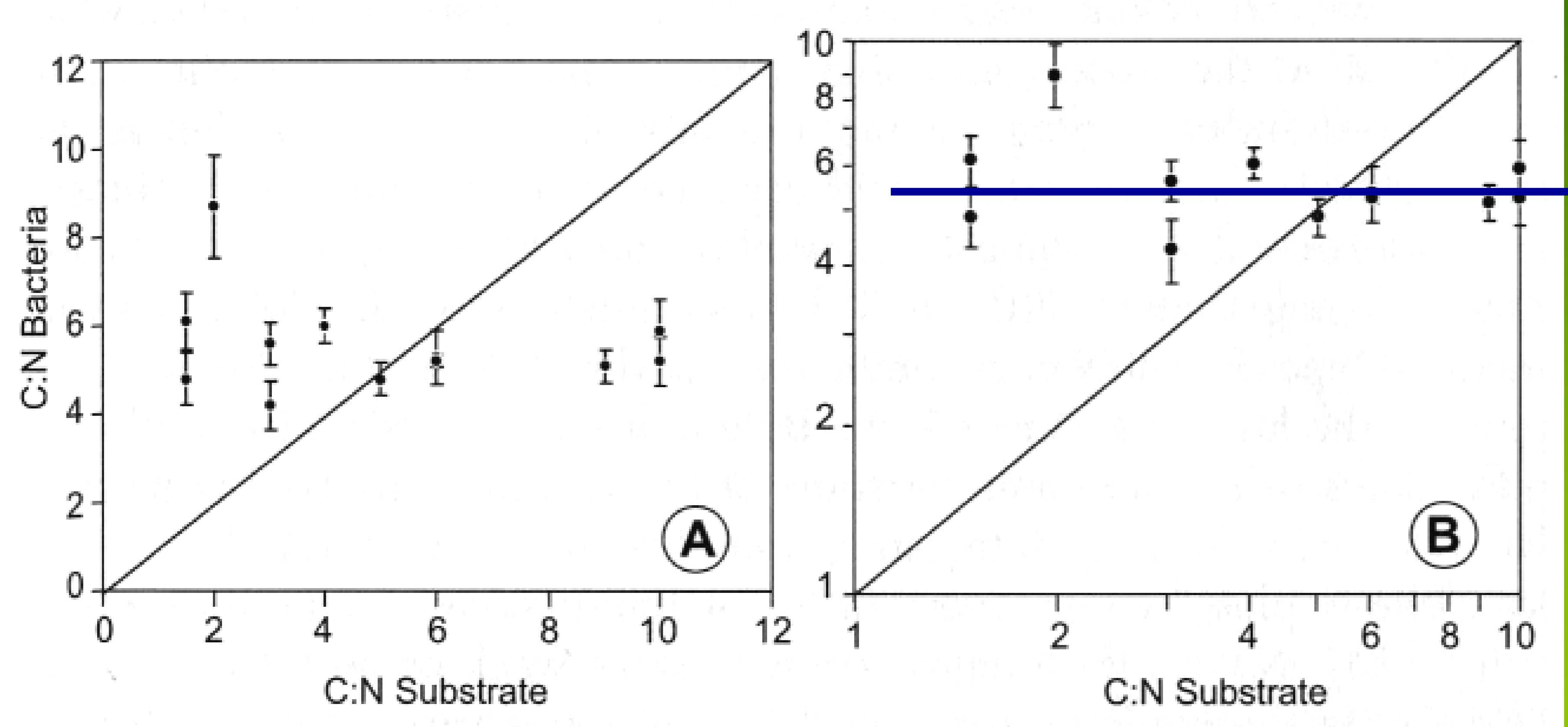
Fytoplankton (*Scenedesmus*)



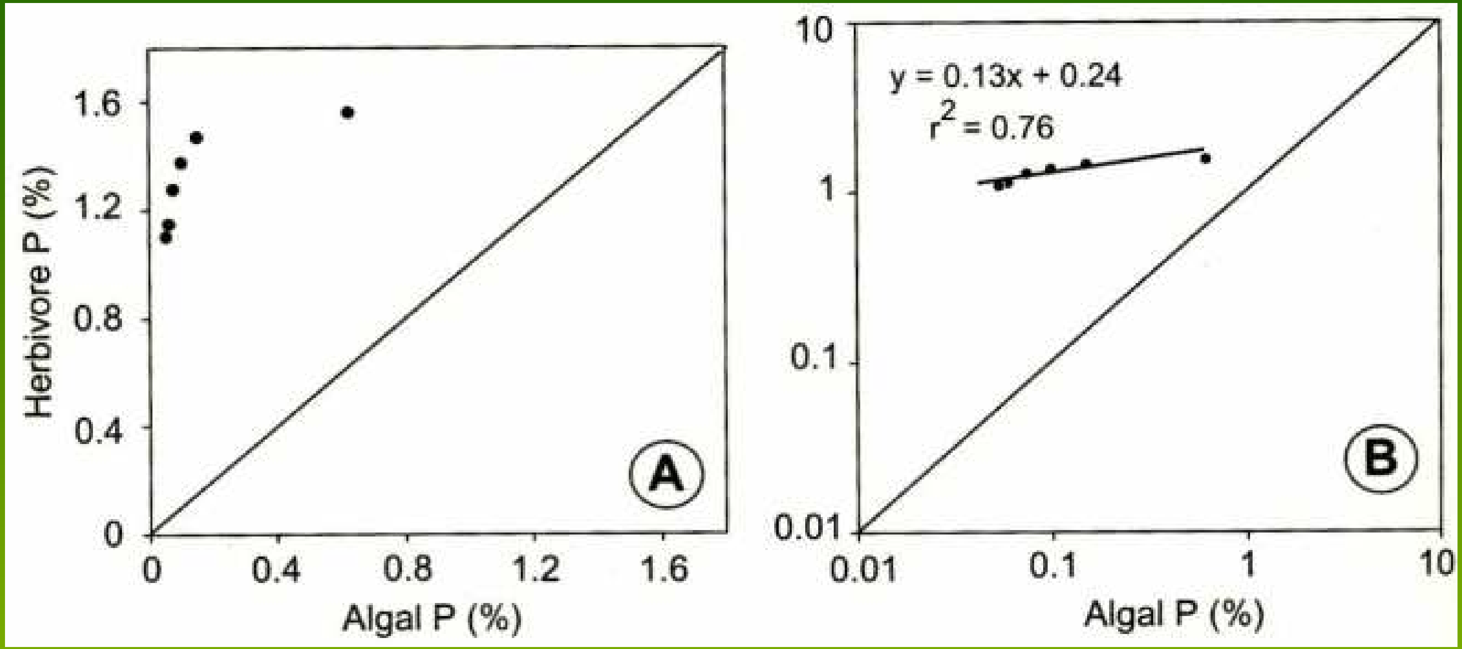
Žádná homeostatická regulace = „you are what you eat"

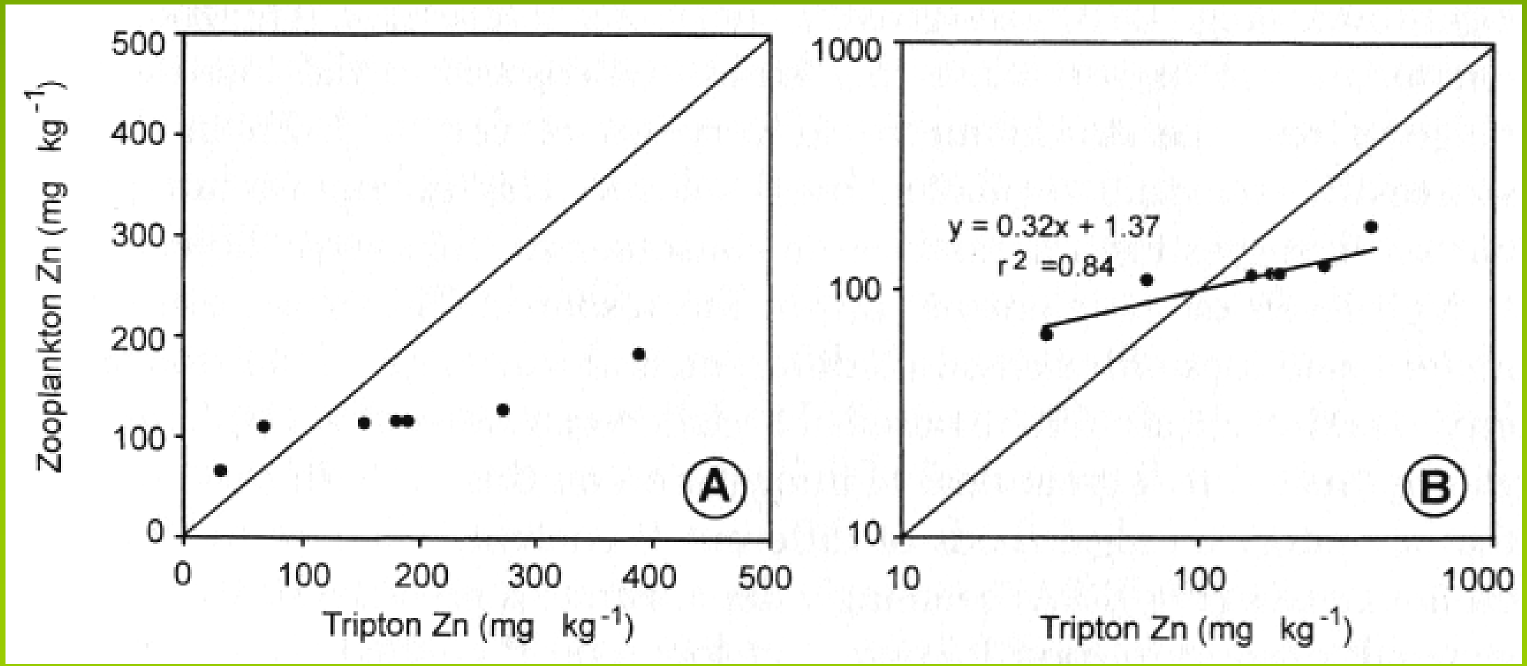
Striktní homeostáze – heterotrofní růst

Bakterie = rovnovážný růst



Silná / striktní homeostáze – Zooplankton

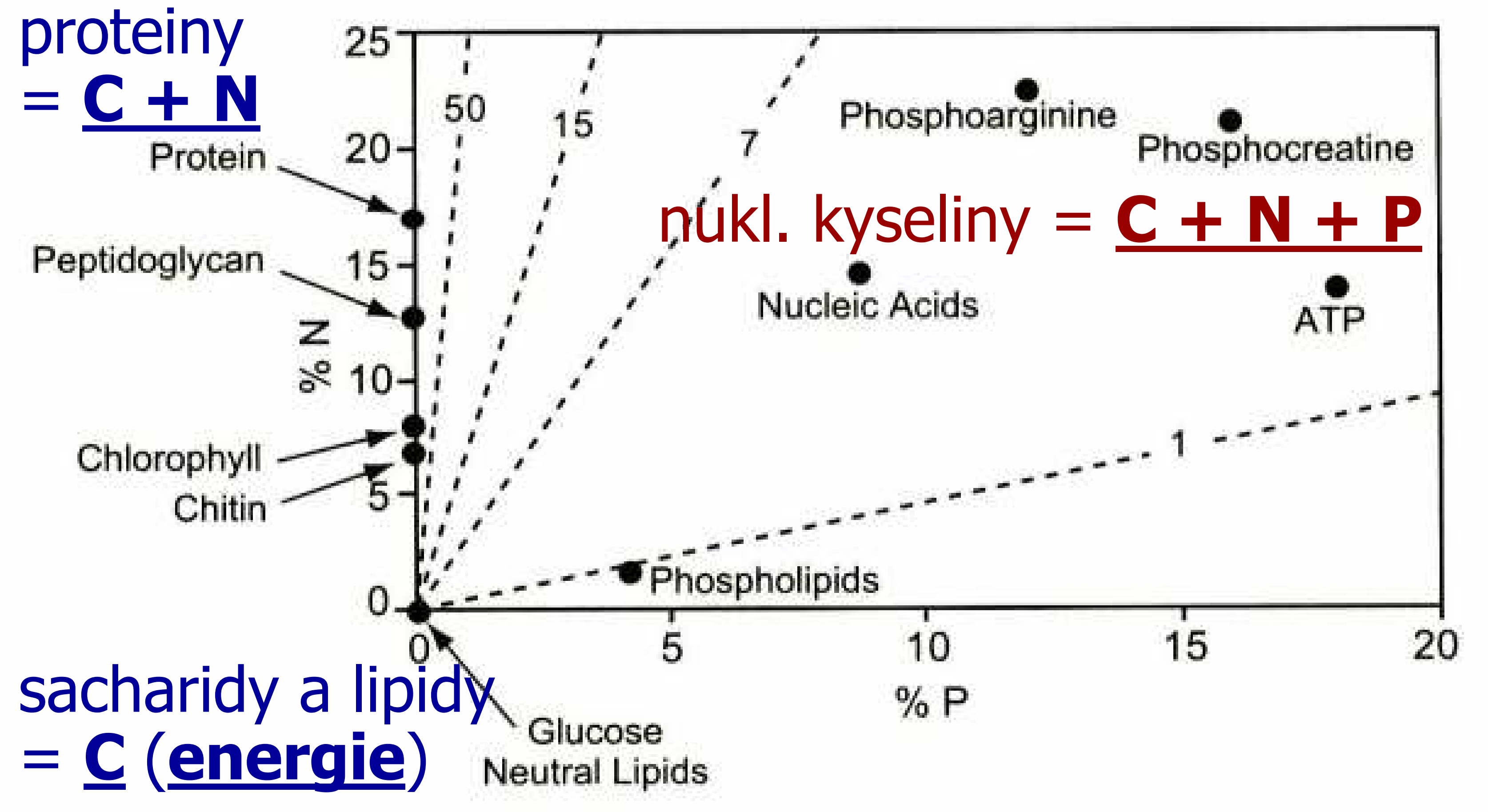




Stechiometrie buňky – buněčná chemie

Složení **biomolekul** – biochemická stechiometrie

Selekce C, N a P v biochemické evoluci



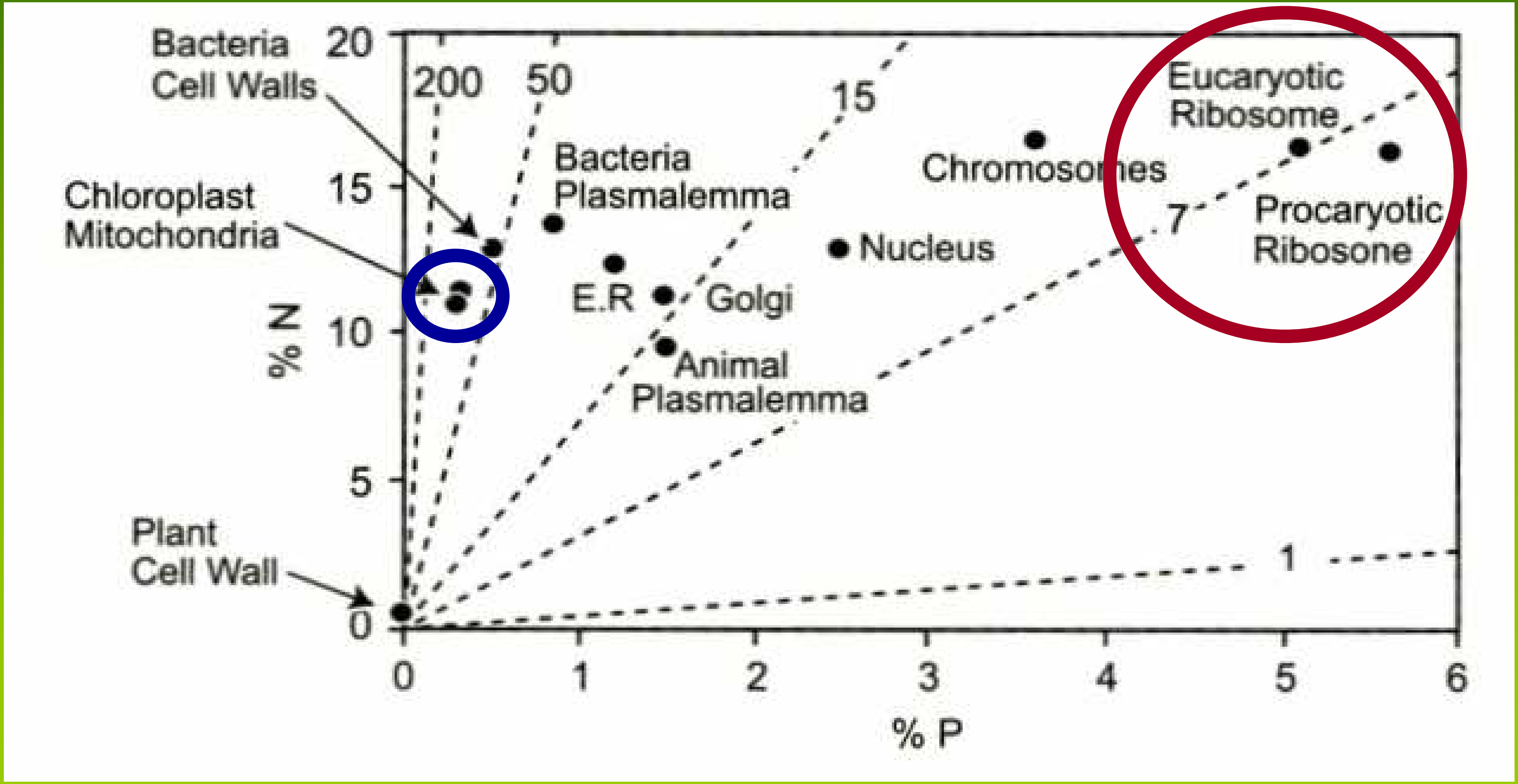
proteiny = **C + N**

nukl. kyseliny = **C + N + P**

sacharidy a lipidy = **C** (**energie**)

Stechiometrie buňky – buněčná chemie

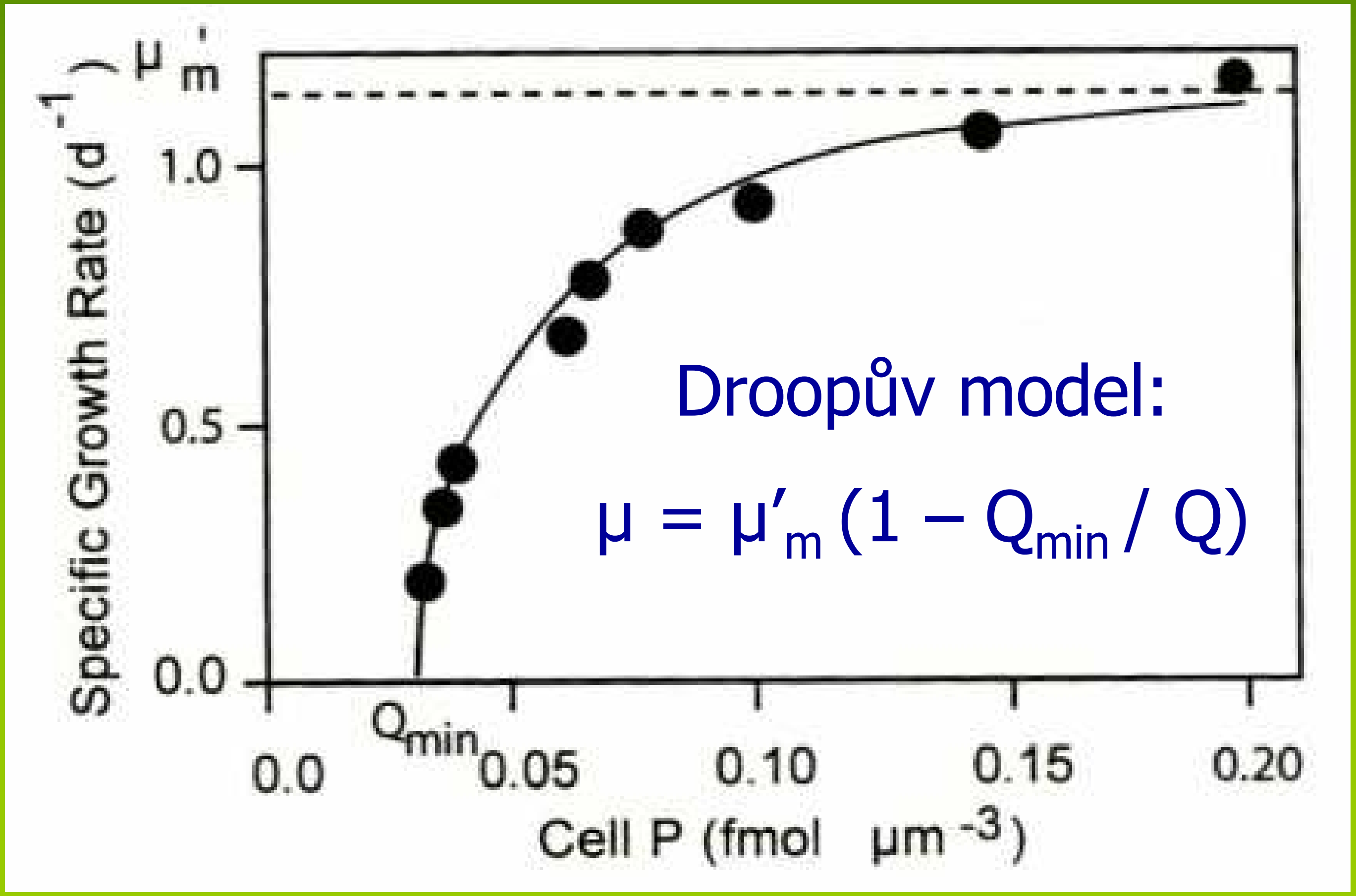
Složení **organel** – vnitrobuněčná stechiometrie



Autotrofní růst (stechiometrie producentů)

Nezastupitelný zdroj — **buněčné minimum** (práh)

Droop (1974) – **cell quota: Q_{min}** (mol cell^{-1}, když μ = 0)



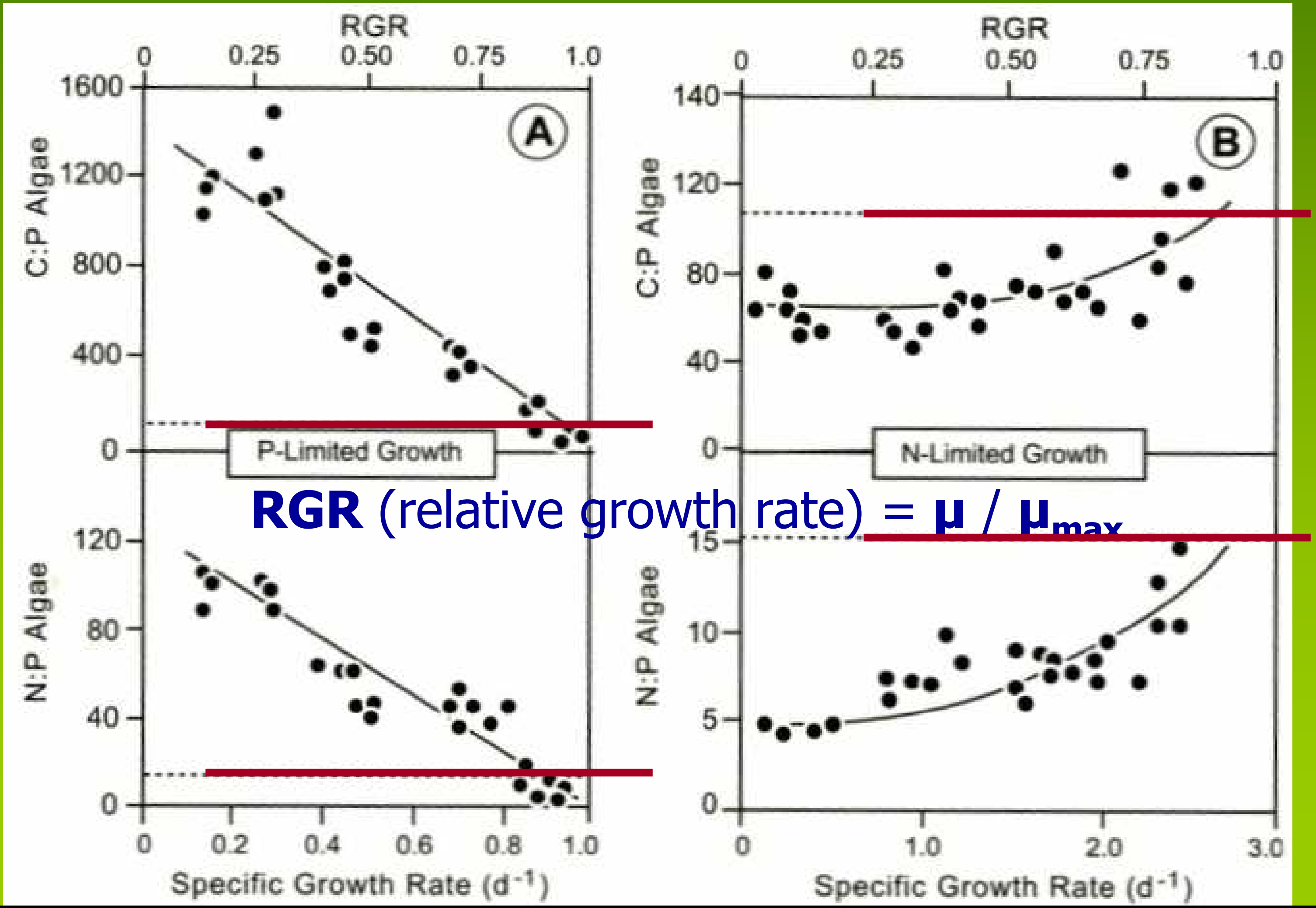
Droopův model:

$$\mu = \mu'_m (1 - Q_{min} / Q)$$

Autotrofní růst (stechiometrie producentů)

Stechiometrie autotrofů závisí na **míře limitace živinami**

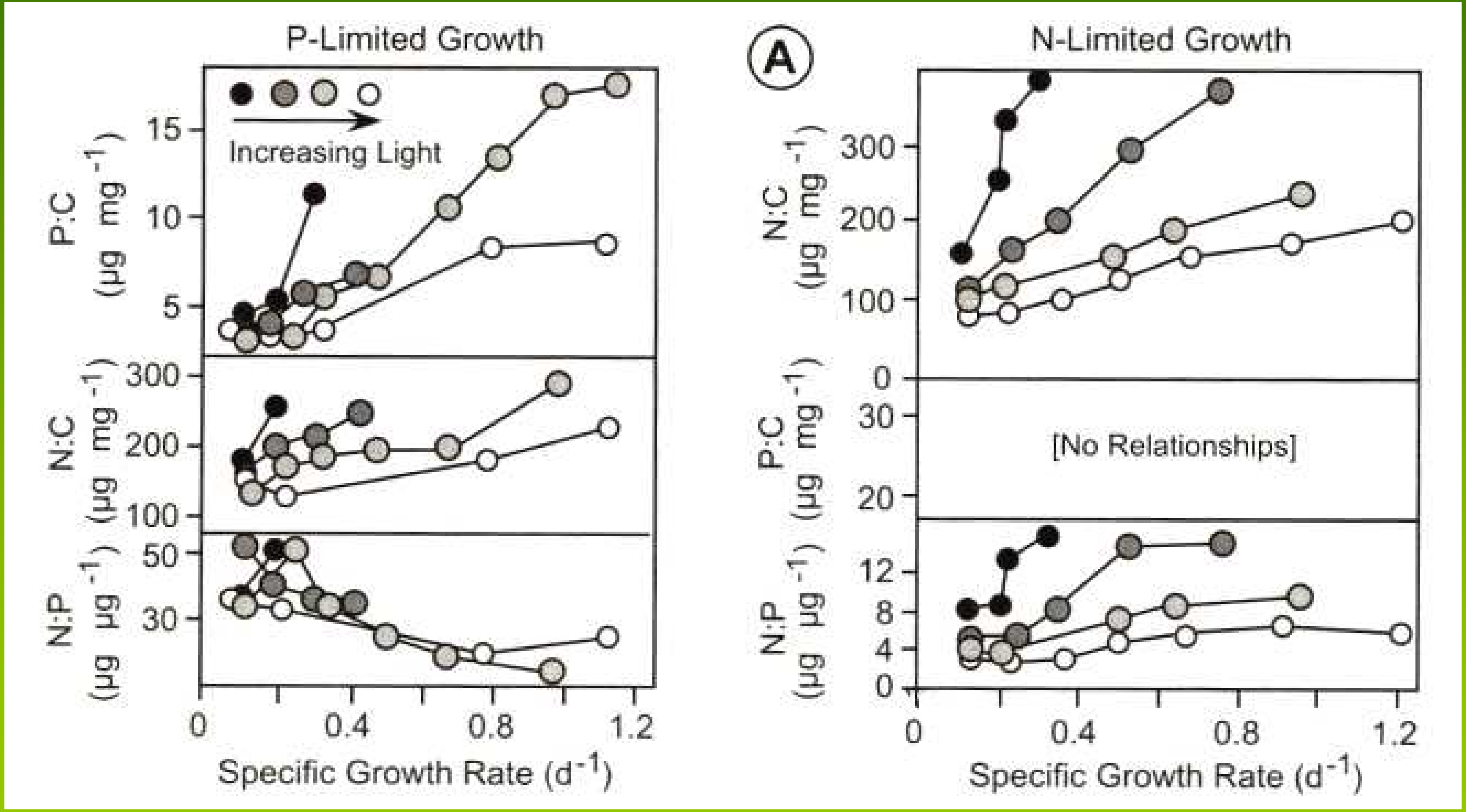
Molární poměry C:N, C:P, N:P



RGR (relative growth rate) = μ / μ_{max}

Autotrofní růst (stechiometrie producentů)

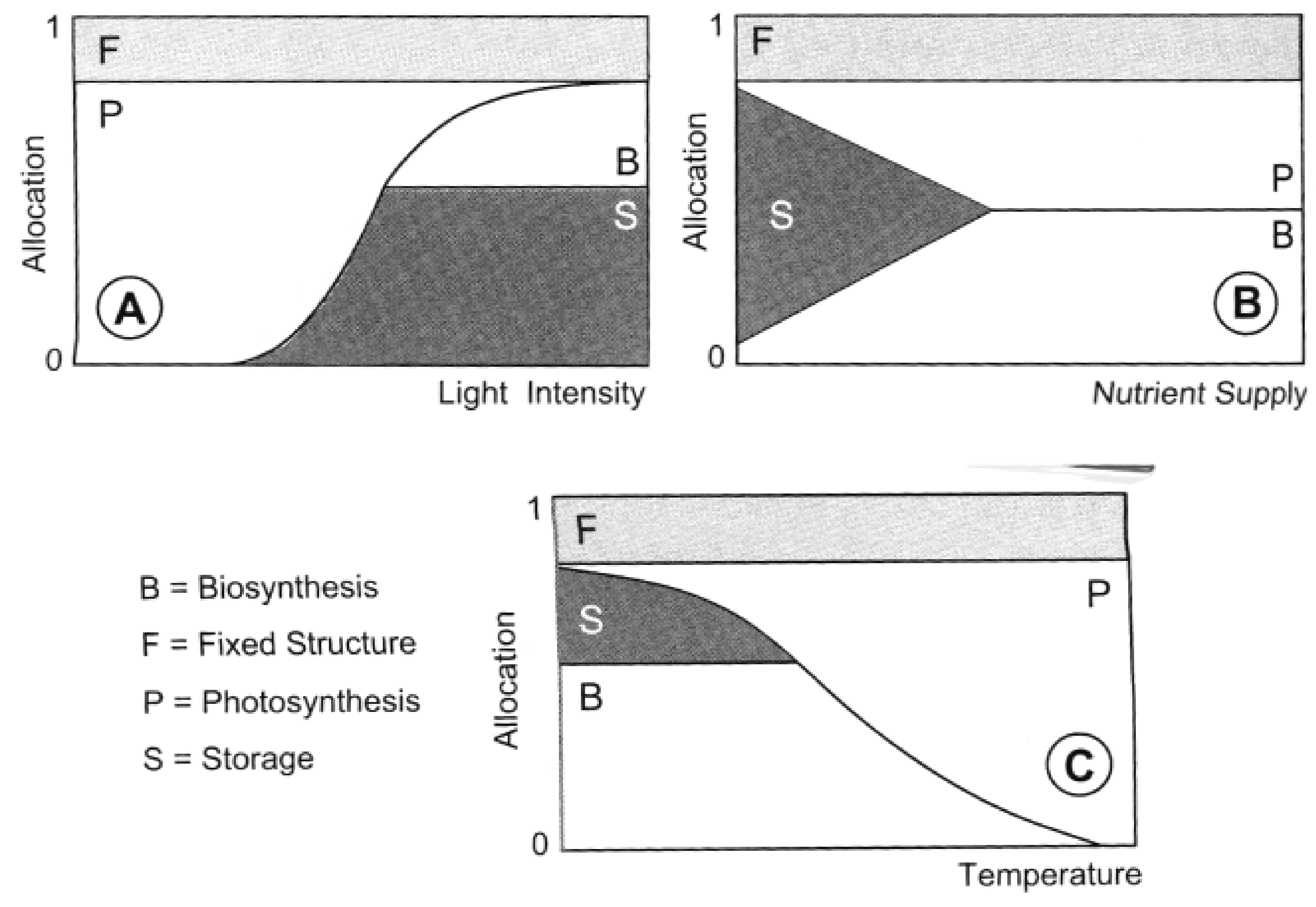
Vliv světla ? – poměr světlo:živiny



Maximální světlo neznamená optimální růst !

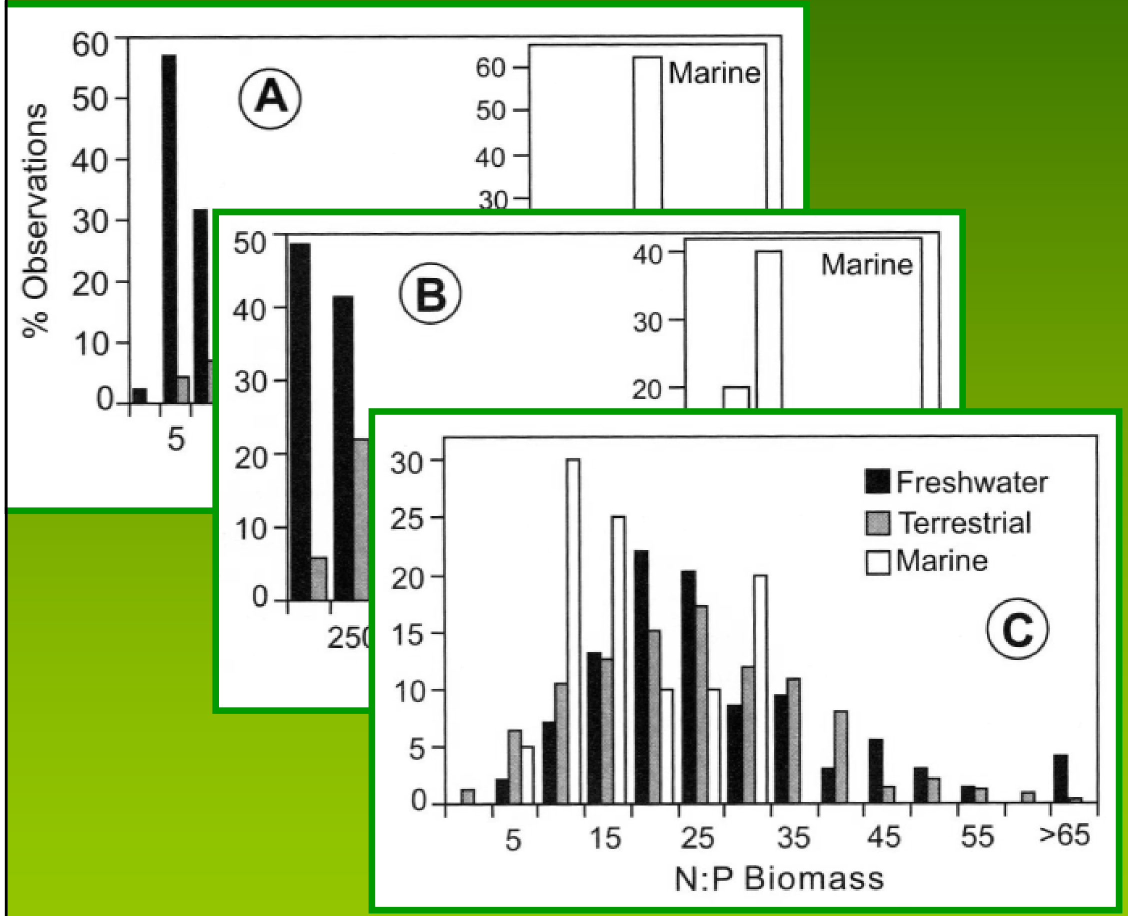
Autotrofní růst (stechiometrie producentů)

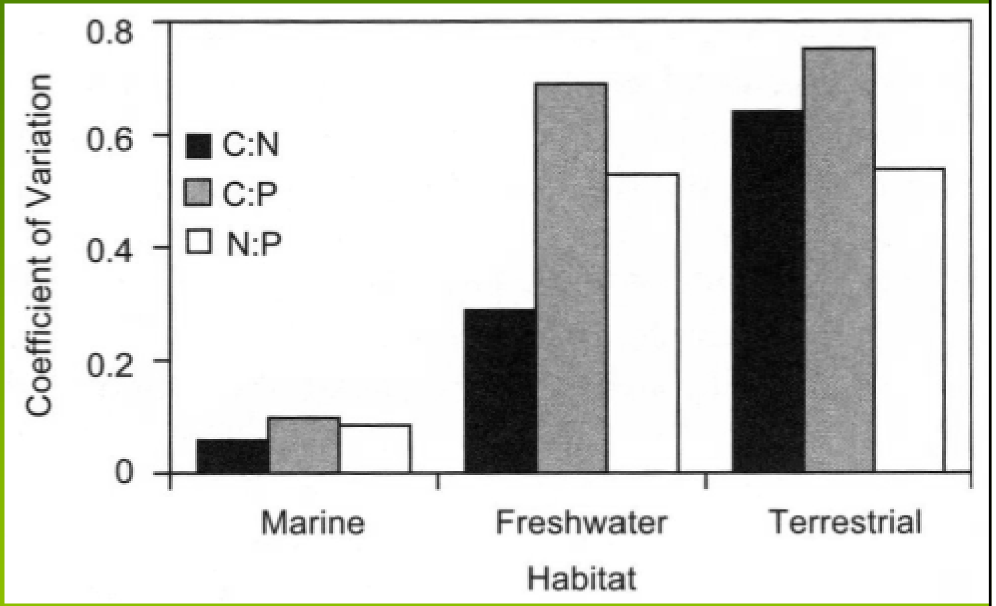
Prediktivní model **alokace u řas** (Shuter 1979)



Autotrofní růst (stechiometrie producentů)

Variabilita v základu potravních sítí (potr. pyramidy)



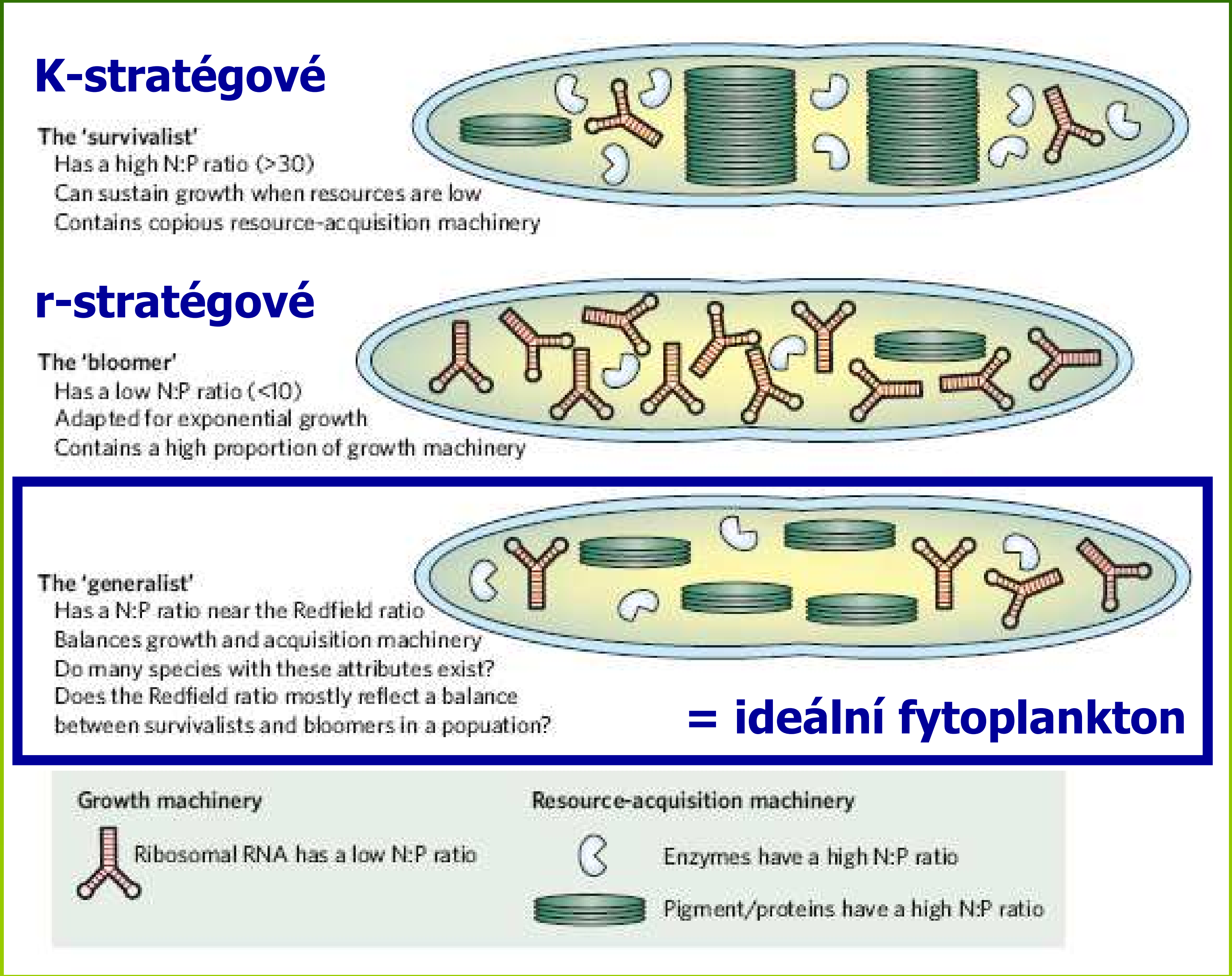


oceány – **stabilní** stechiometrie hl. živin (**C:N:P** = Redfieldův poměr)

kontinenty (terestrické i vodní ekosystémy) **– variabilní C:N:P**

Průměrný fytoplankton – stechiometrická fikce ?

N_2 fixátoři
N:P > 40



K-stratégové

The 'survivalist'
Has a high N:P ratio (>30)
Can sustain growth when resources are low
Contains copious resource-acquisition machinery

r-stratégové

The 'bloomer'
Has a low N:P ratio (<10)
Adapted for exponential growth
Contains a high proportion of growth machinery

The 'generalist'
Has a N:P ratio near the Redfield ratio
Balances growth and acquisition machinery
Do many species with these attributes exist?
Does the Redfield ratio mostly reflect a balance
between survivalists and bloomers in a popuation?

= ideální fytoplankton

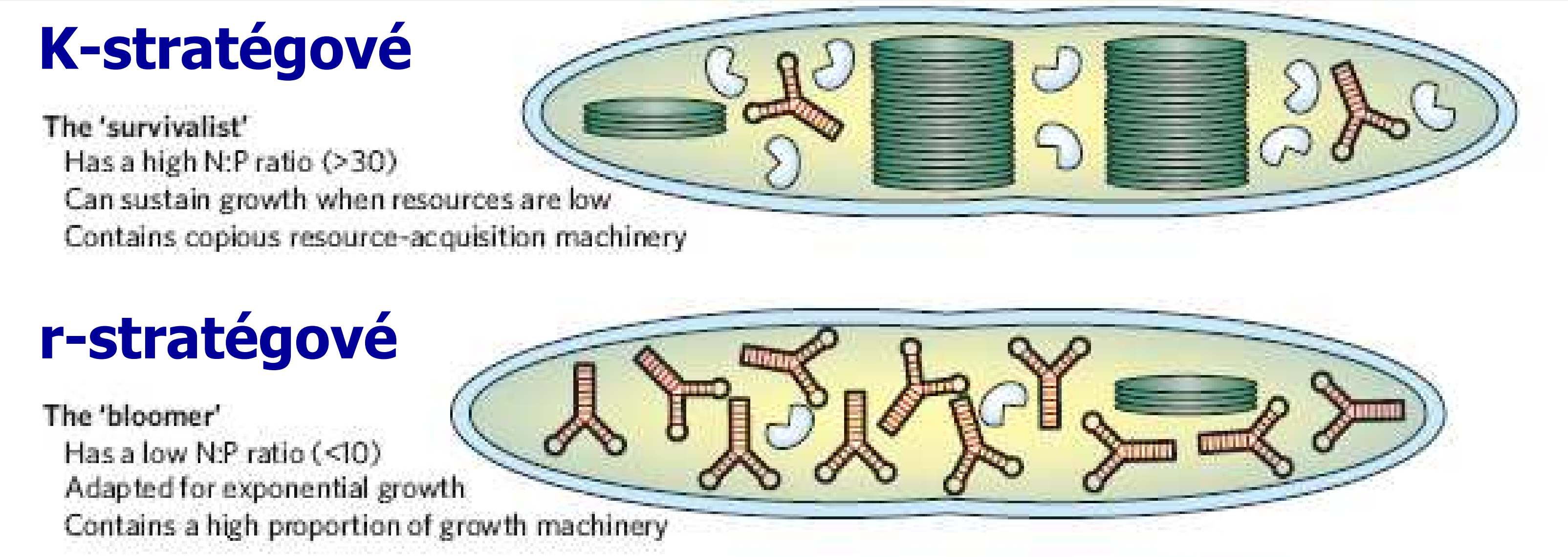
Growth machinery
Ribosomal RNA has a low N:P ratio

Resource-acquisition machinery
Enzymes have a high N:P ratio
Pigment/proteins have a high N:P ratio

Stechiometrie fytoplanktonu – **evoluční rozdíly**

„Chlorophyta“ – poměr **C:N:P ~ 200:27:1** (jezera!)

N_2 fixátoři
N:P > 40



K-stratégové

The 'survivalist'
Has a high N:P ratio (>30)
Can sustain growth when resources are low
Contains copious resource-acquisition machinery

r-stratégové

The 'bloomer'
Has a low N:P ratio (<10)
Adapted for exponential growth
Contains a high proportion of growth machinery

„Rhodophyta“ – poměr **C:N:P ~ 70:10:1** (bakterie!)

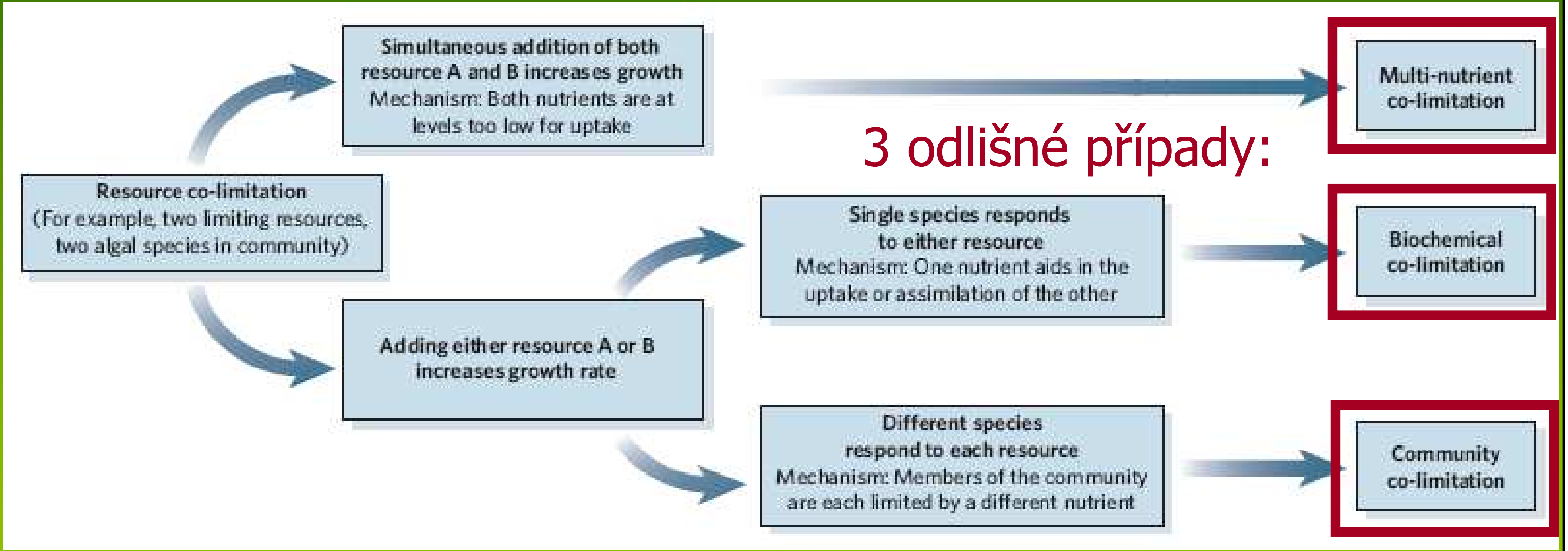
Eutrofizace povrchových vod = **změna diverzity!**

Growth machinery
Ribosomal RNA has a low N:P ratio

Resource-acquisition machinery
Enzymes have a high N:P ratio
Pigment/proteins have a high N:P ratio

Multiple resource co-limitation

současná limitace producenta více nezastupitelnými zdroji



Resource co-limitation (For example, two limiting resources, two algal species in community)

Simultaneous addition of both resource A and B increases growth
Mechanism: Both nutrients are at levels too low for uptake

Multi-nutrient co-limitation

3 odlišné případy:

Adding either resource A or B increases growth rate

Single species responds to either resource
Mechanism: One nutrient aids in the uptake or assimilation of the other

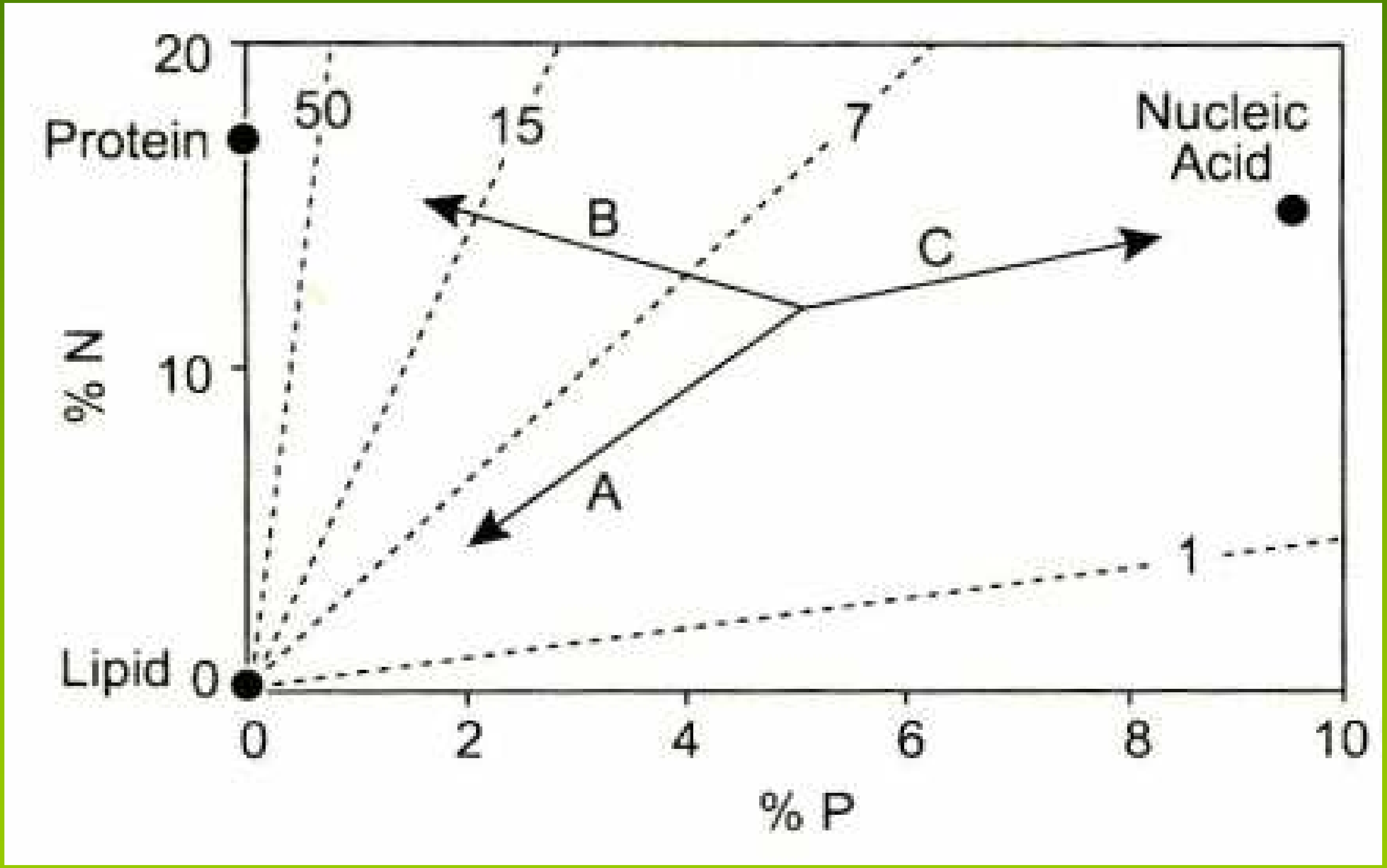
Biochemical co-limitation

Different species respond to each resource
Mechanism: Members of the community are each limited by a different nutrient

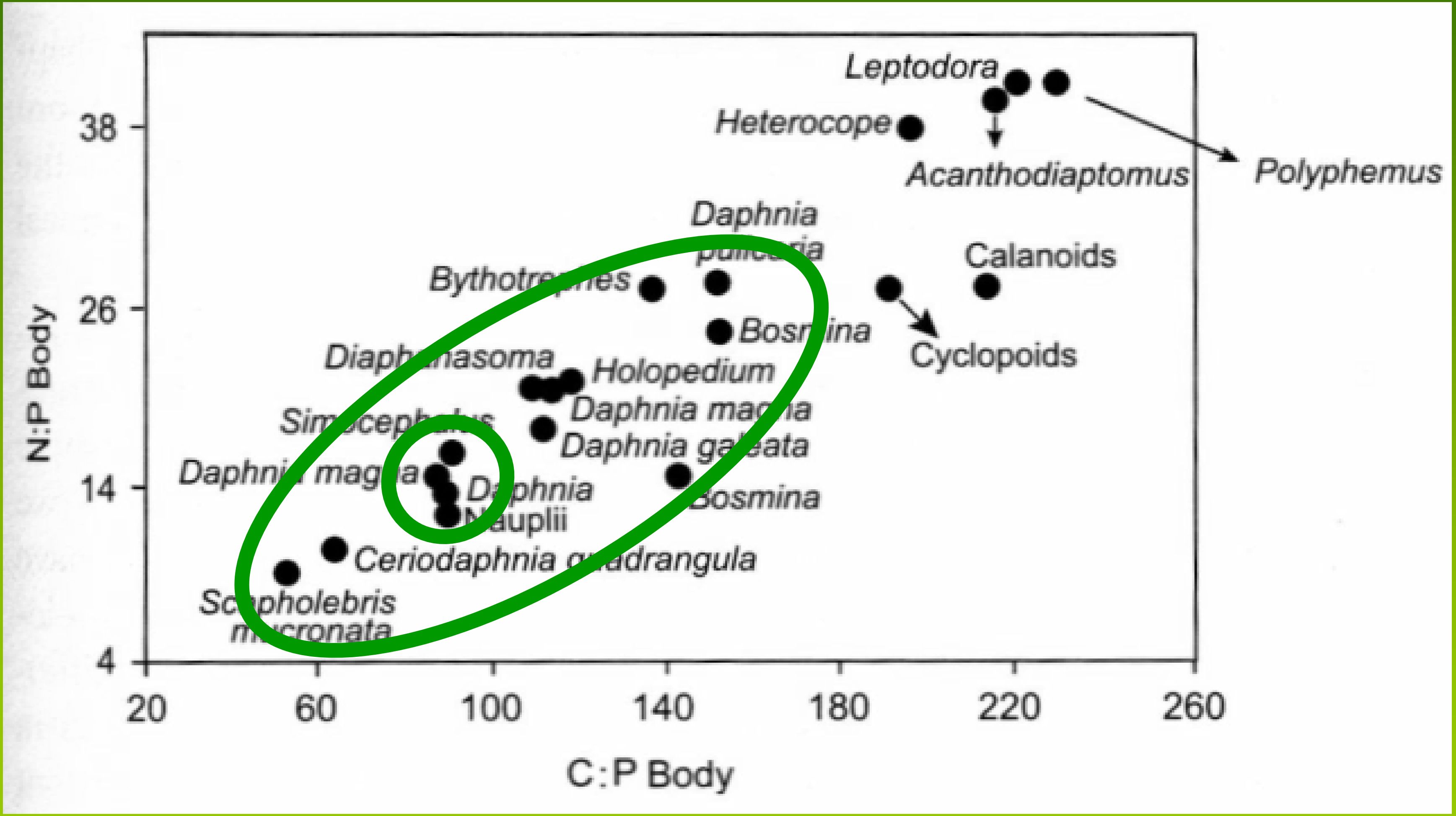
Community co-limitation

Heterotrofní homeostáze
(stechiometrie konzumentů)

Růst — využití zdrojů = **<u>změna stechiometrie</u>**

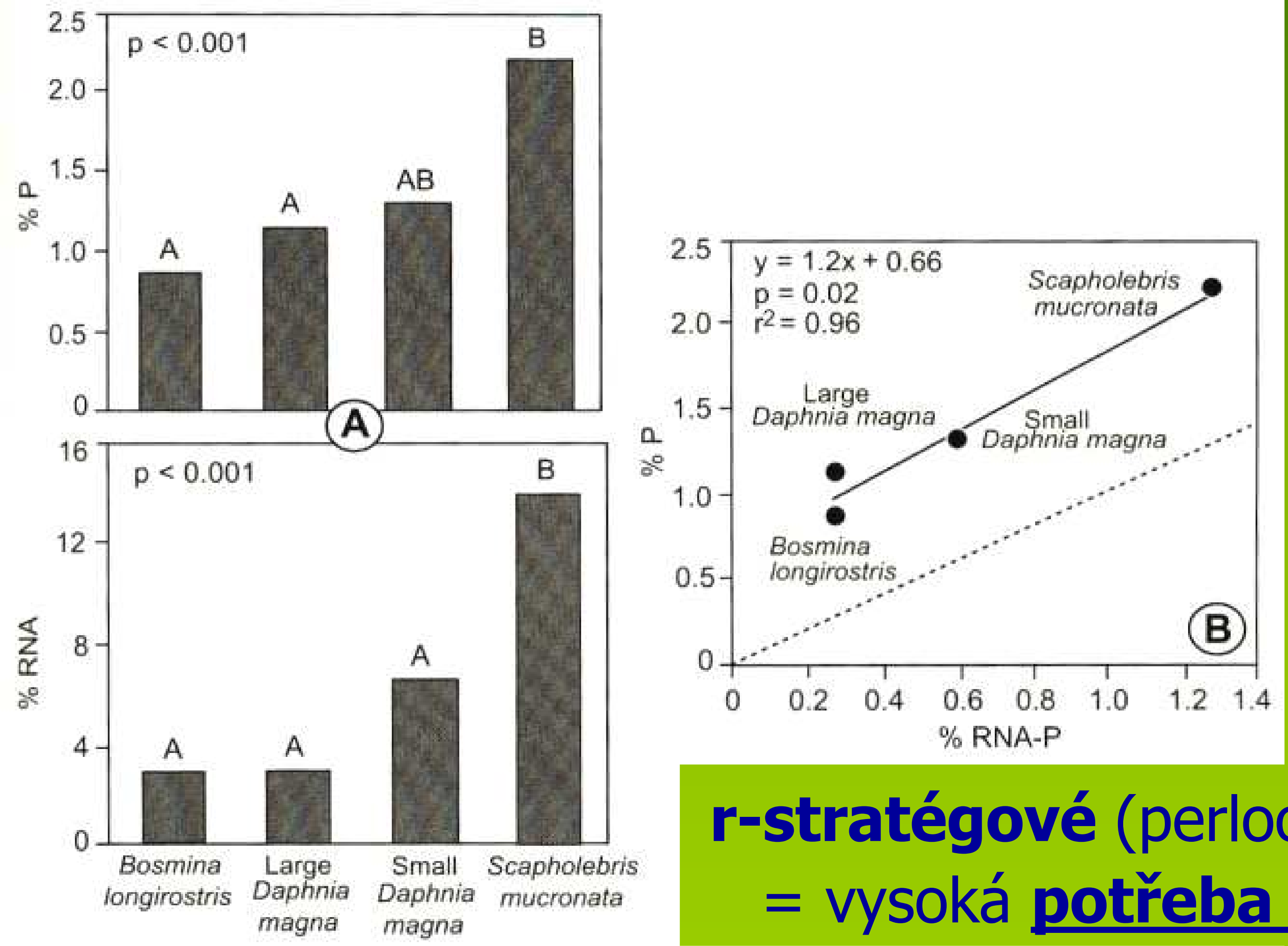


Heterotrofní homeostáze – Zooplankton (stechiometrie bezobratlých)



Heterotrofní homeostáze – Zooplankton
(stechiometrie bezobratlých)

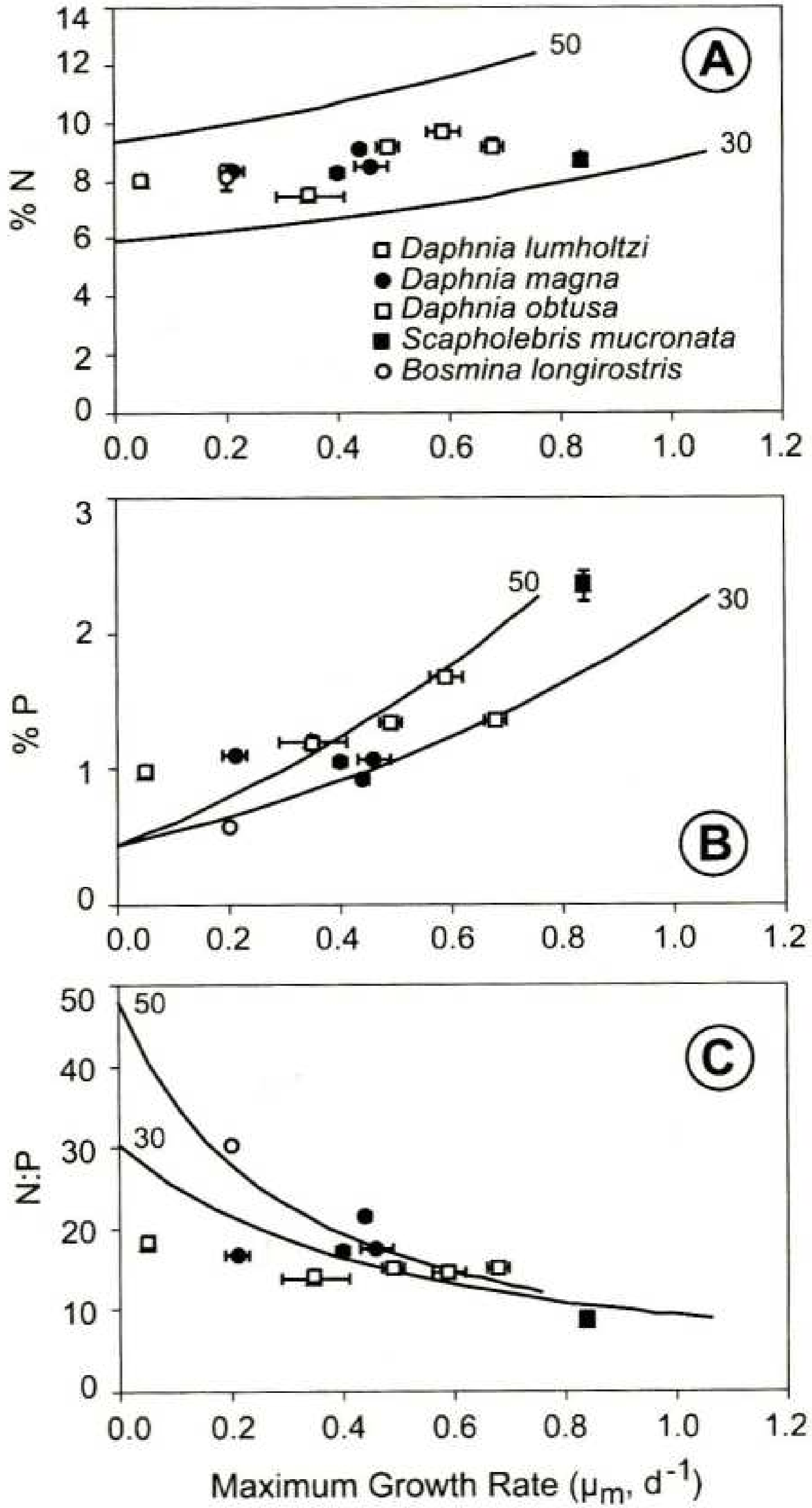
Growth **R**ate **H**ypothesis (**GRH**) = **ribozómy**



r-stratégové (perloočky)
= vysoká **potřeba P !**

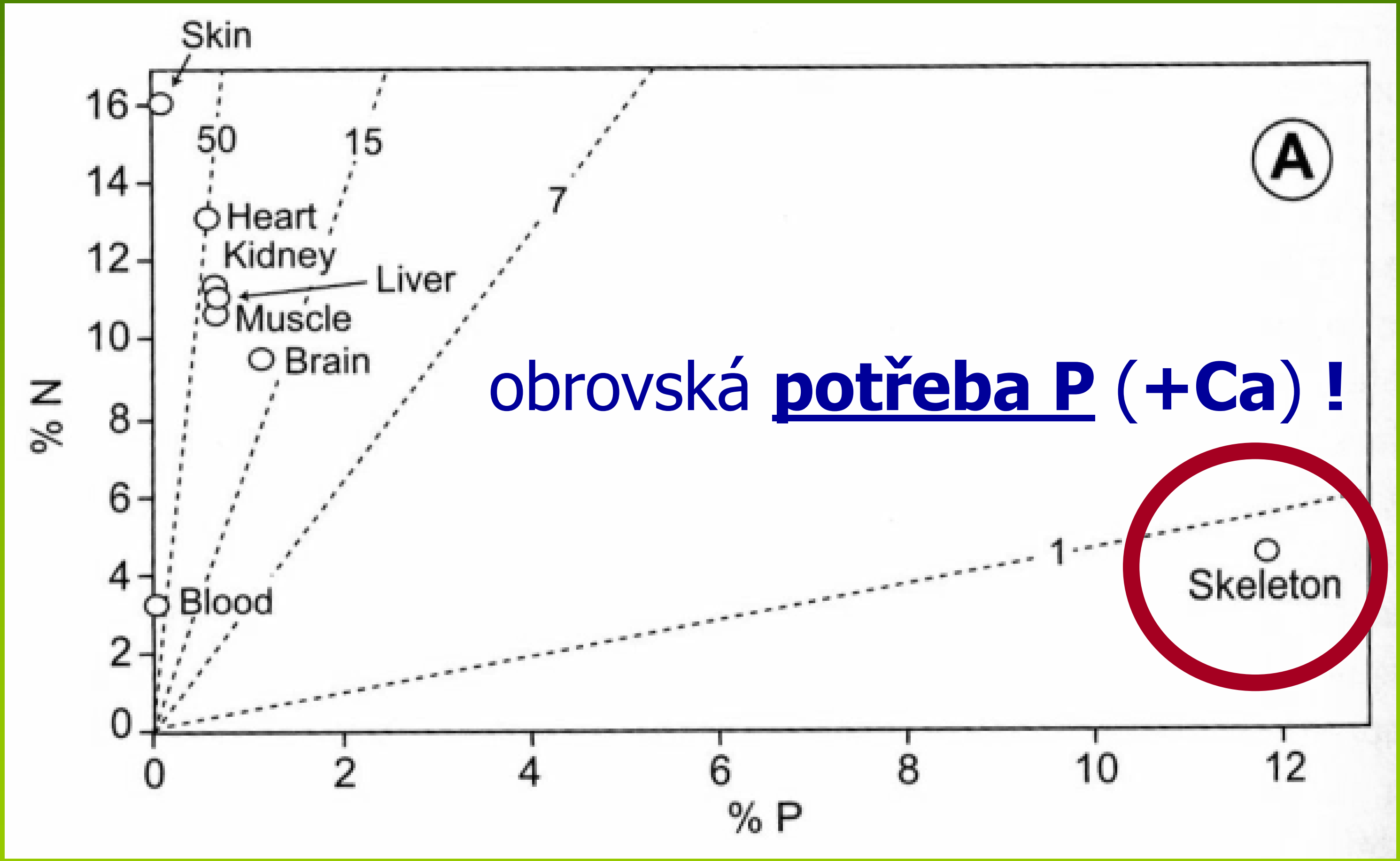
DE ribosome kinetics

(Dobberfuhl a Elser)



Heterotrofní homeostáze – Ryby (stechiometrie obratlovců)

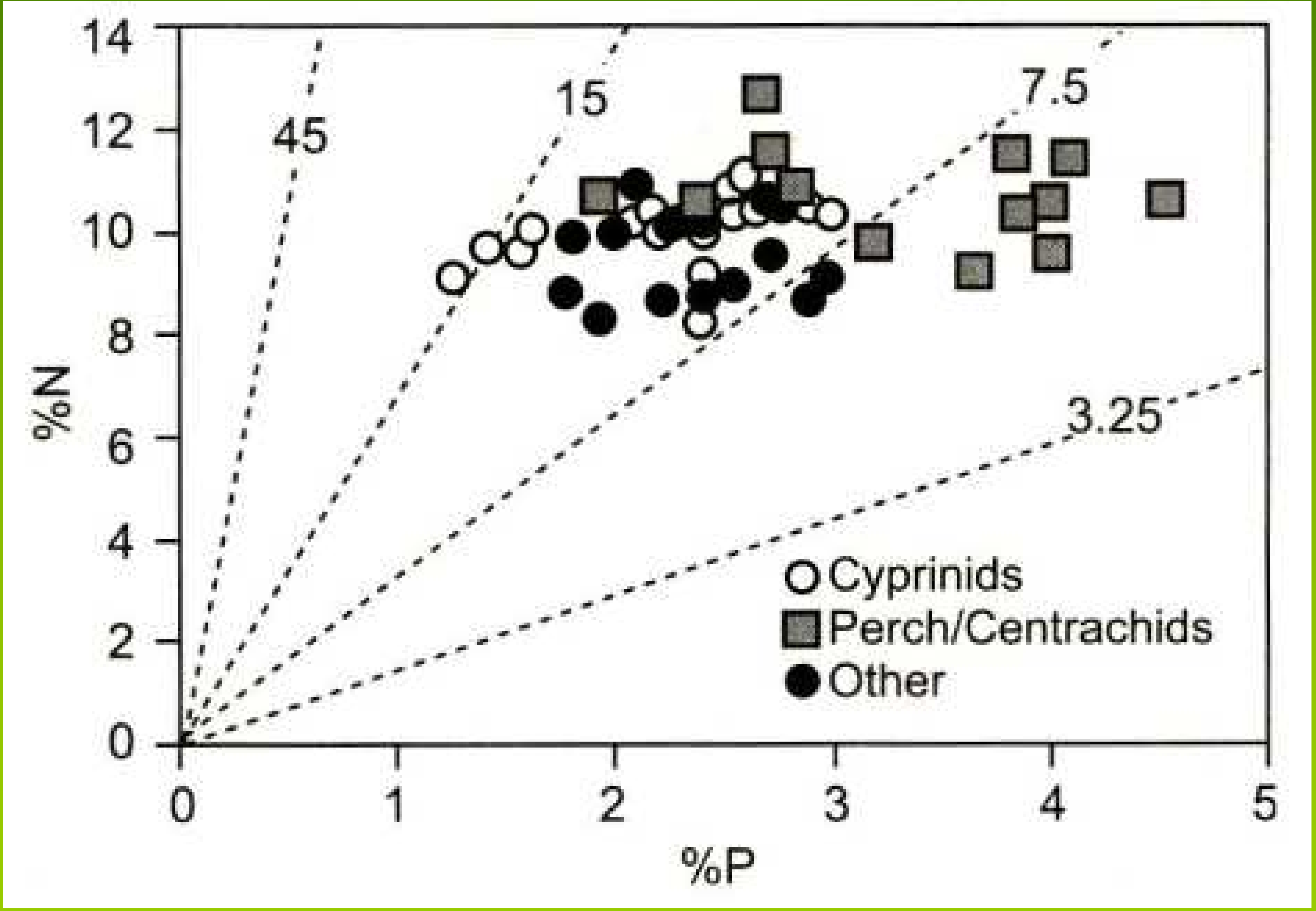
Strukturní investice = <u>kostra</u>



obrovská **<u>potřeba P</u>** (**+Ca**) **!**

Heterotrofní homeostáze – Ryby
(stechiometrie obratlovců)

Strukturní investice = kostra



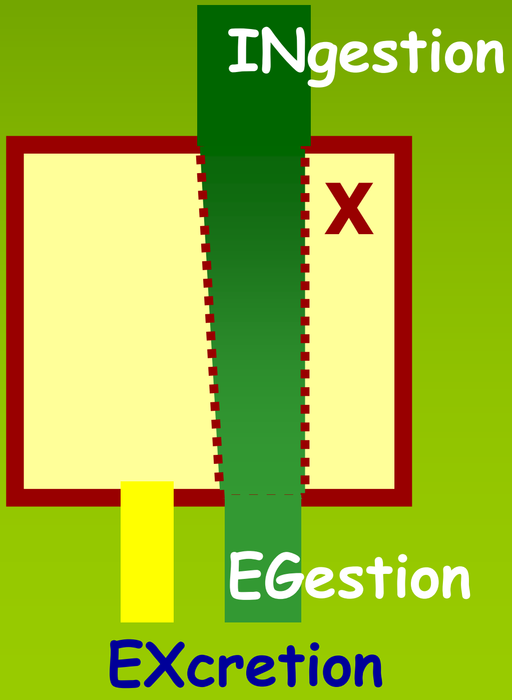
Nerovnováha zdrojů a růst živočichů

Zákon zachování hmoty = stechiometrický vztah

konzument–zdroj:

X biomasa konz. + Y zdroj ⟶ X biomasa konz. +

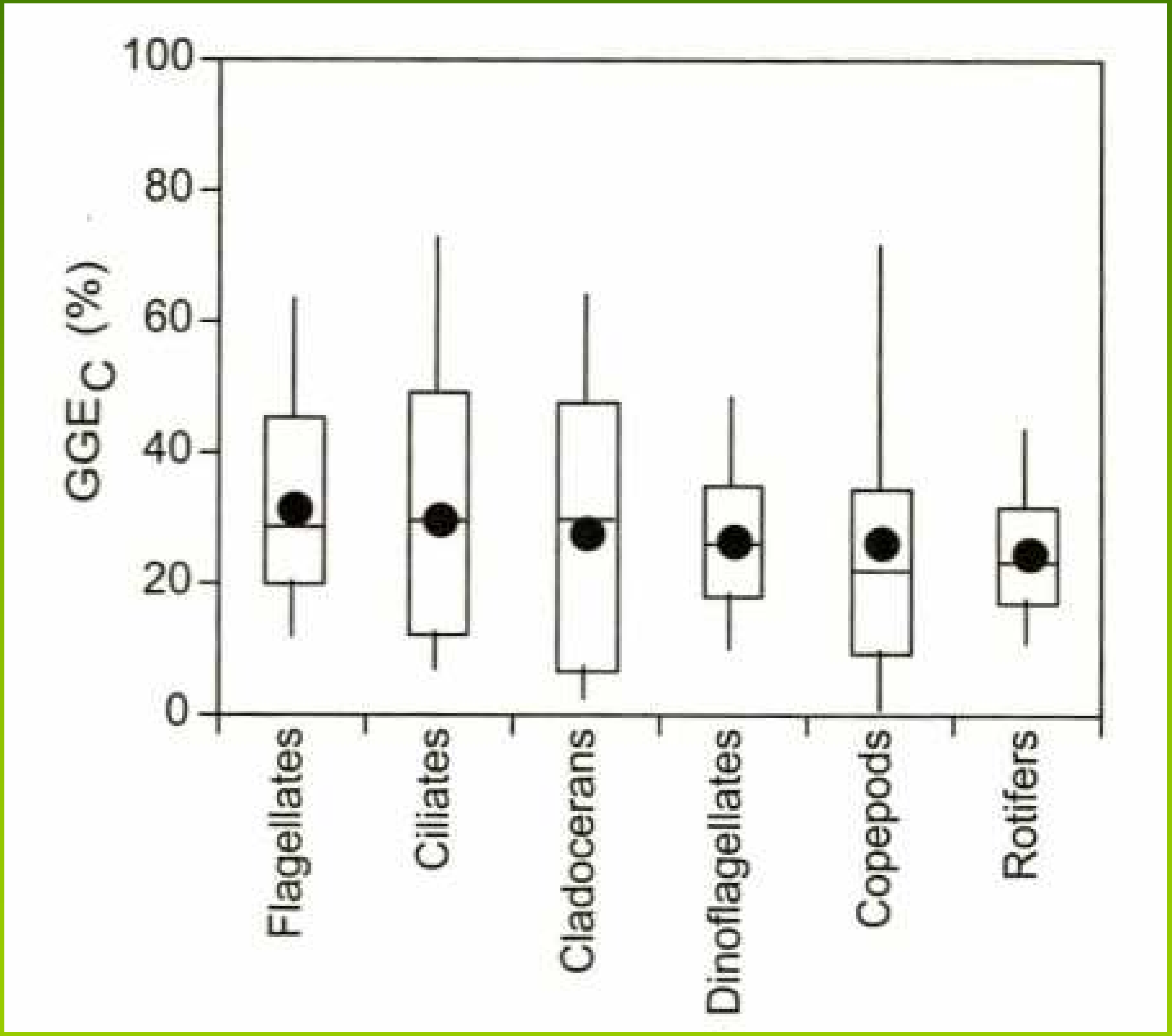
aY biomasa konz. + (1 - a)Y odpadní produkt



$g' = IN - (EG + EX)$	[growth rate]
$GGE = g'/IN = S \cdot NGE$	[gross growth efficiency]
$NGE = g'/(IN - EG)$	[net growth efficiency]
$S = (IN - EG)/IN$	[assimilation efficiency]

Nerovnováha zdrojů – yield (výtěžek)

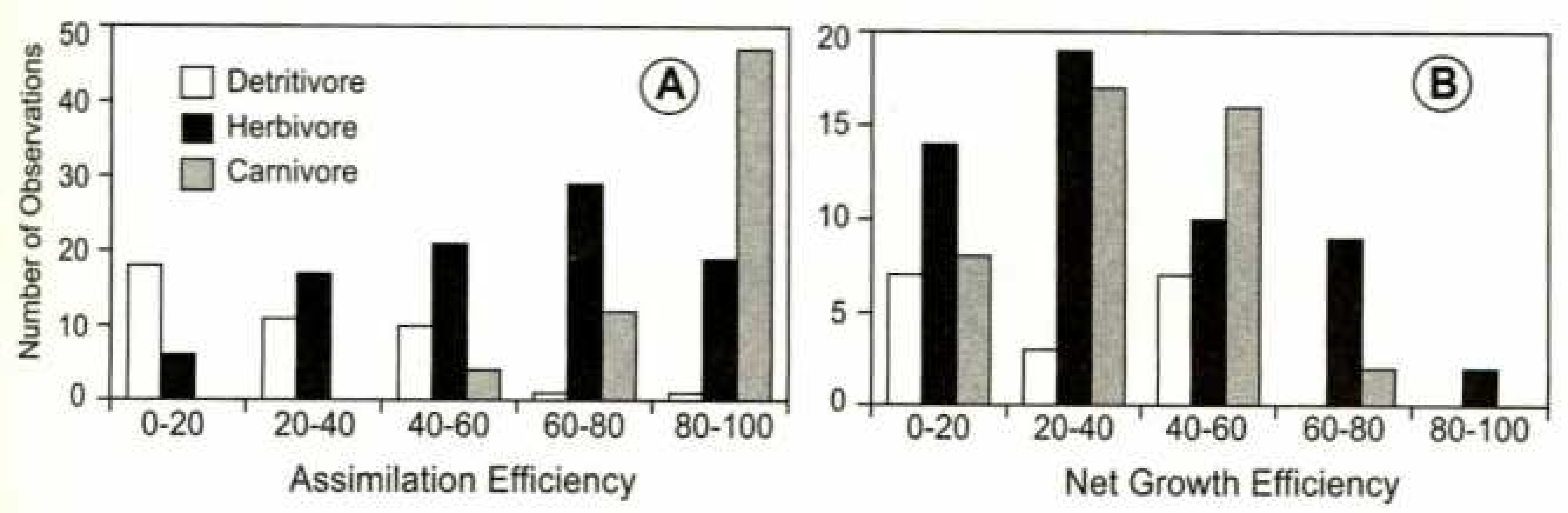
Velká variabilita GGE_C – taxonomické rozdíly



Nerovnováha zdrojů – yield (výtěžek)

Účinnosti se liší podle kvality zdroje **= <u>stechiometrie</u>!**

– detritivoři, herbivoři, karnivoři:



Limitovaný růst heterotrofů – hypotéza TER

Threshold **E**lement **R**atio (prahový poměr prvků/živin)

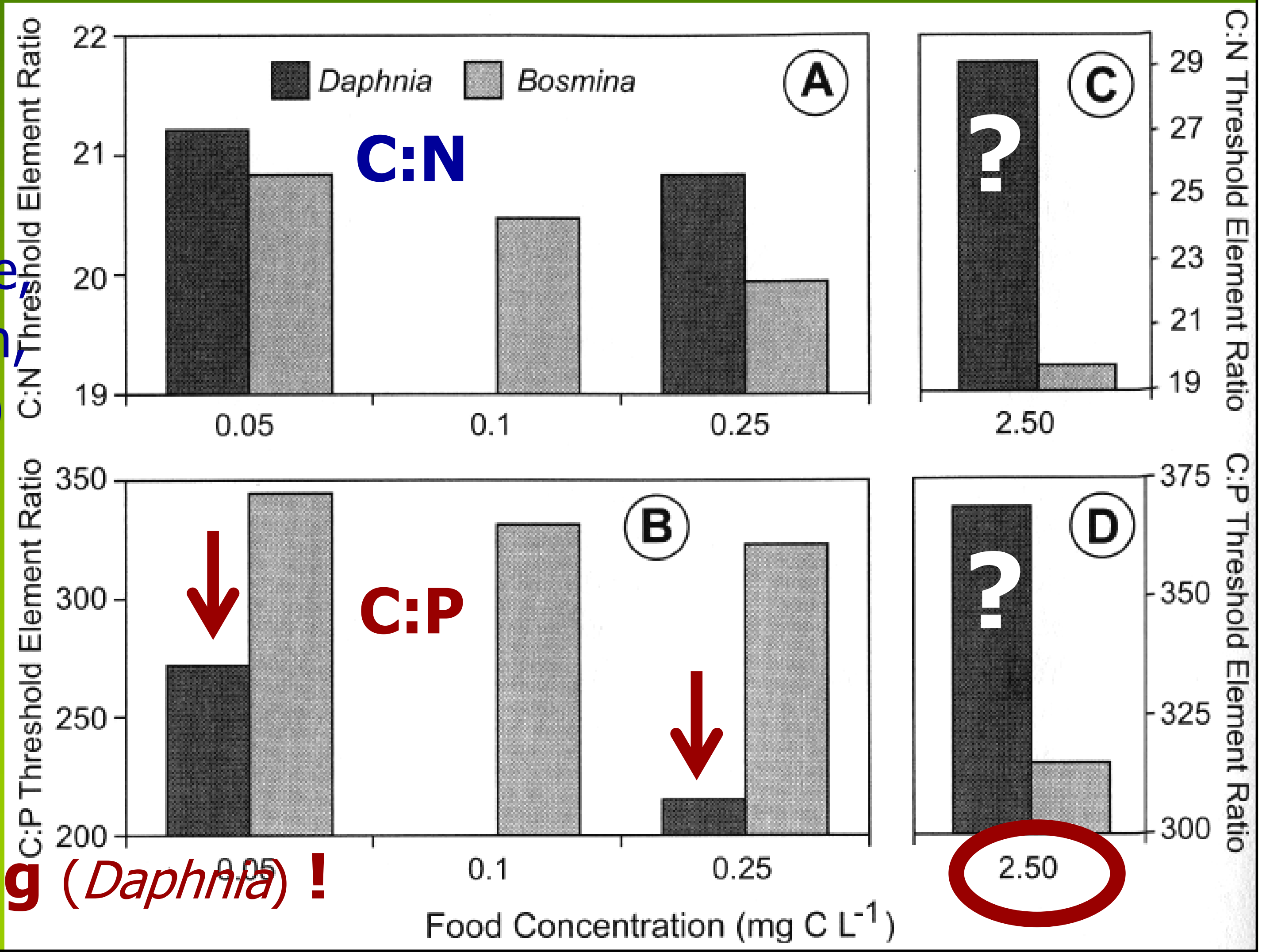
Liebigův zákon minima + <u>stechiometrie</u> (např. Fe, I, Se, Zn…)

Zooplankton

C:N:P

(Urabe & Watanabe, Anderson & Hessen, Sterner & Elser aj.)

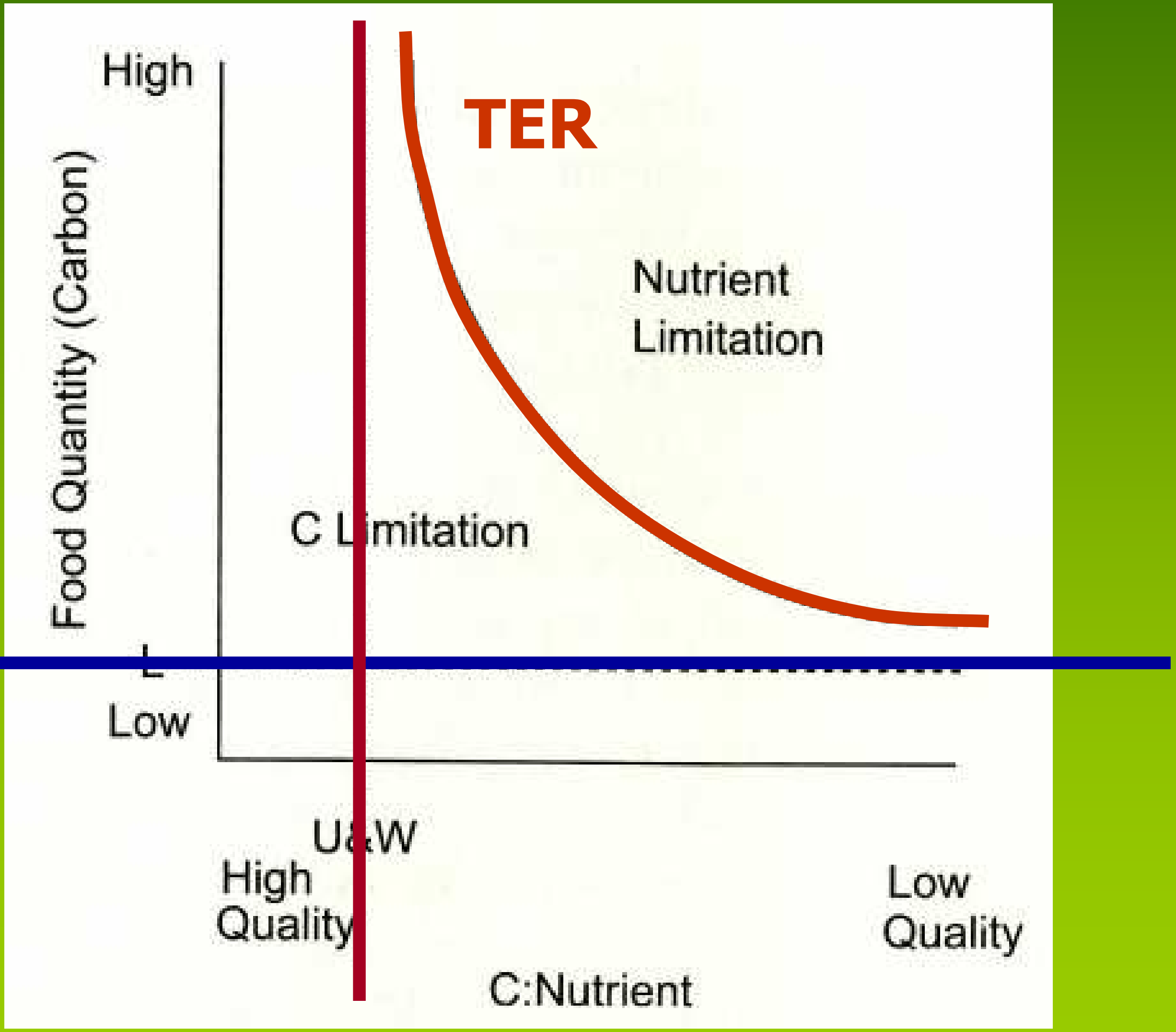
Daphnia = <u>**+ P**</u>



Sloppy feeding (*Daphnia*) **!**

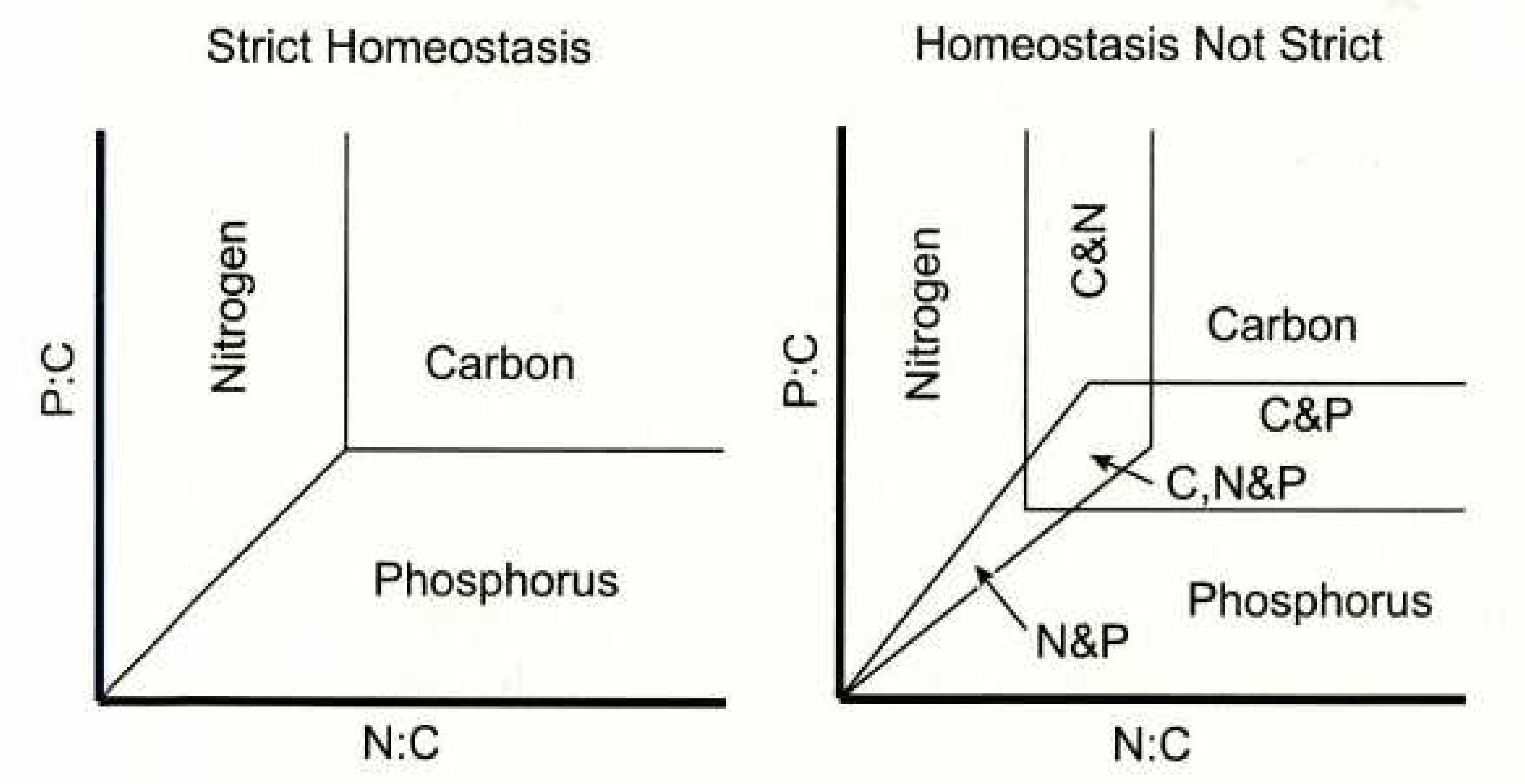
Limitovaný růst heterotrofů – hypotéza TER

Citlivost TER modelů na **kvalitu i kvantitu** zdroje



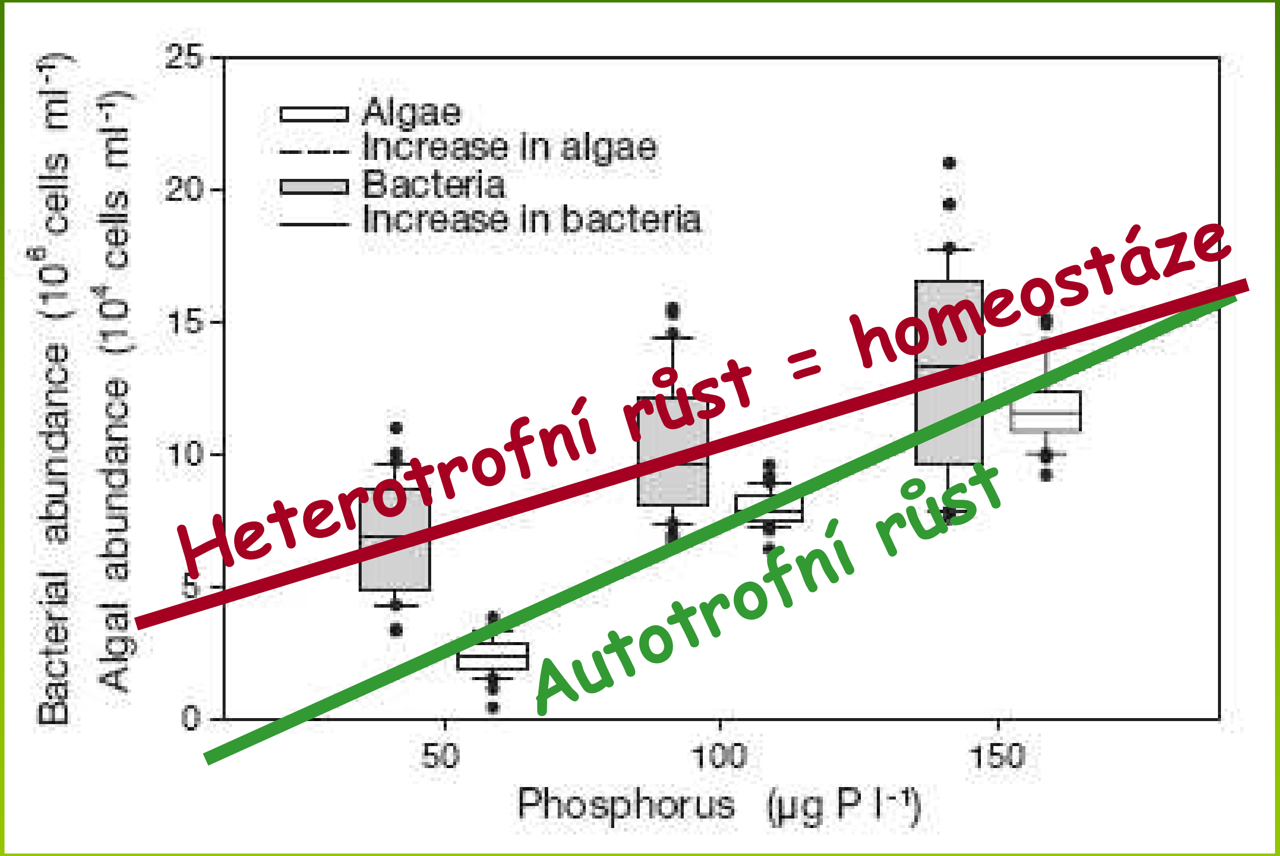
TER vs. multiple resource co-limitation

Bakterie – homeostáze C:N:P (Thingstadt aj.)

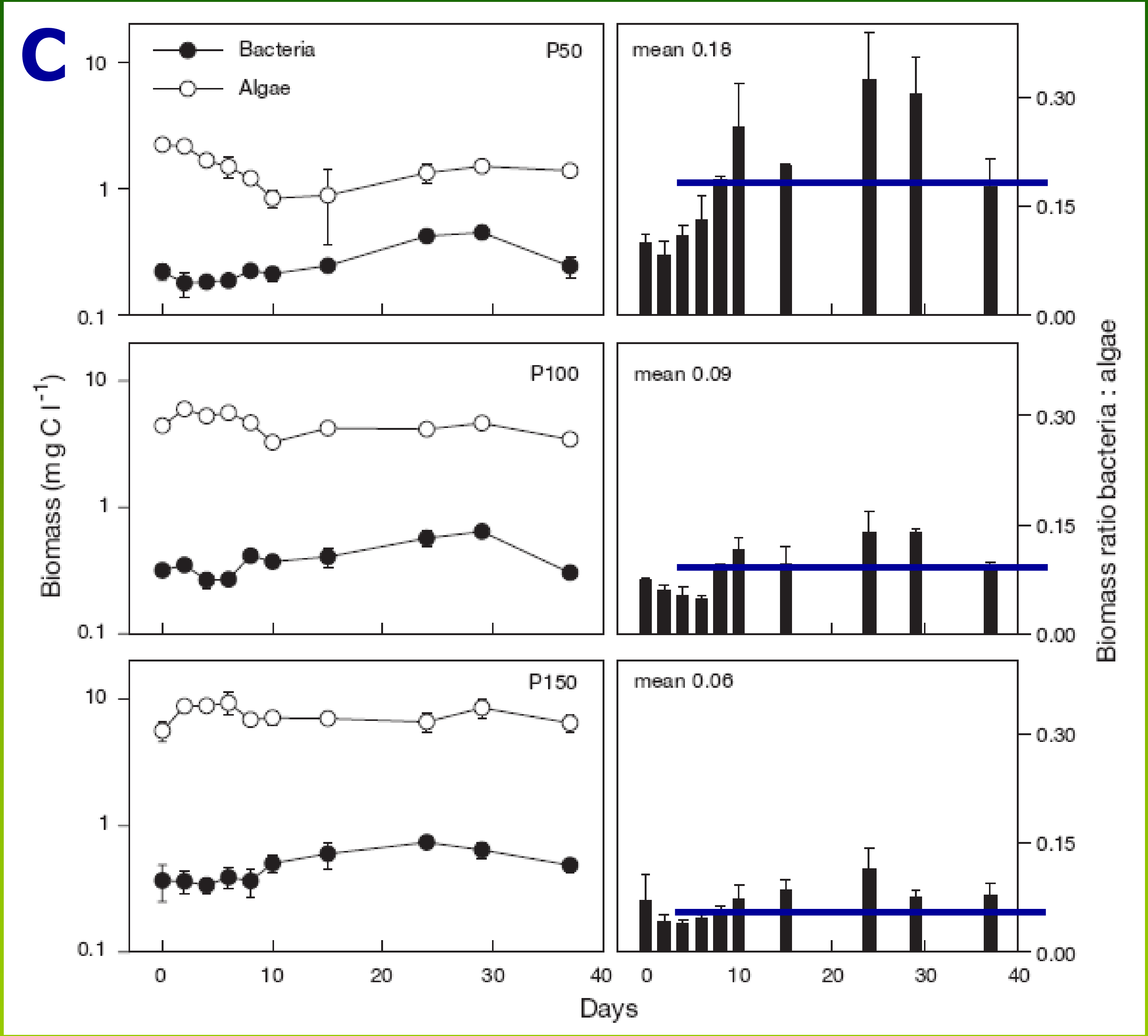


TER vs. konkurence o limitující zdroj (**P**)

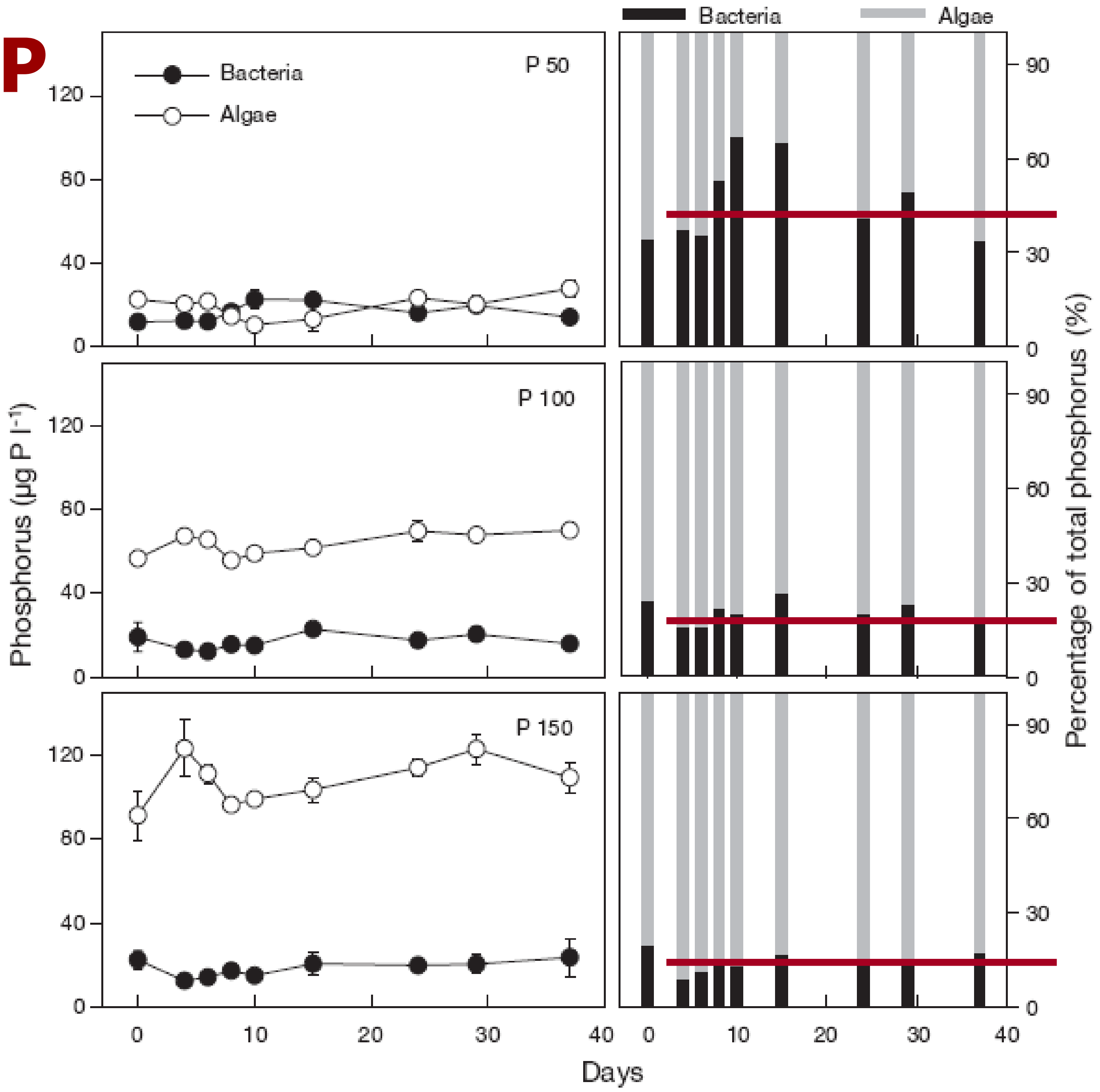
Revize paradoxu fytoplankton–bakterie (Thingstadt)



Konkurence = **komensalismus** nebo **nepřímá predace ?**


C
Bacteria
Algae
P50
P100
P150
mean 0.18
mean 0.09
mean 0.06
10
1
0.1
0.30
0.15
0.00
Biomass (mg C l^{-1})
Biomass ratio bacteria : algae
0
10
20
30
40
Days

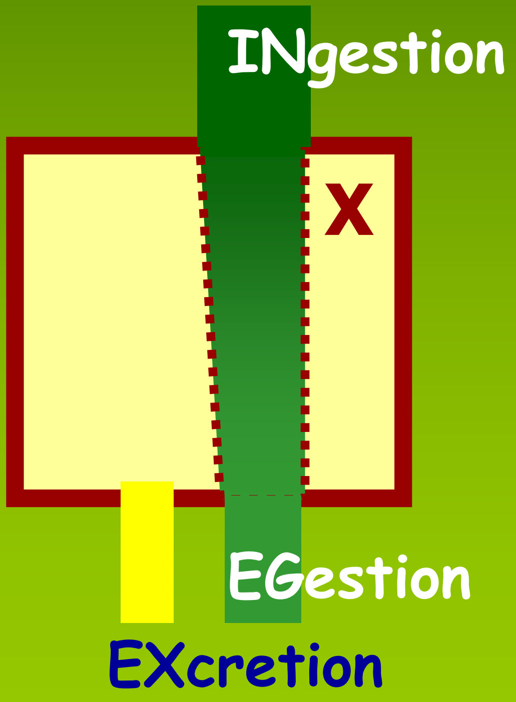
P

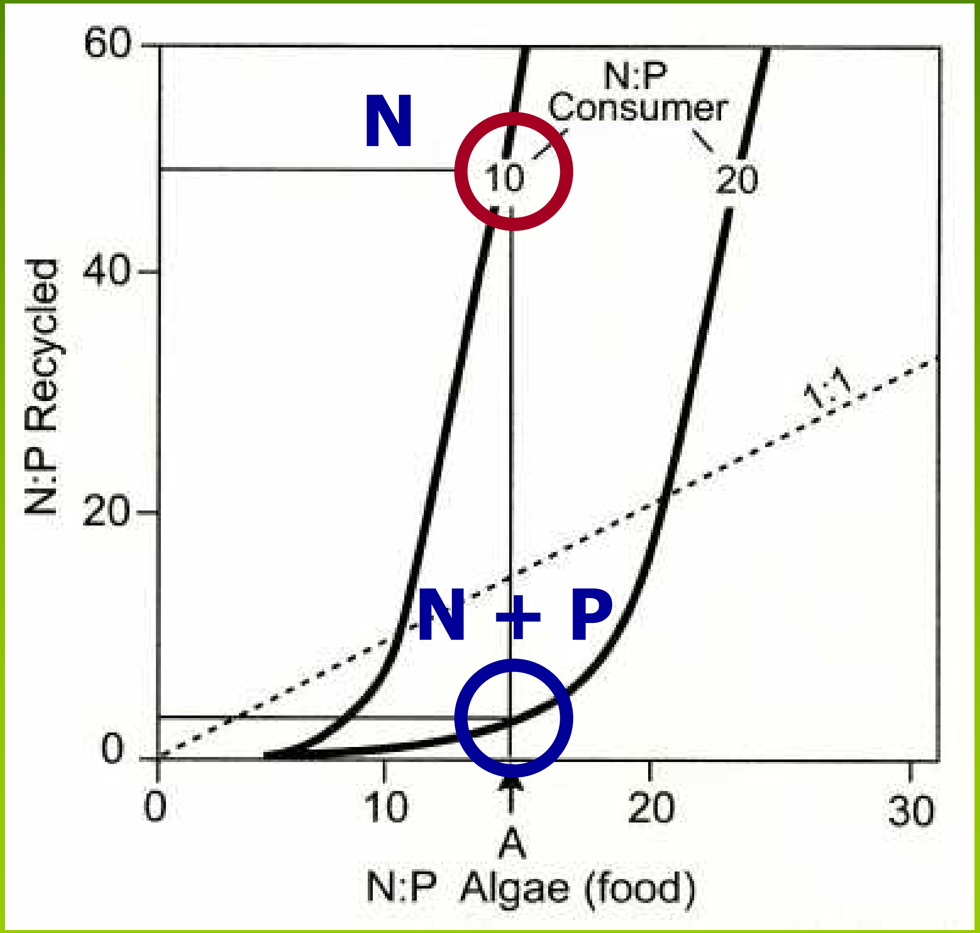

Bacteria
Algae
P 50
P 100
P 150
Phosphorus (µg P l⁻¹)
Percentage of total phosphorus (%)
Days
0
40
80
120
0
10
20
30
40
0
30
60
90

Nerovnováha zdrojů + homeostáze = **CNR**

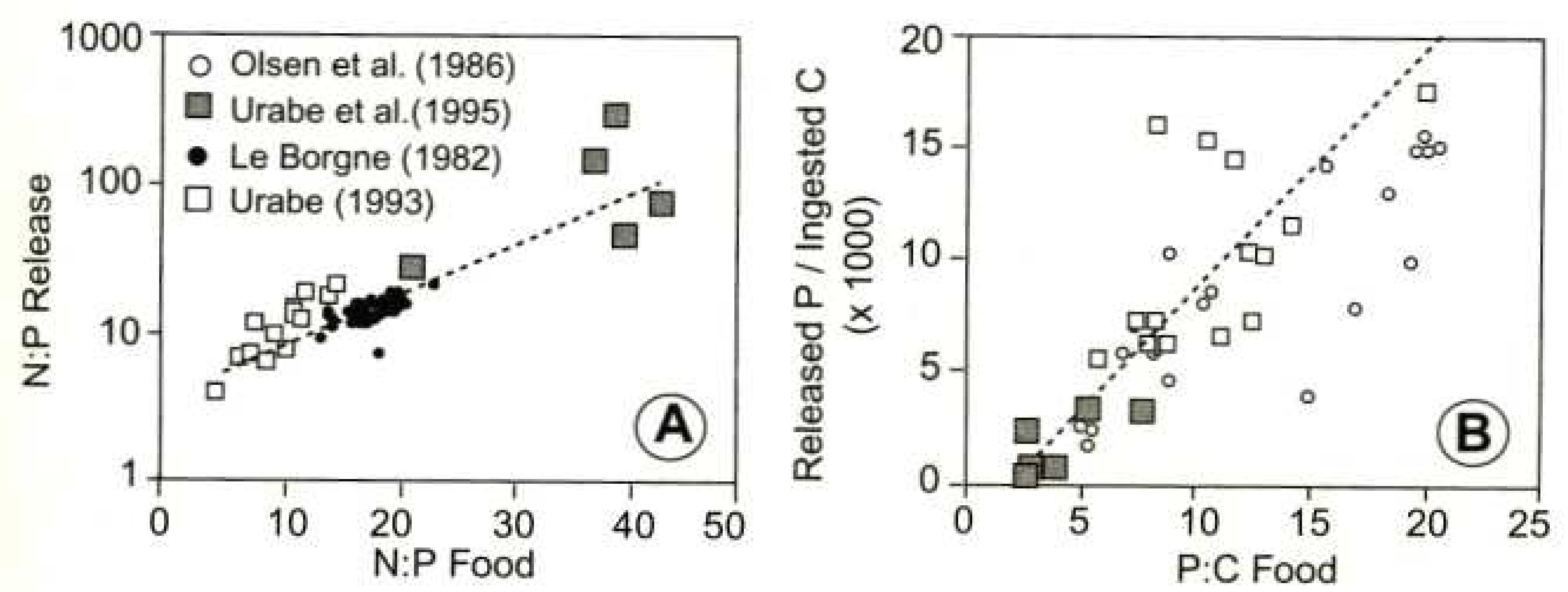
Consumer-driven **N**utrient **R**ecycling

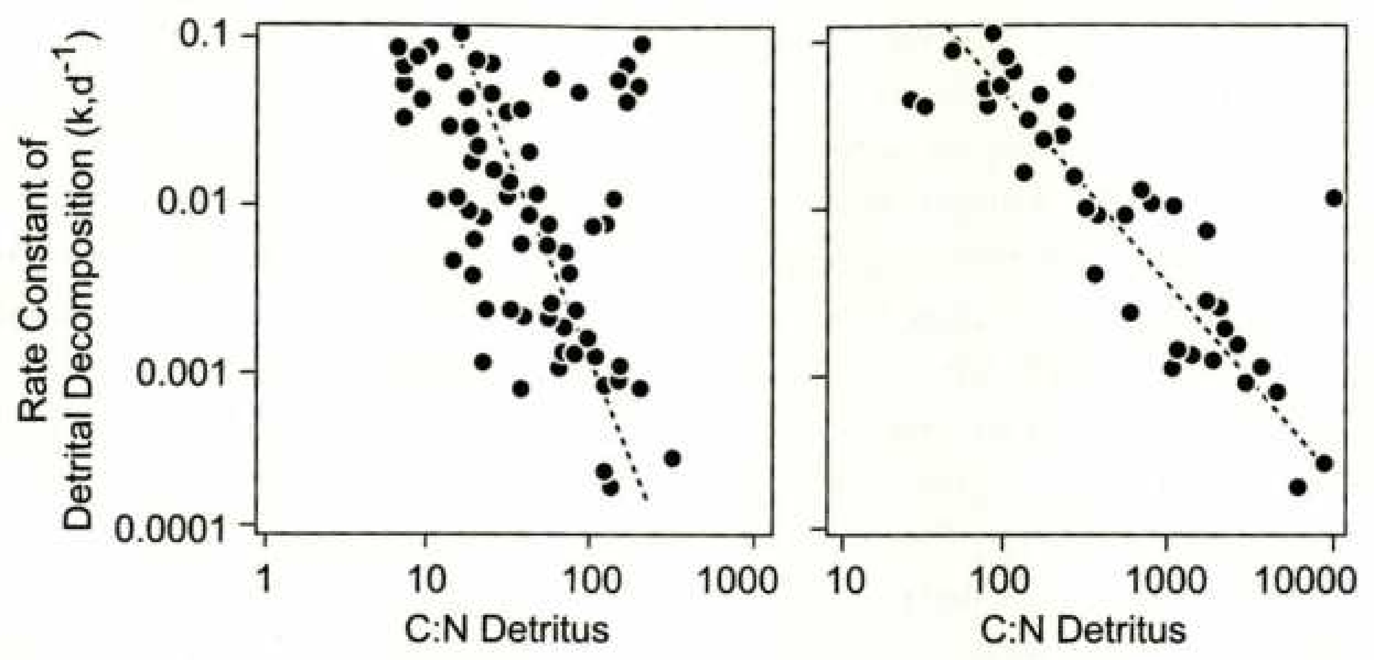
Regenerace N a P = stechiometrie konzumenta



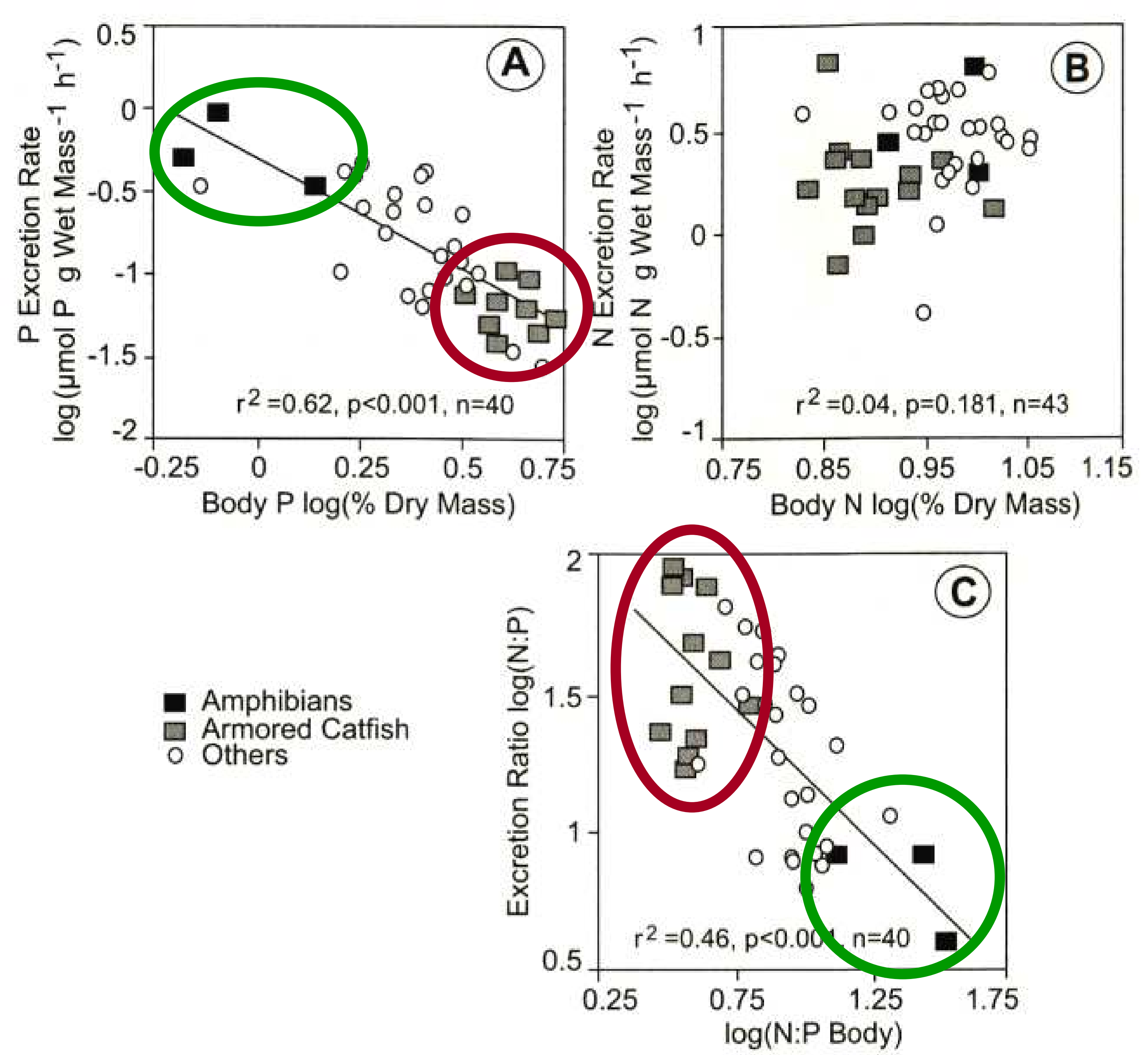


CNR – zooplankton, mikrobiální dekompozice

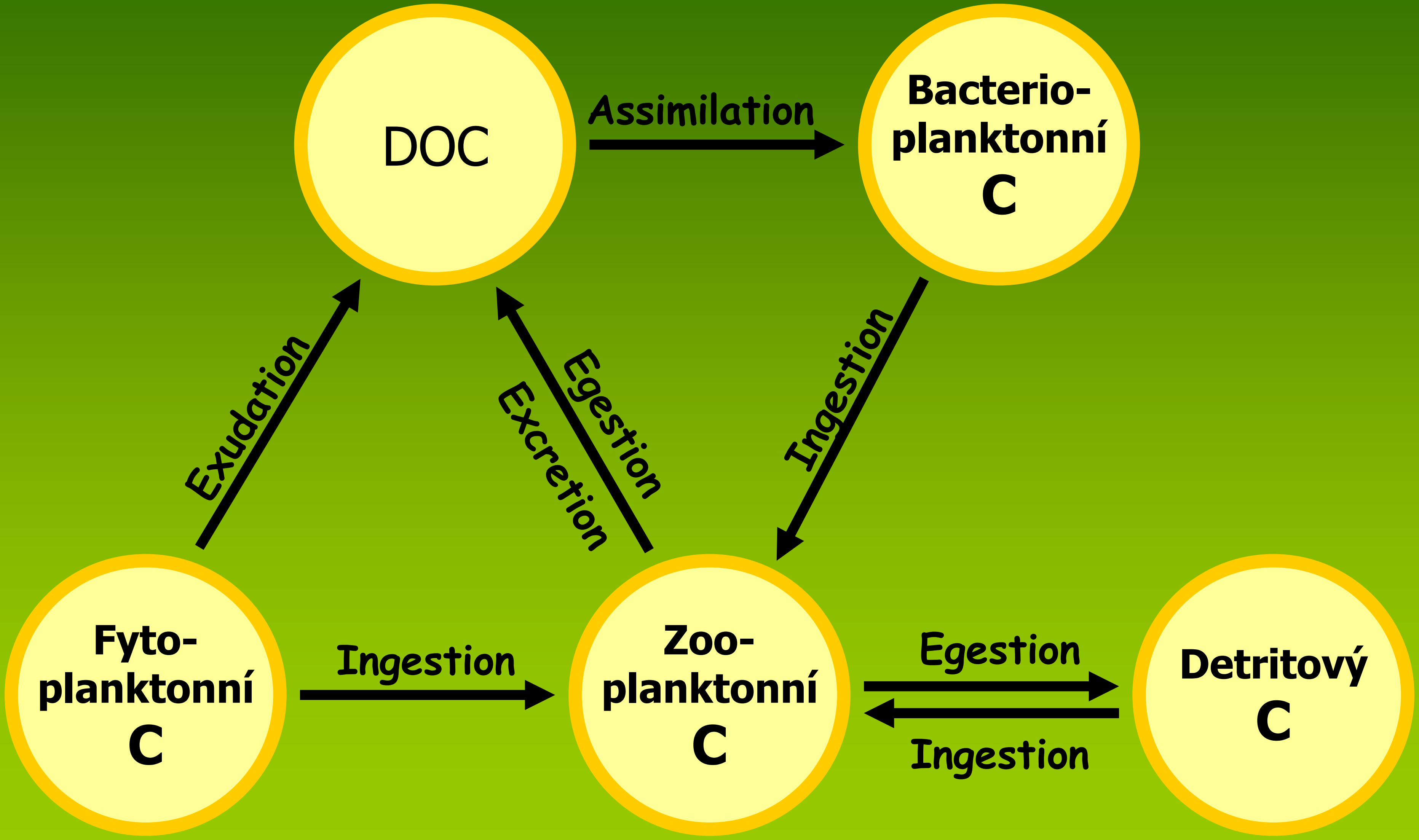




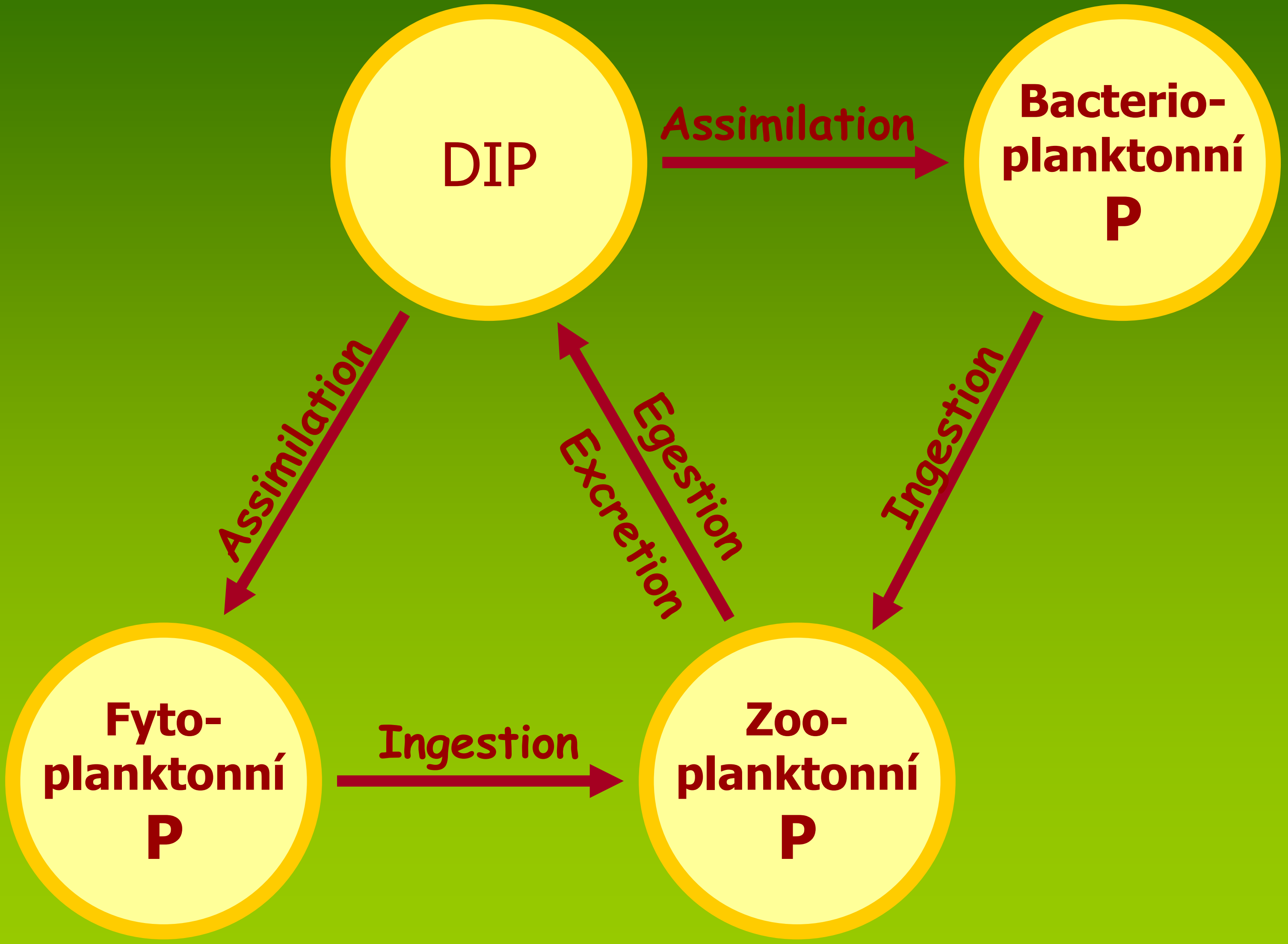
CNR – obratlovci



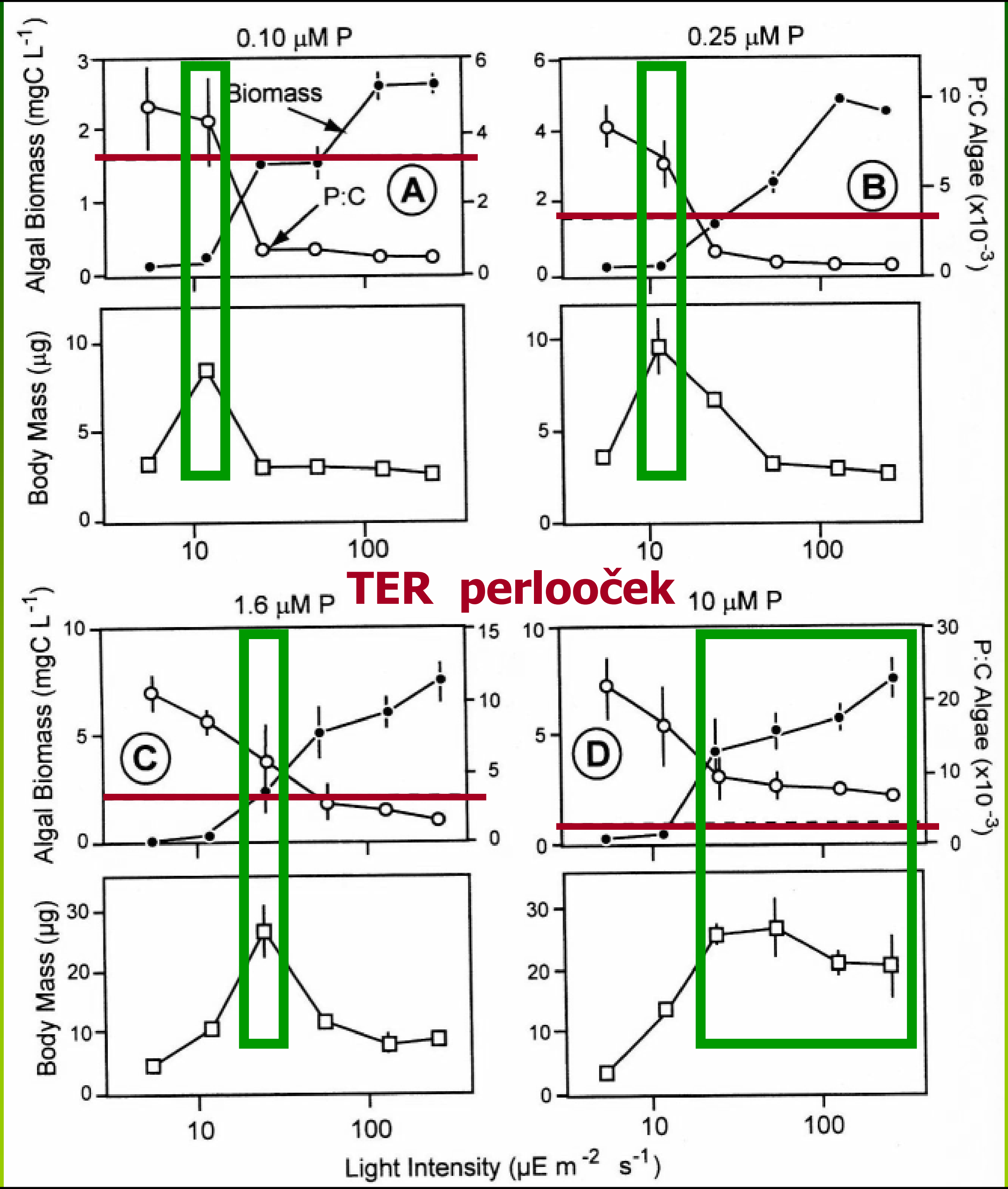
Stechiometrie společenstev



Stechiometrie společenstev



světlo ?



TER perlooček

Stechiometrie

světlo:živiny

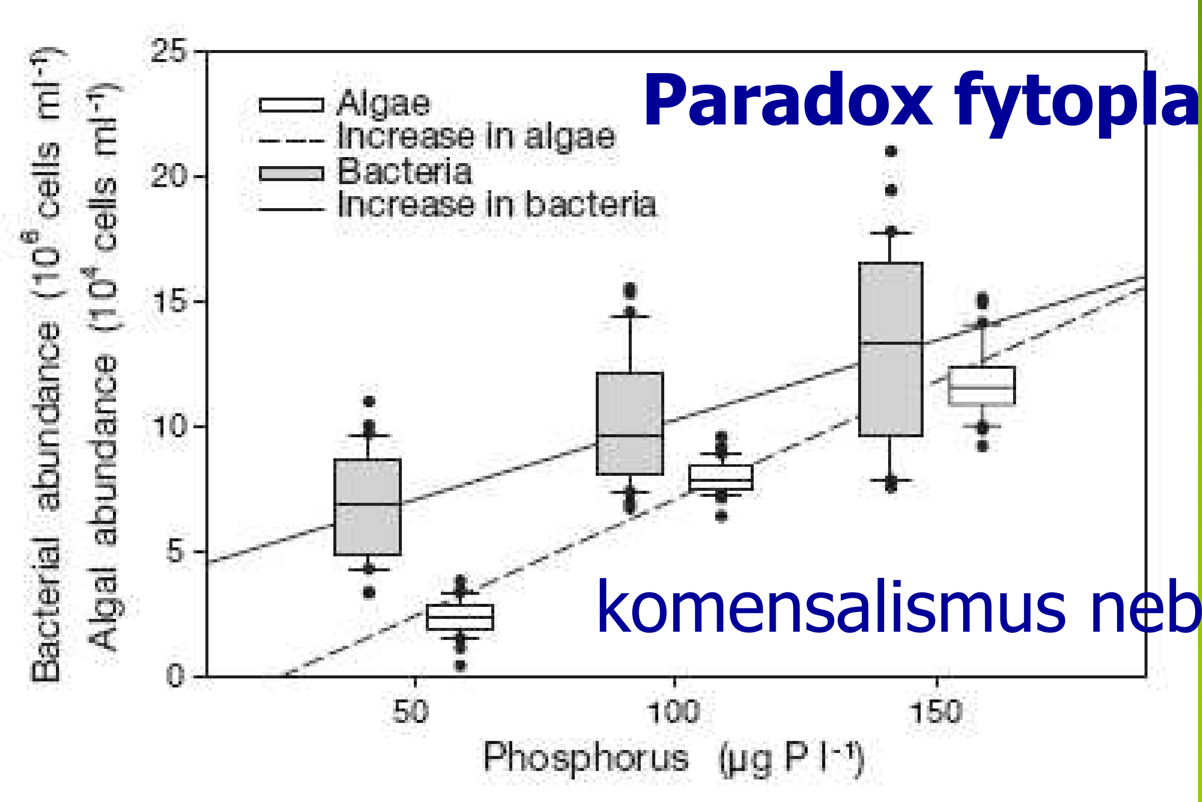
(~C:P)

Stechiometrie společenstev – integrace:

dvojí vliv stechiometrie na **ekologické interakce**

- **kvantitativní ~ energie**
- **kvalitativní ~ funkce + informace**

} niky druhů



Paradox fytoplankton–bakterie:

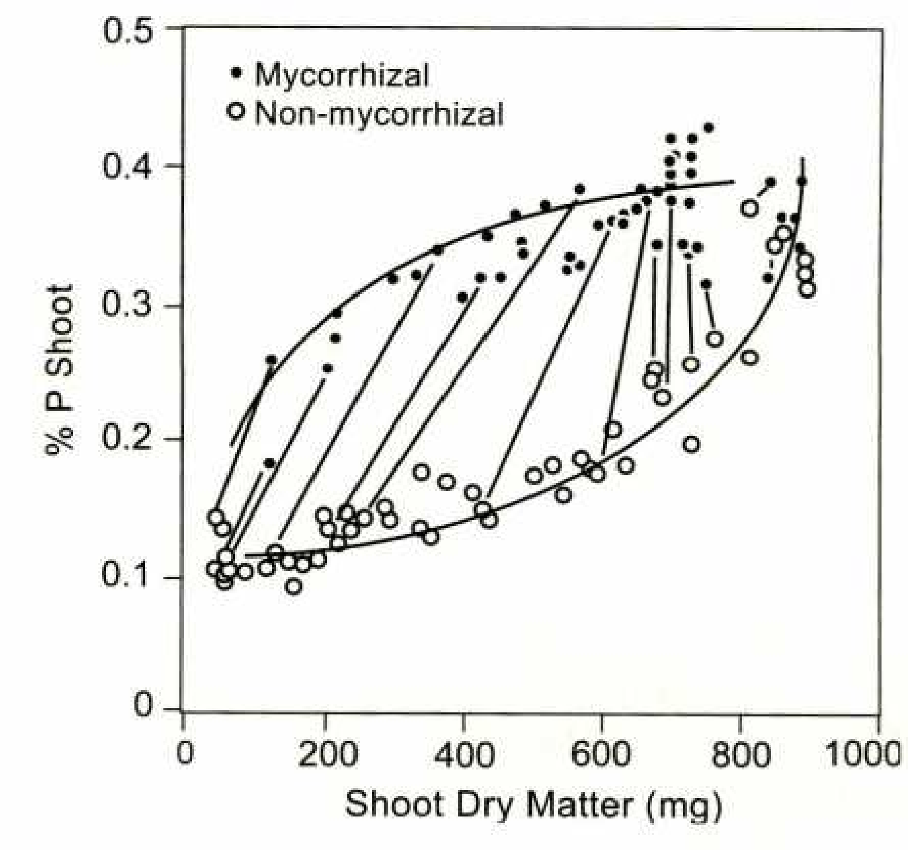
komensalismus nebo nepřímá predace?

Stechiometrie společenstev – integrace:

dvojí vliv stechiometrie na **ekologické interakce**

- **<u>kvantitativní</u> ~ energie**
- **<u>kvalitativní</u> ~ funkce + informace**

} niky druhů



Mykorhiza:

stechiometrie **mutualismu**

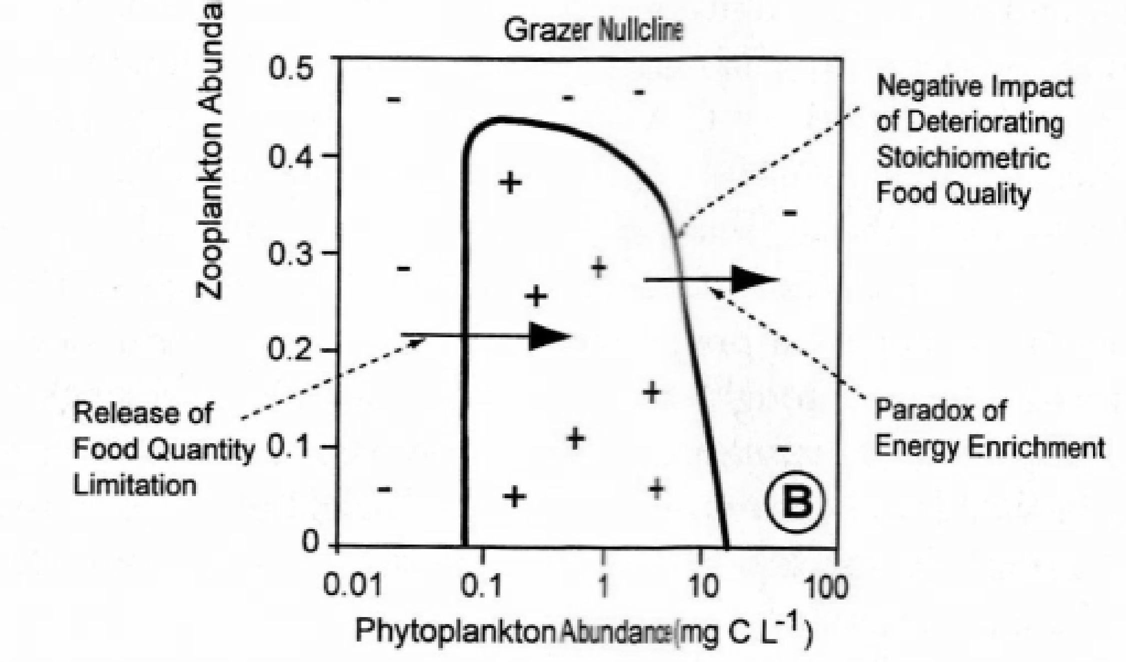
Stechiometrie společenstev – integrace:

dvojí vliv stechiometrie na **ekologické interakce**

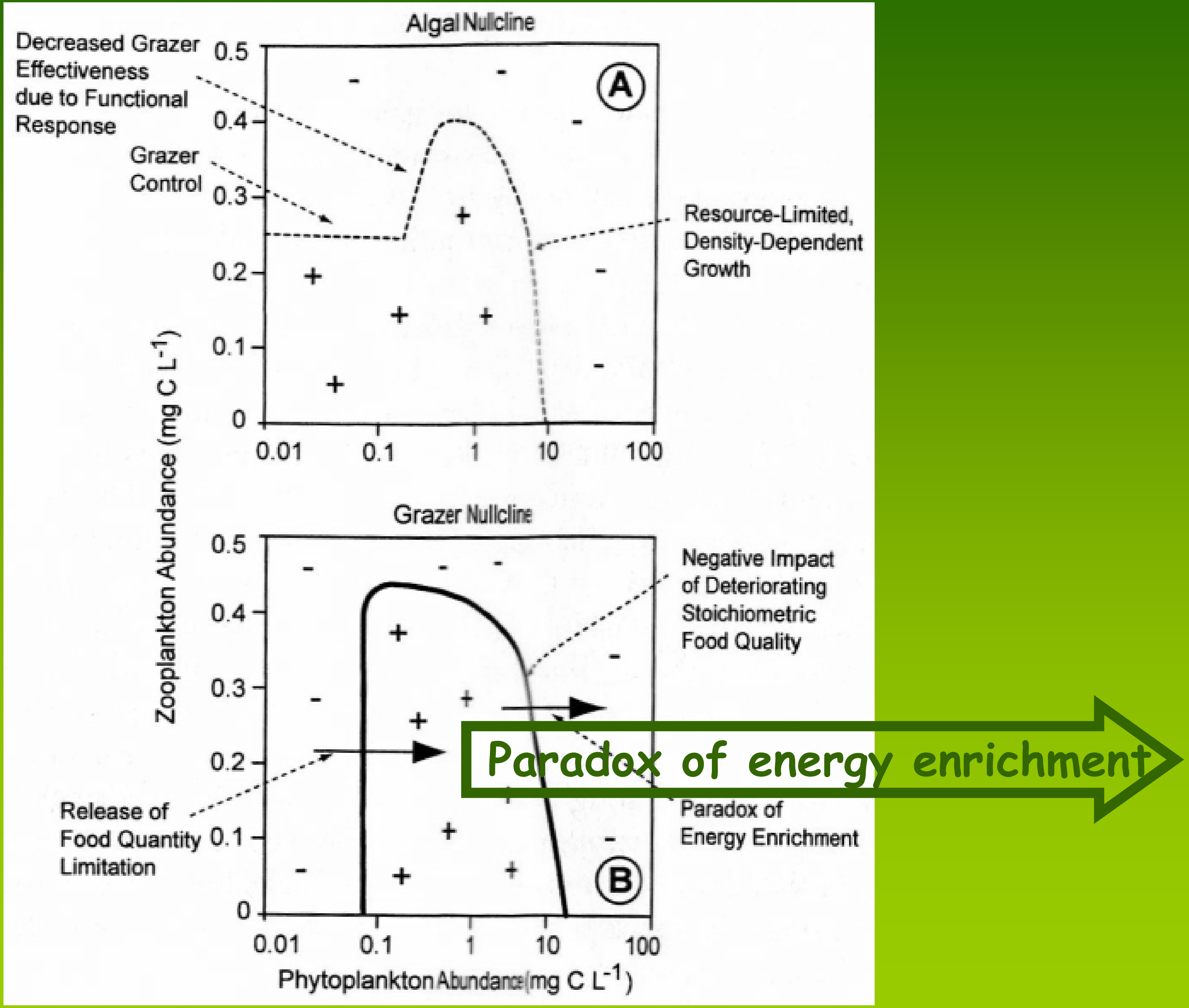
- **kvantitativní ~ energie**
- **kvalitativní ~ funkce + informace**

} niky druhů

Herbivorní filtrátoři (*Daphnia*): **Paradox of energy enrichment**



Stechiometrie vztahu **živiny–řasy–zooplankton**



Paradox of energy enrichment

Stechiometrie **pastevního potravního řetězce:**

Andersenův stechiometrický **model**

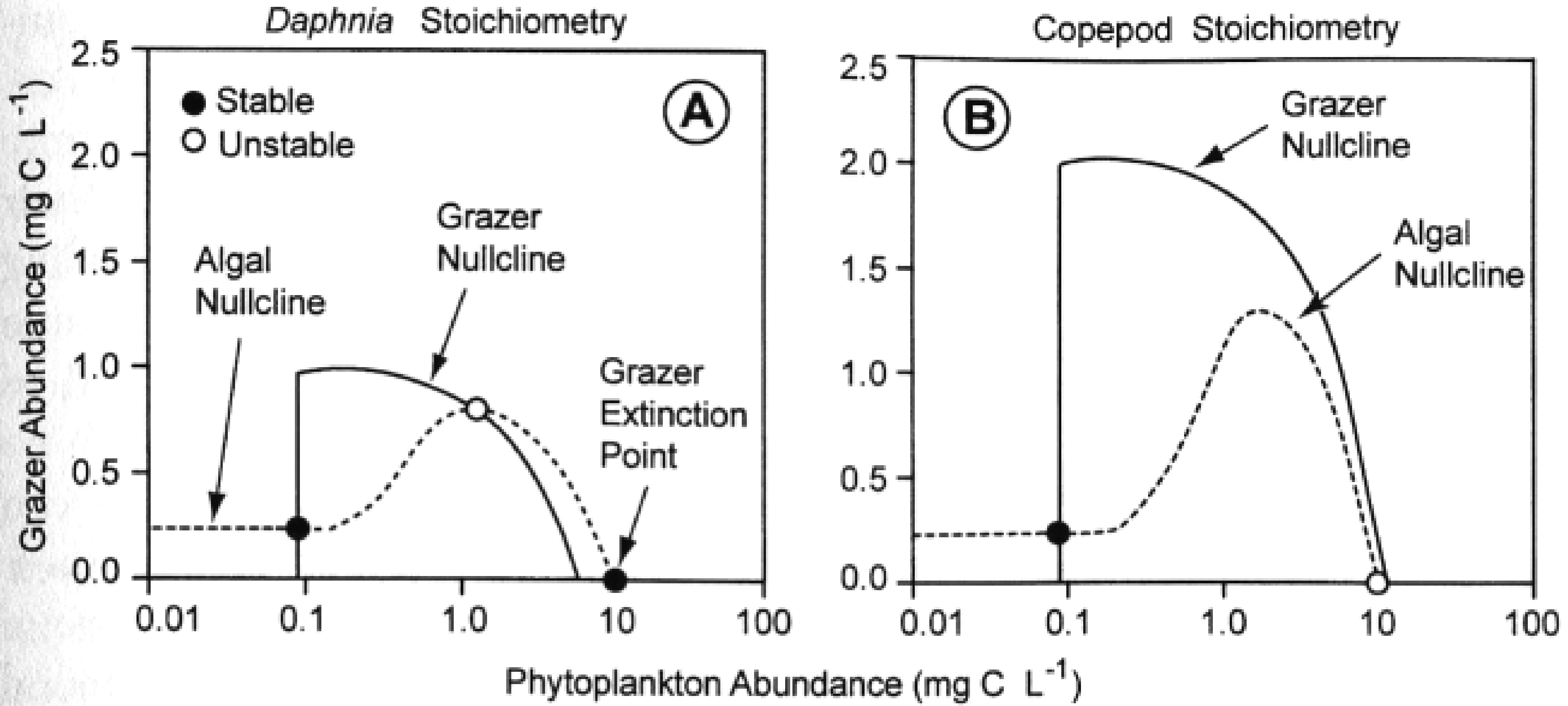
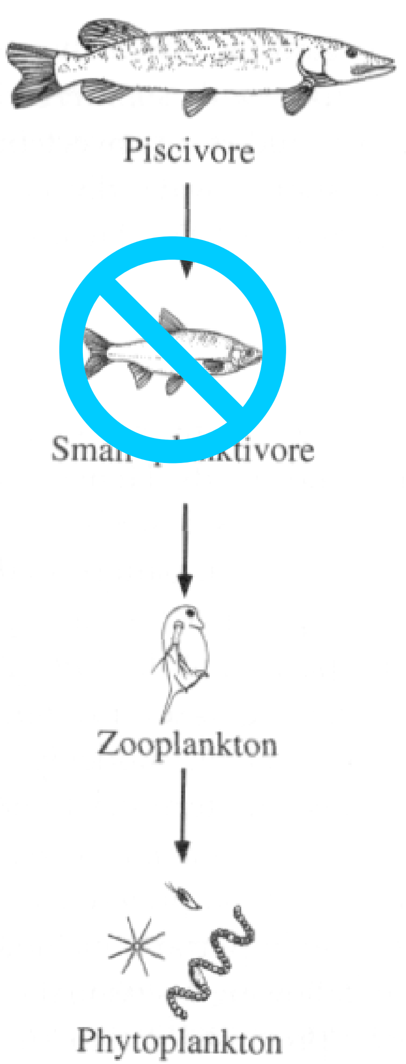


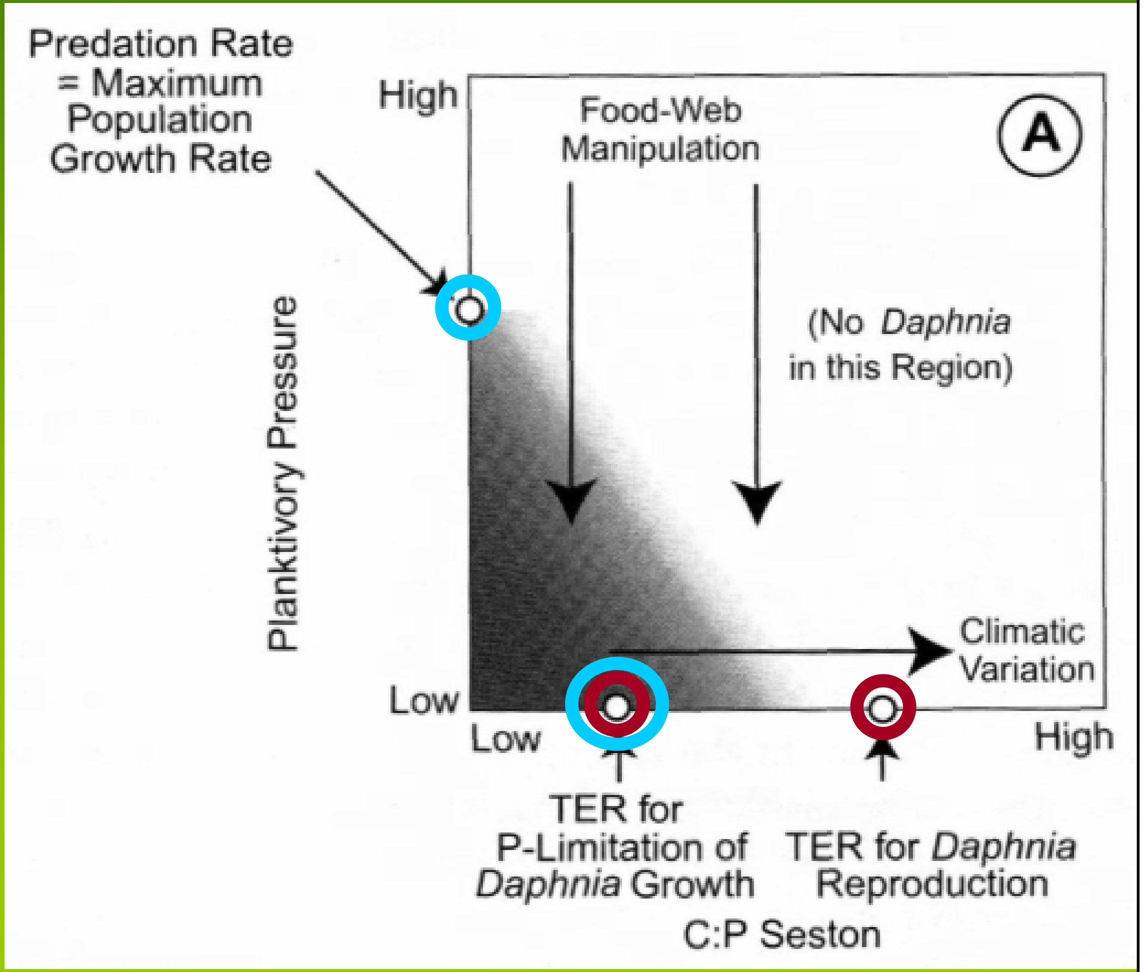
Fig. 7.7. Some of the community equilibria in the Andersen stoichiometry model, contrasting a low-C:P grazer (e.g., *Daphnia*) (A) with a high-C:P grazer (e.g., copepods) (B). For calculation of nullclines, only the grazer C:P was changed. Solid circles represent stable equilibria and open circles represent unstable equilibria. Multiple stable equilibria occur in the model with the low-C:P grazer.

Stechiometrie **potravních sítí**

aneb stechiometrie (ne/úspěšné) **biomanipulace**

Cascading **T**rophic **I**nteractions (**CTI**)

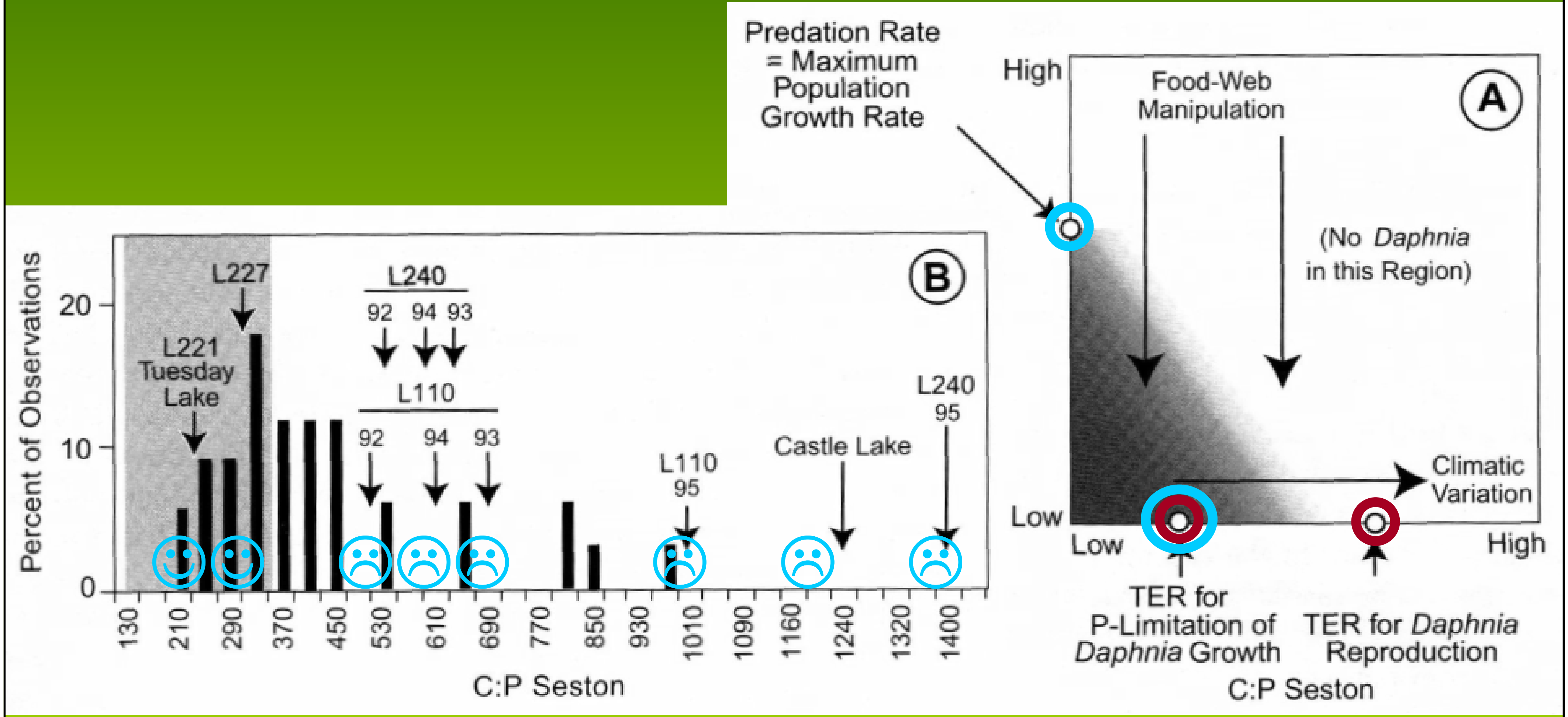




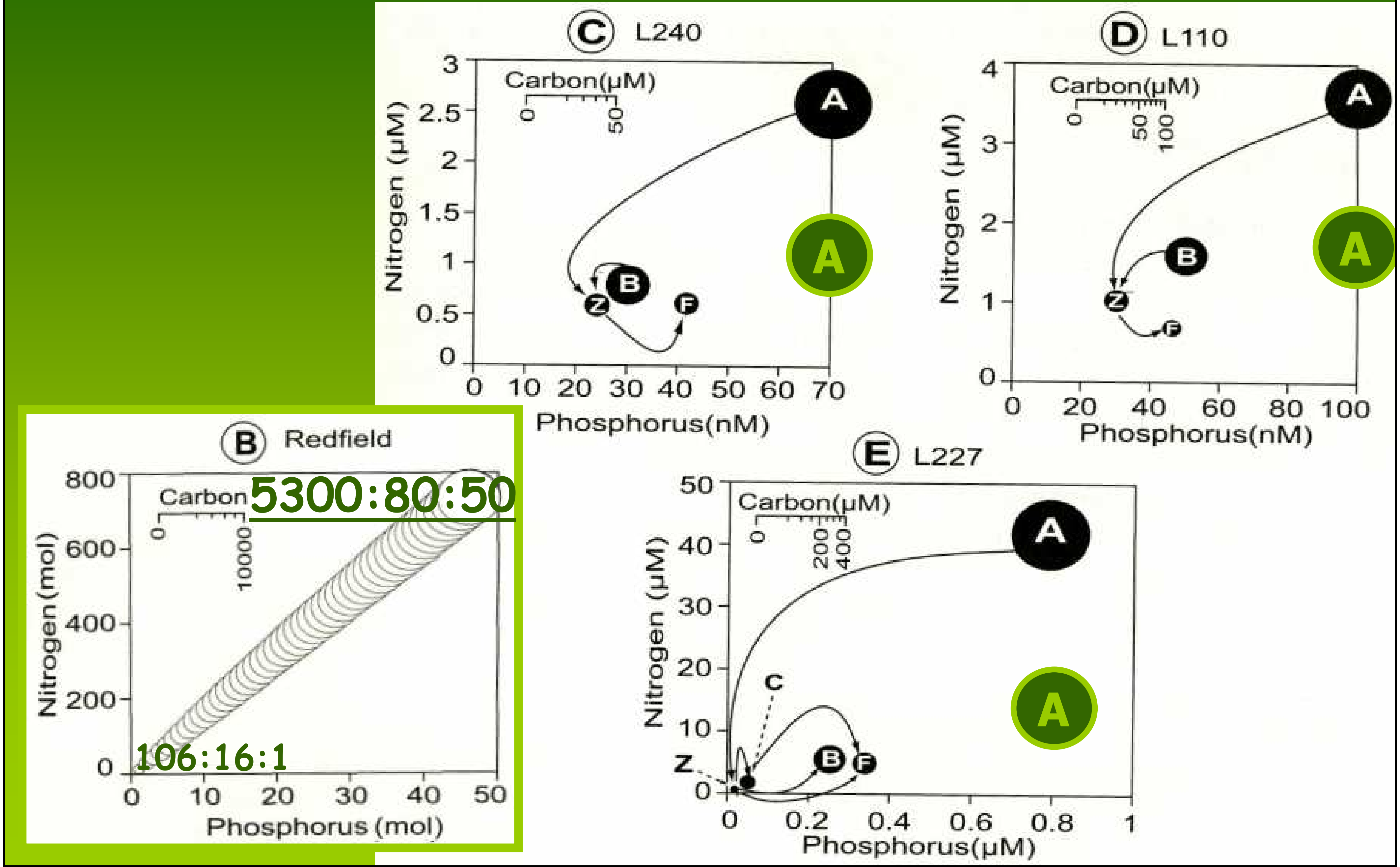
Stechiometrie **potravních sítí**

aneb stechiometrie (ne/úspěšné) **biomanipulace**

Cascading **T**rophic **I**nteractions (**CTI**)



Stechiometrie ekosystémů

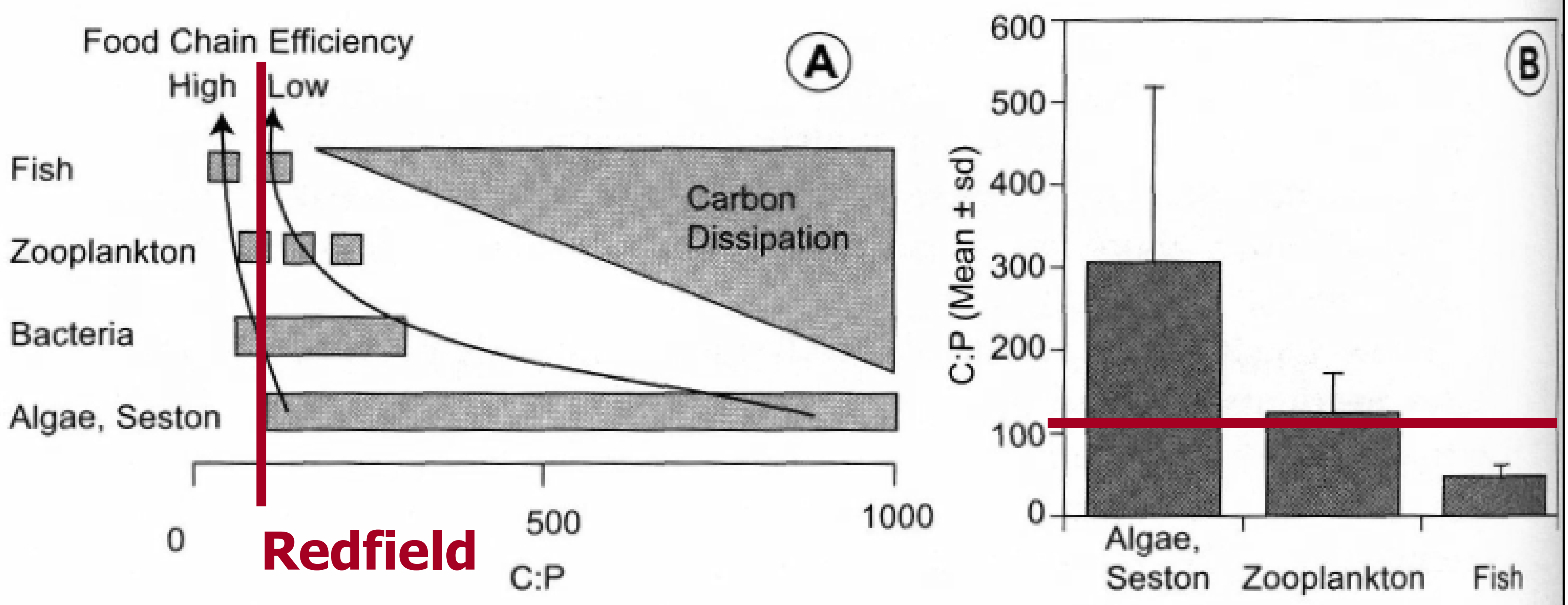


5300:80:50

106:16:1

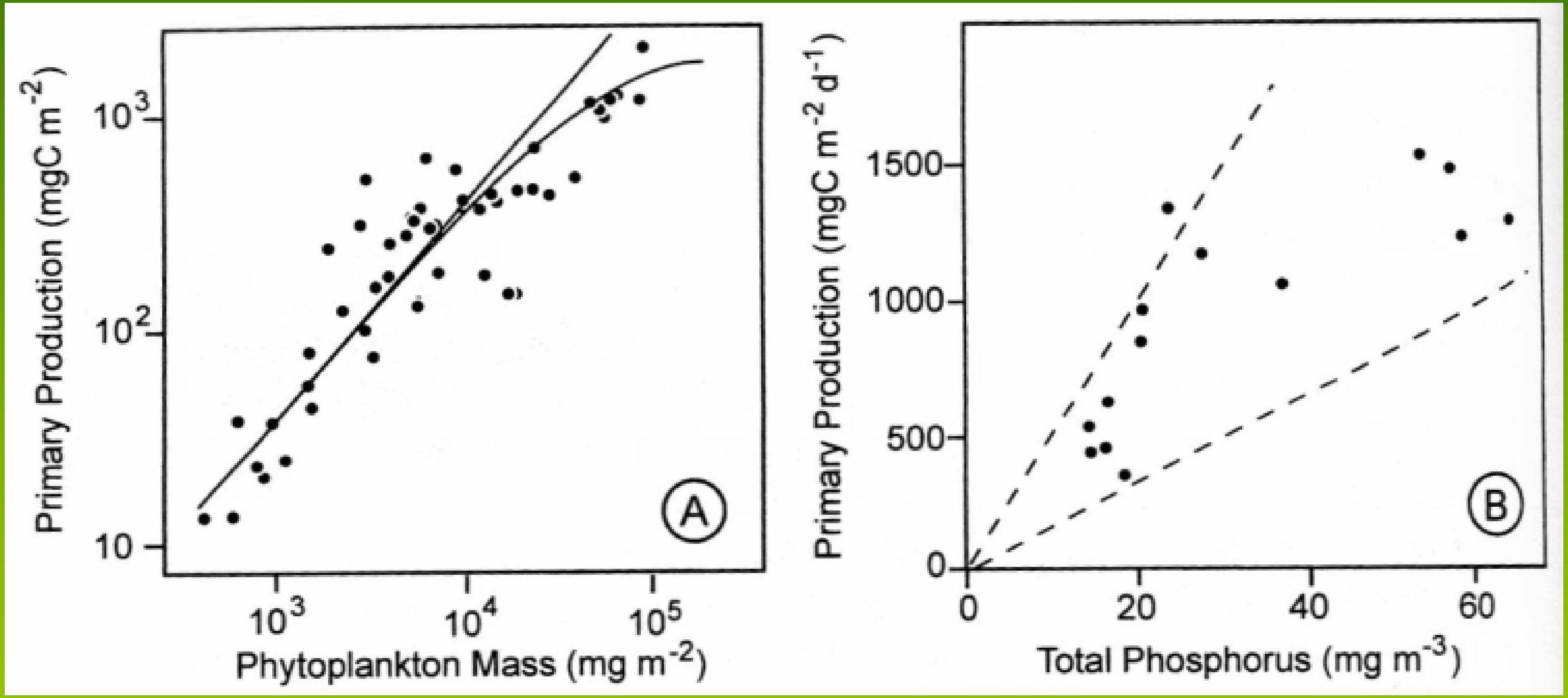
Stechiometrie ekosystémů

Trofické úrovně (**GGE$_C$**) = **disipace <u>uhlíku + energie</u> !**



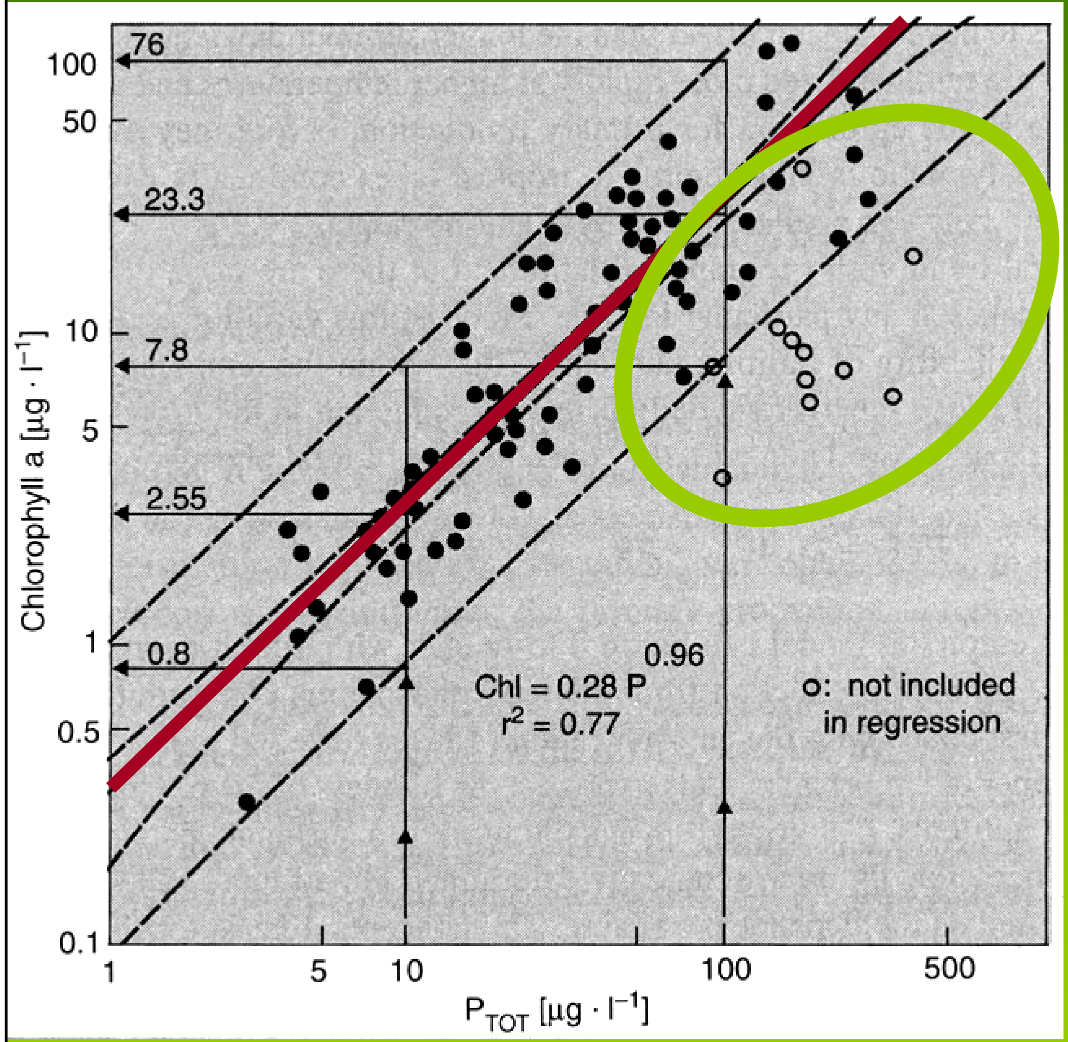
Stechiometrie ekosystémů

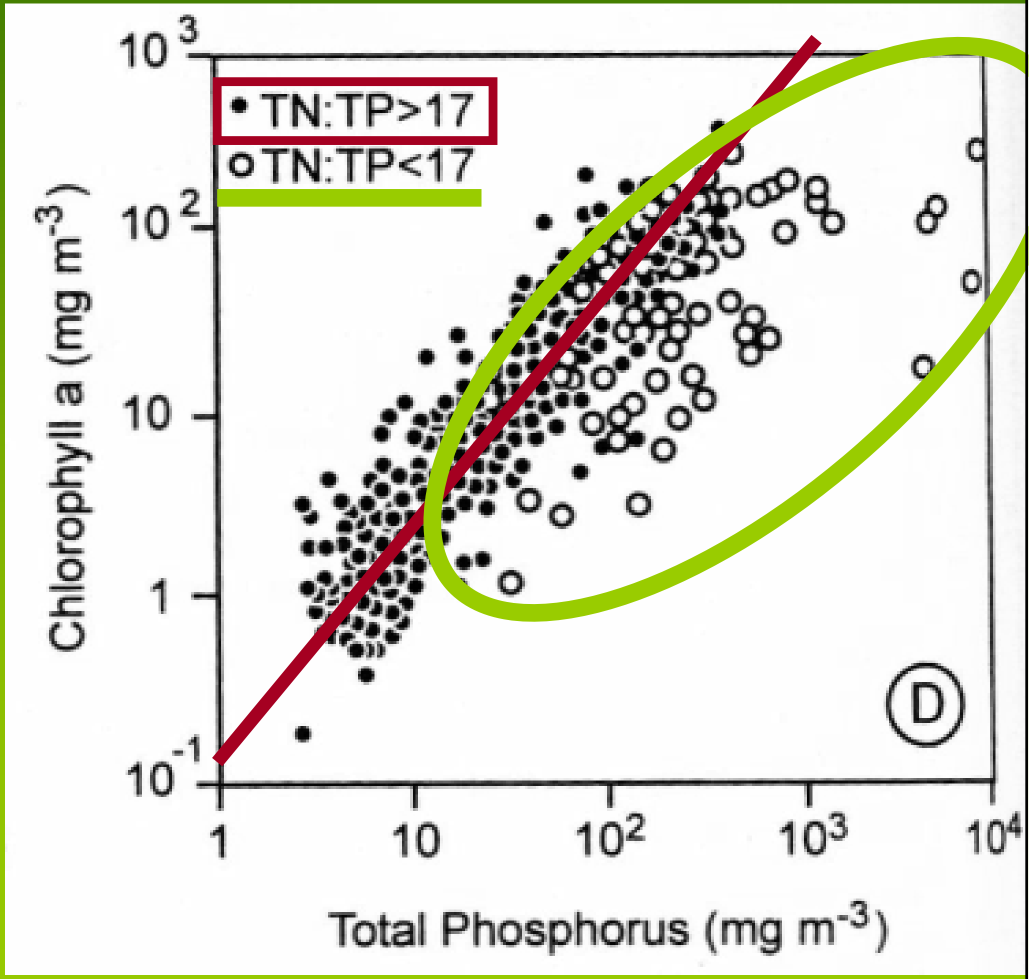
Trofie jezer a (stechiometrie) **eutrofizace**



Stechiometrie ekosystémů

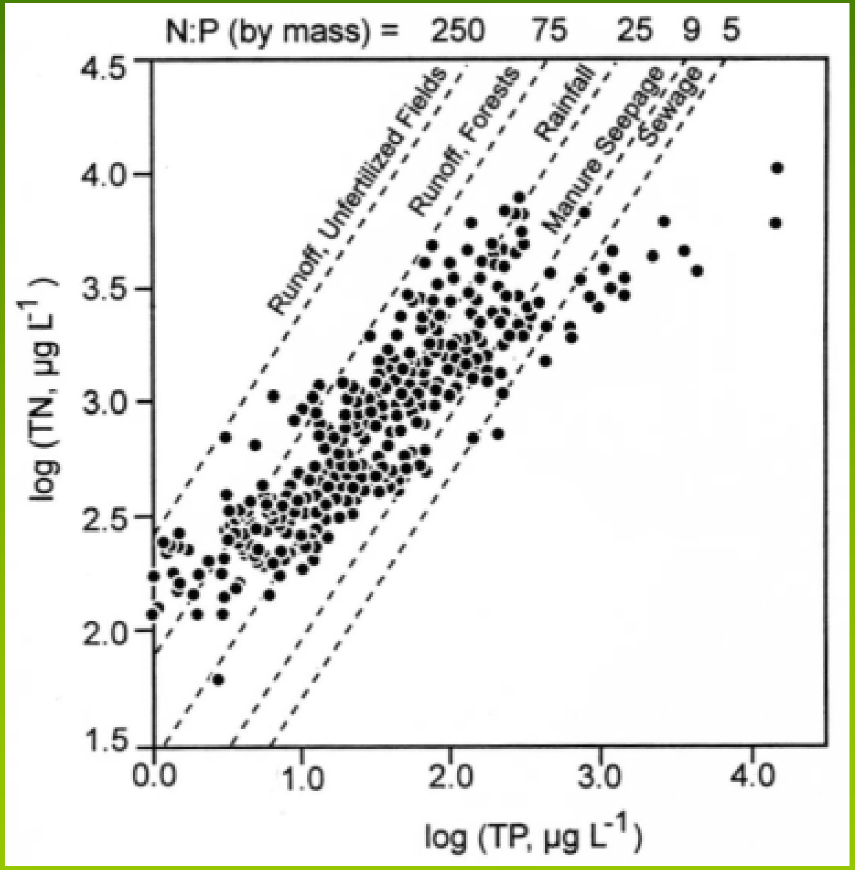
Model OECD (Vollenweider): vztah chlorofyl–TP





Stechiometrie ekosystémů

Antropogenní vlivy = hnojení a eutrofizace

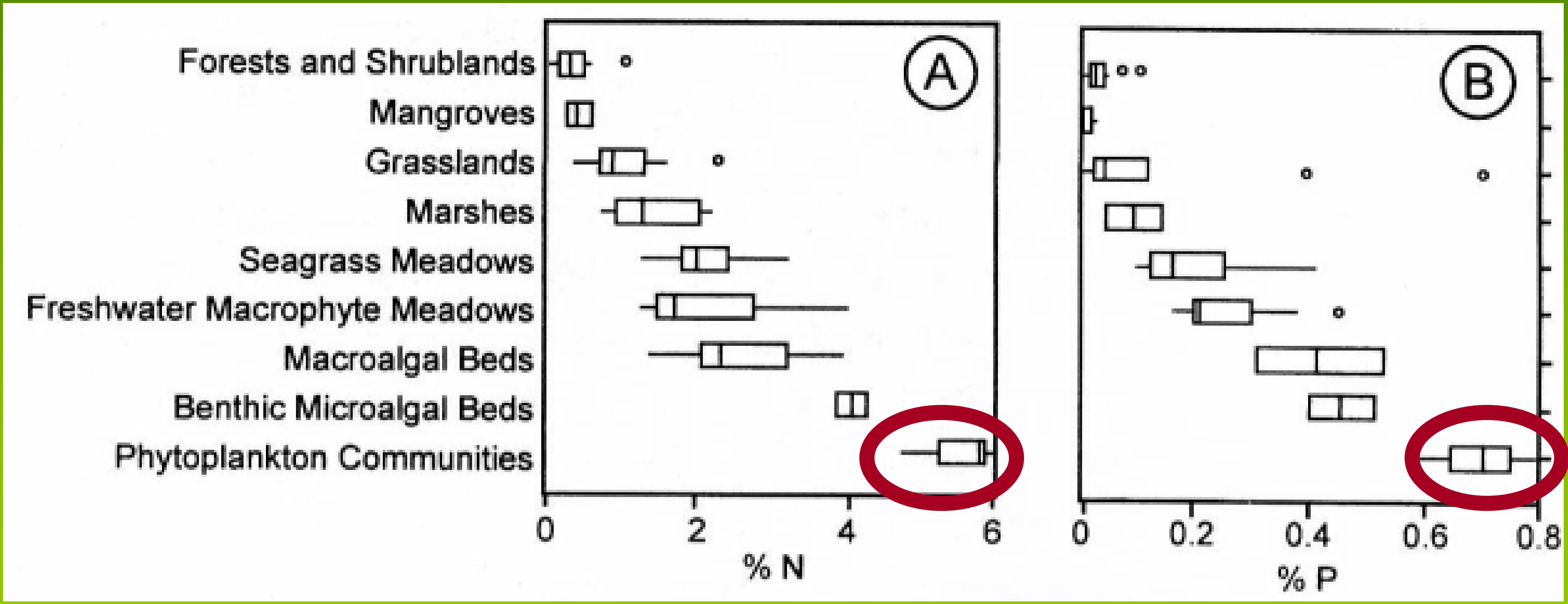


„Lidská činnost mění krajinu i planetu
v jeden velký exktrement…“

Stechiometrie ekosystémů – produktivita ?

Rozdíly stechiometrie terestrických a vodních producentů

Terestr. ekosystém: **vysoký C:N:P = velká (strukturní !) biomasa**

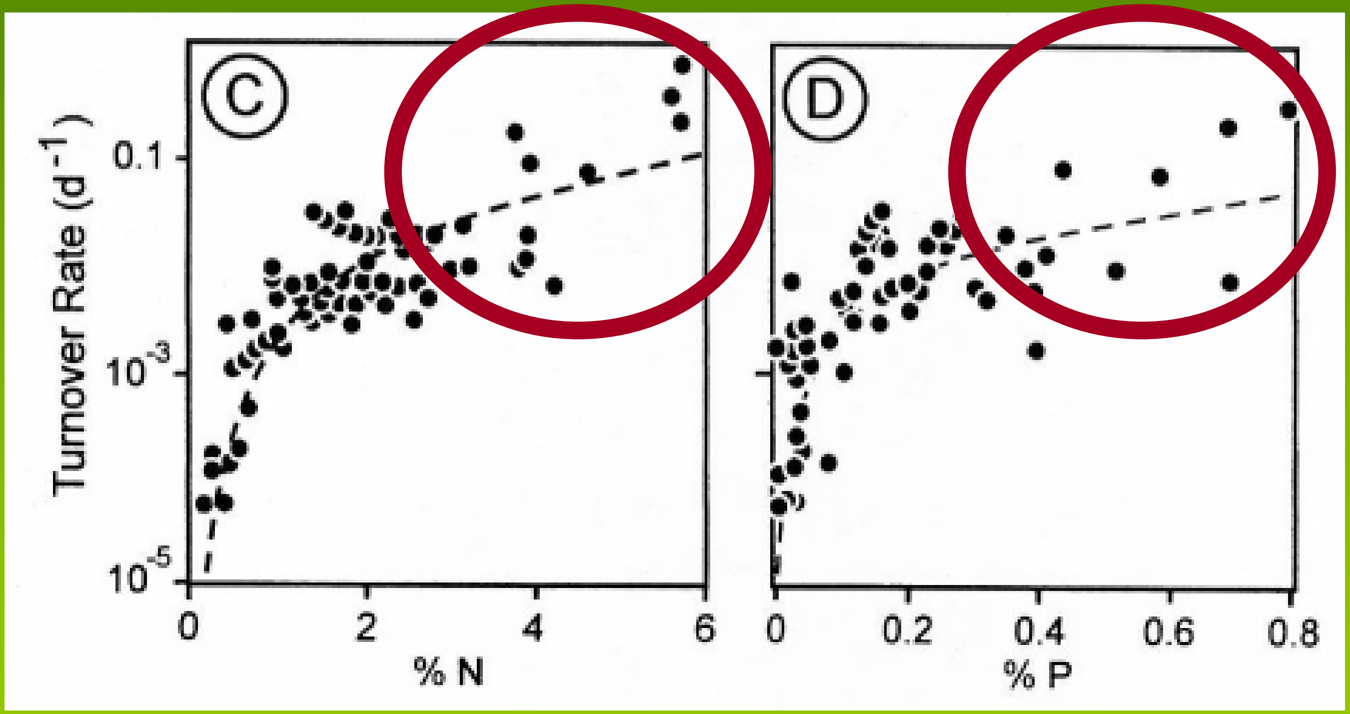


Vodní ekosystém: **nizký C:N:P = malá biomasa, vysoká produkce !**

Stechiometrie ekosystémů – produktivita ?

Rozdíly stechiometrie terestrických a vodních producentů

Terestr. ekosystém: **vysoký C:N:P = velká (strukturní !) biomasa**



Vodní ekosystém: **nizký C:N:P = malá biomasa, vysoká produkce !**

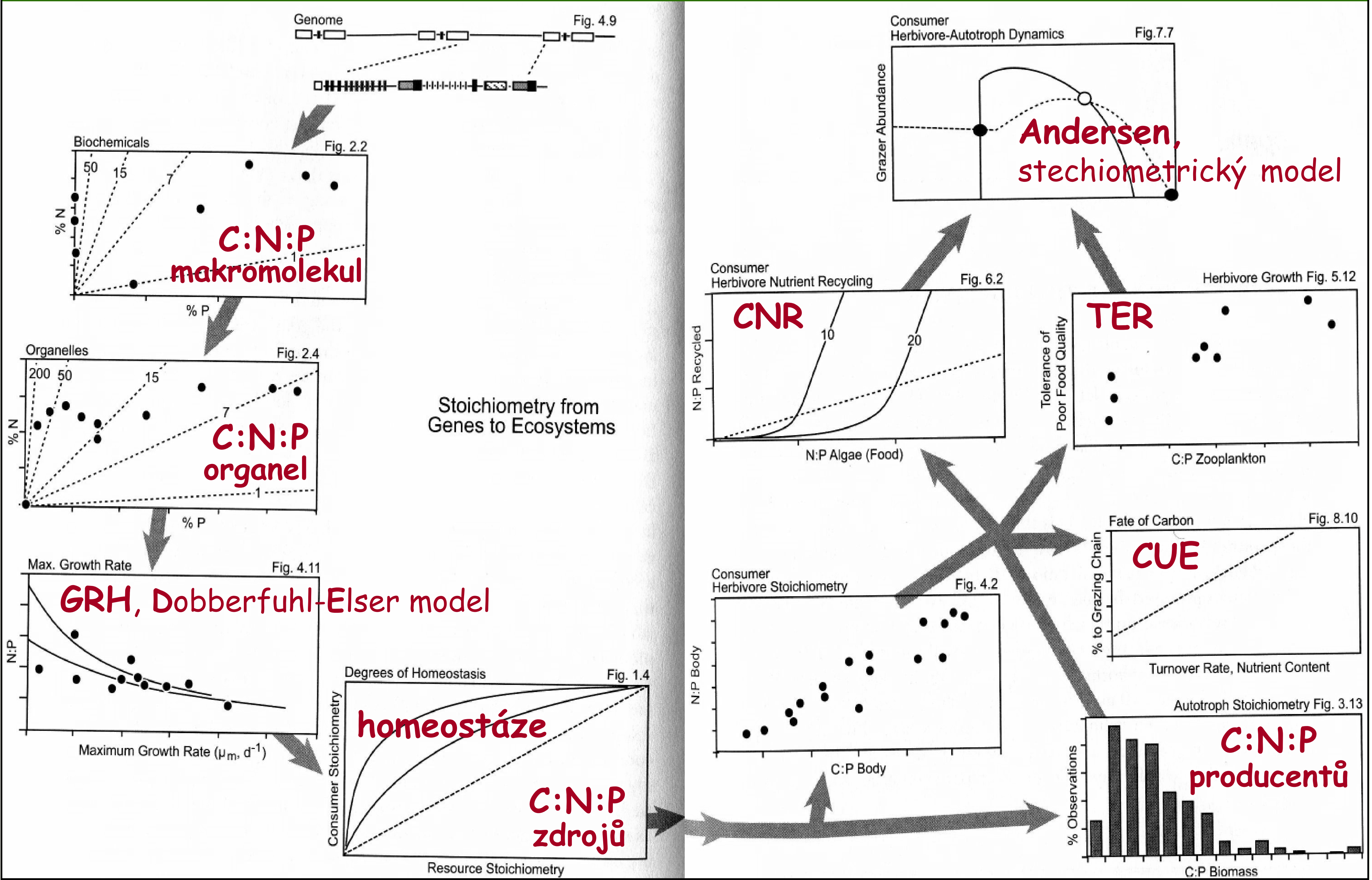
Stechiometrie ekosystémů – CUE

Carbon **U**se **E**fficiency – stechiometrie účinnosti produkce

vysoká variabilita CUE mezi jezery

	George	Chad	Lanao	Malawi	Tanganyika
GPP (g O_2 m^{-2} d^{-1})	**11.1**	**4.0**	**8.7**	**3.1**	**3.5**
NPP (g C_2 m^{-2} d^{-1})	**1.5**	**1.0**	**1.7**	**0.7**	**0.8**
Fish yiled (kg ha^{-1} y^{-1})	**136**	**14**	**60**	**40**	**125**
CUE (% annual PP)	**0.25**	**0.038**	**0.097**	**0.16**	**0.43**

Ekologická stechiometrie – syntéza



C:N:P makromolekul

C:N:P organel

GRH, Dobberfuhl-Elser model

homeostáze

C:N:P zdrojů

Andersen, stechiometrický model

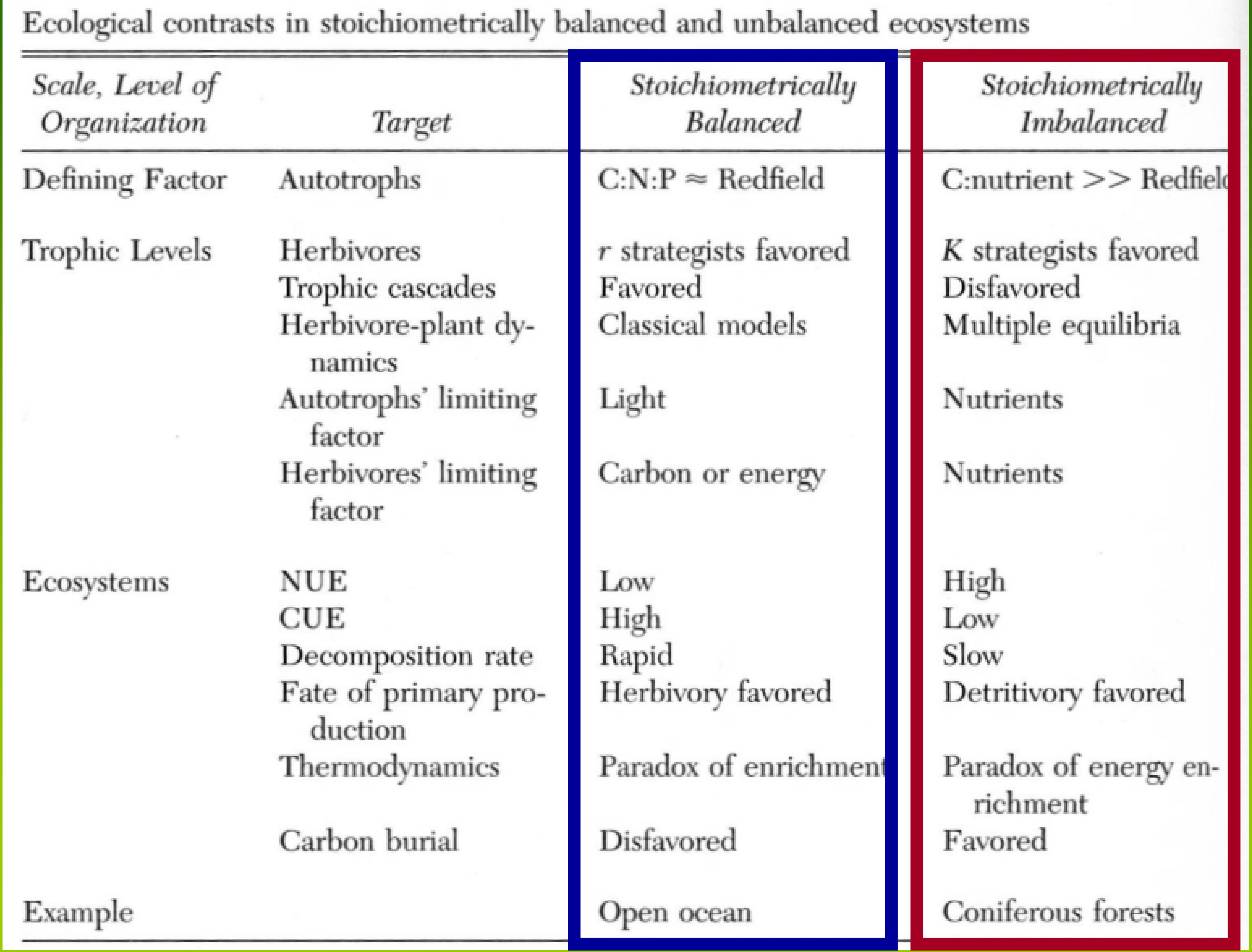
CNR

TER

CUE

C:N:P producentů

Ekologická stechiometrie – syntéza



Ecological contrasts in stoichiometrically balanced and unbalanced ecosystems

Scale, Level of Organization	*Target*	*Stoichiometrically Balanced*	*Stoichiometrically Imbalanced*
Defining Factor	Autotrophs	C:N:P ≈ Redfield	C:nutrient >> Redfiel
Trophic Levels	Herbivores	*r* strategists favored	*K* strategists favored
	Trophic cascades	Favored	Disfavored
	Herbivore-plant dynamics	Classical models	Multiple equilibria
	Autotrophs' limiting factor	Light	Nutrients
	Herbivores' limiting factor	Carbon or energy	Nutrients
Ecosystems	NUE	Low	High
	CUE	High	Low
	Decomposition rate	Rapid	Slow
	Fate of primary production	Herbivory favored	Detritivory favored
	Thermodynamics	Paradox of enrichment	Paradox of energy enrichment
	Carbon burial	Disfavored	Favored
Example		Open ocean	Coniferous forests

Ekologická stechiometrie – syntéza

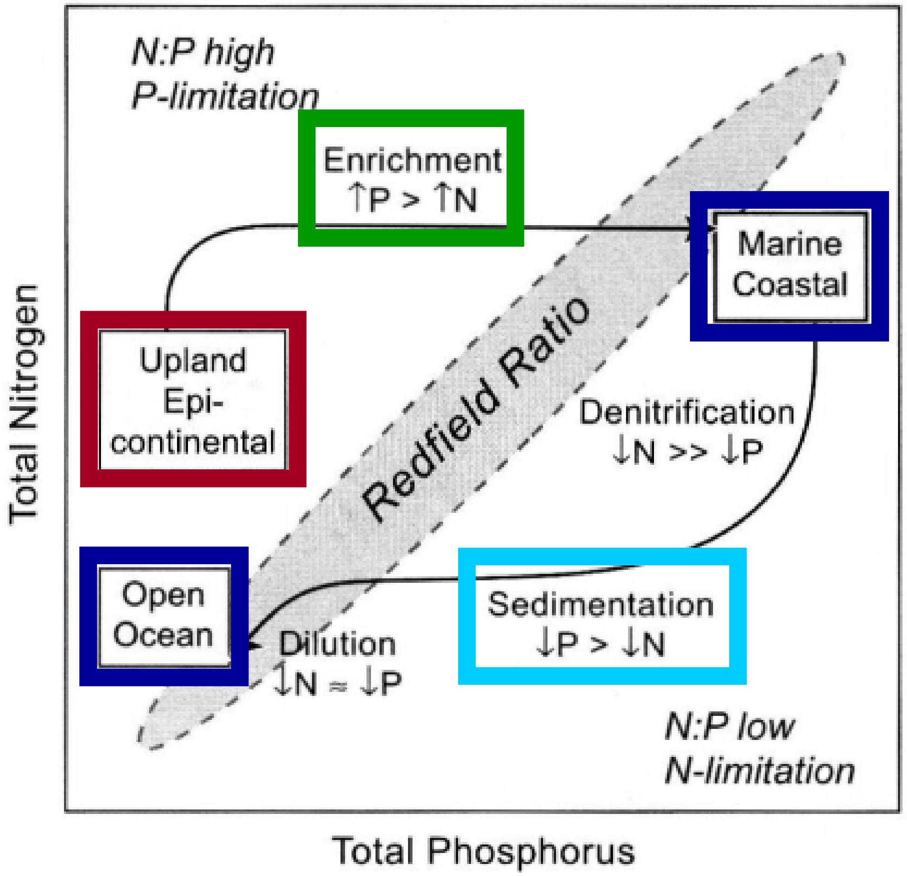
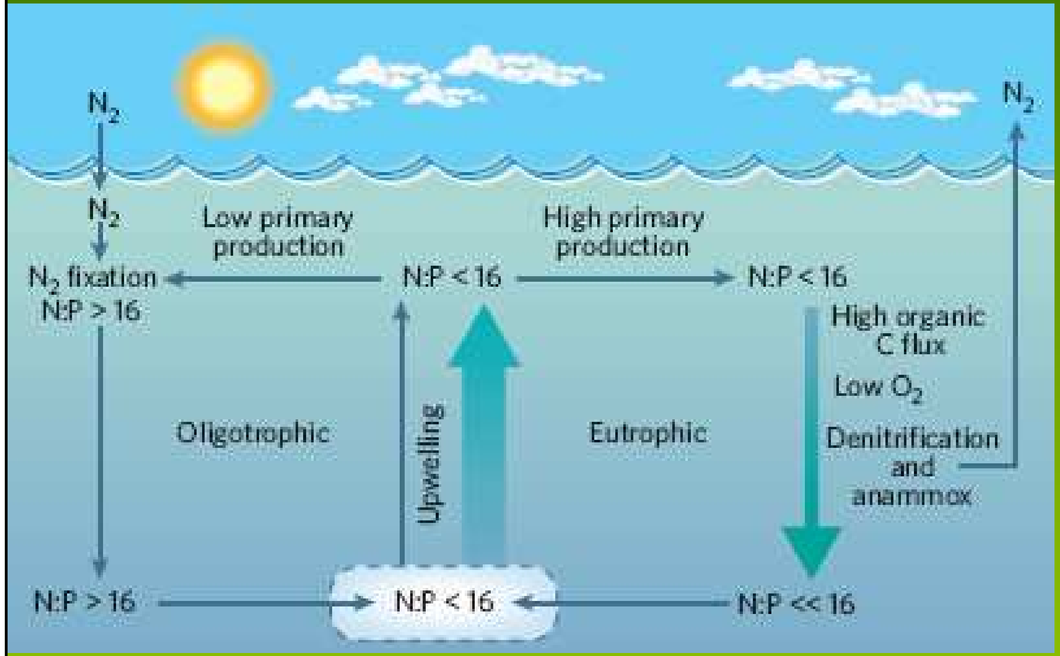
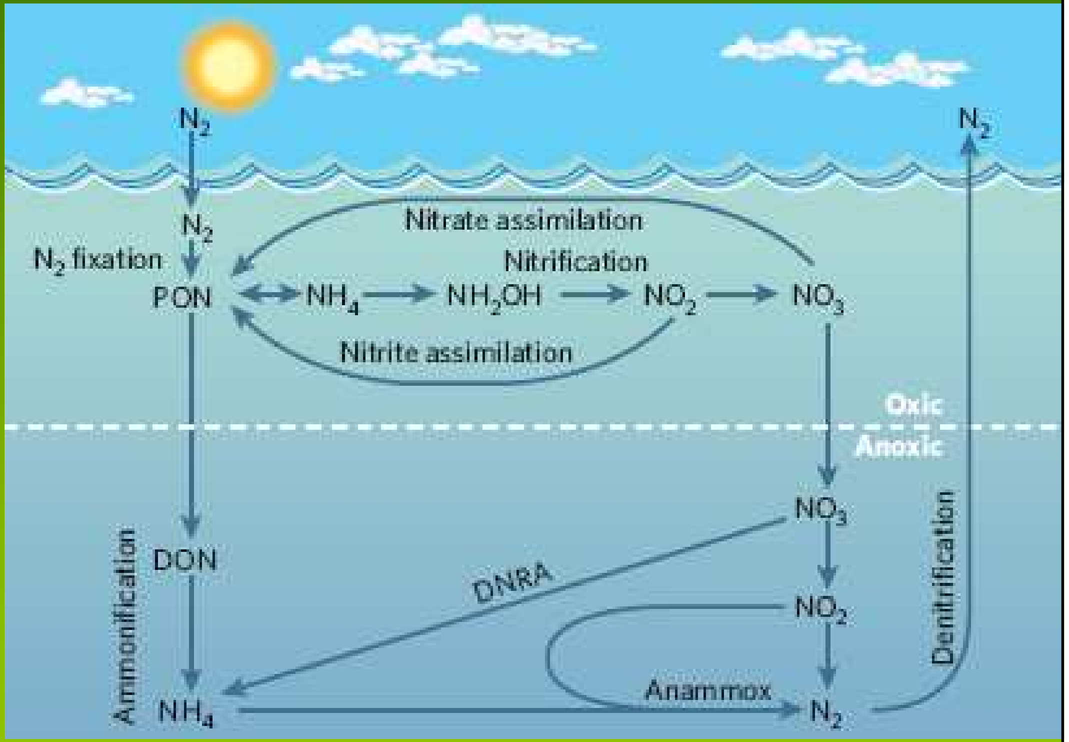


Fig. 8.5. Schematic of hypothesized shifts in total N:P balance from upland epicontinental systems (low-order streams, headwater lakes) subjected mainly to non-anthropogenic nutrient loading through enrichment producing lower N:P and emptying into marine coastal environments. There, high rates of denitrification coupled to other processes again raise N:P such that it is somewhat higher than the Redfield ratio (indicated by oval area). Moving offshore, sedimentation and dilution lower N and P, and increase N:P. For comparison to real data, see Figures 1.11 and 8.4.

Ekologická stechiometrie – syntéza

Gaia – globální ekosystém = <u>**homeostáze oceánů**</u>





Arrigo K.R.: Marine microorganisms and global nutrient cycles. **Nature 437, 349–355, 2005.**