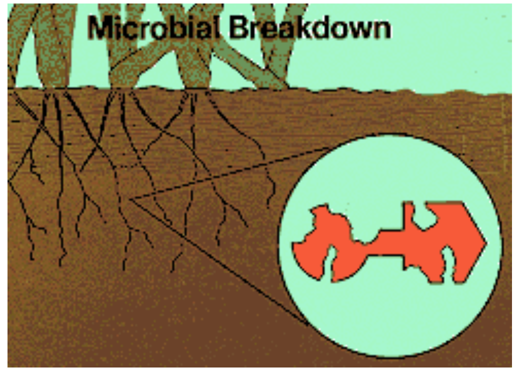
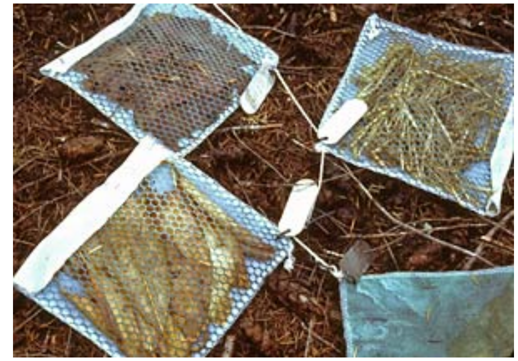
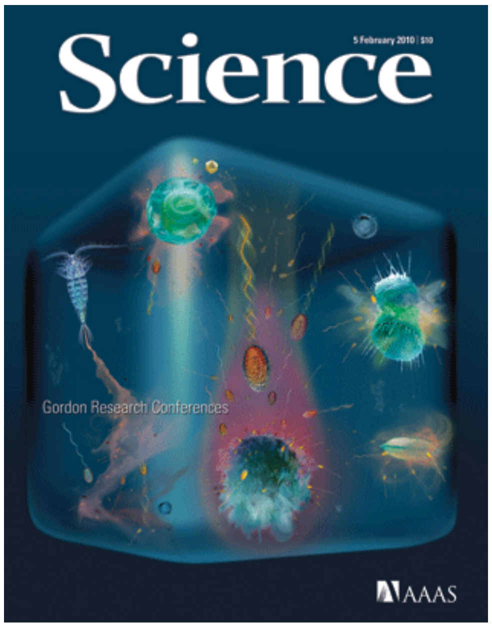
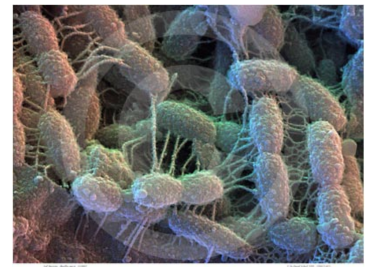


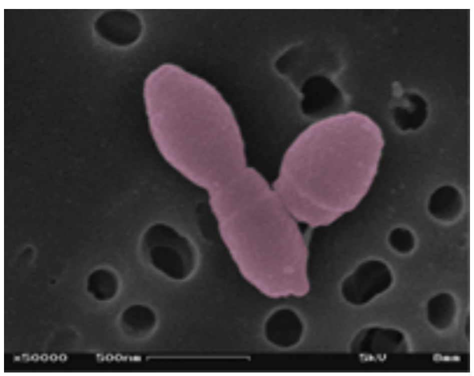


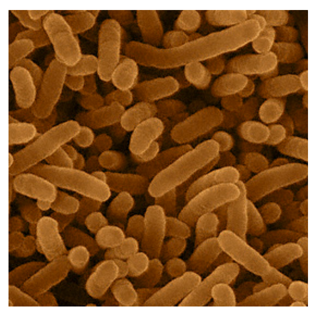


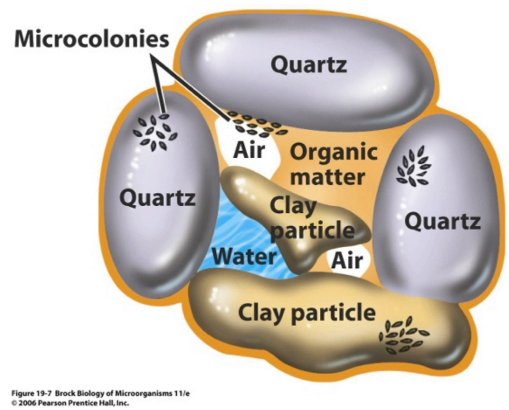
The Carbon Cycle from the Microbial Perspective, Part 2: Heterotrophy



With some material courtesy of Raina Maier



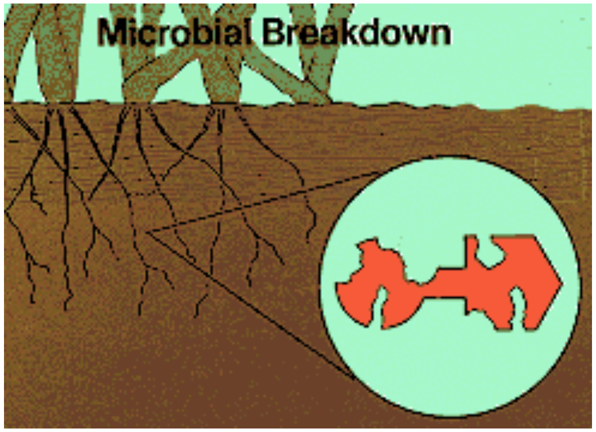




Microbes & the C Cycle: B. Heterotrophy

- Heterotrophs get their C from others by breaking down (oxidizing) complex (reduced) C compounds, via:
  - predation & herbivory of living tissues
  - scavenging of dead biomass
- Decomposition provides energy for microbial growth
- Releases nutrients
- Results in breakdown of OM

Microbes are master decomposers



https://courses.worldcampus.psu.edu/welcome/turf230/images/microbial

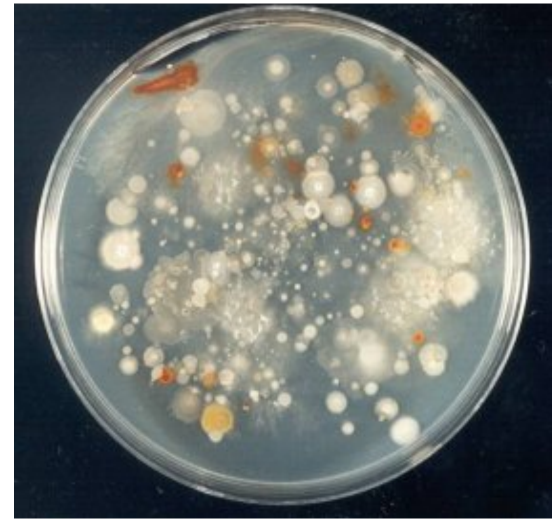
The breakdown of organic matter….

http://inkwellnotions.files.wordpress.com/2011/05/earthworm.jpg

Macrobe vs. microbe <u>decomposers</u>:

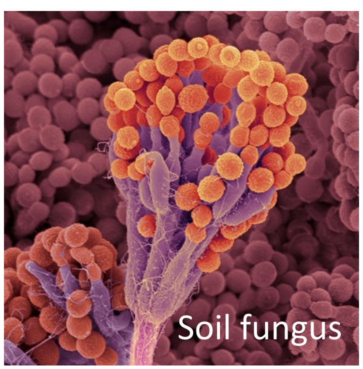
- Substrate complexity?

- Redox conditions?



What are major terrestrial (eg forest) C inputs?

William S. Currie



forces.si.edu

i. plant materials

cellulose	15 – 60%
hemicellulose	10-30%
lignin	5- 30%
protein/nucleic acids	2-15%

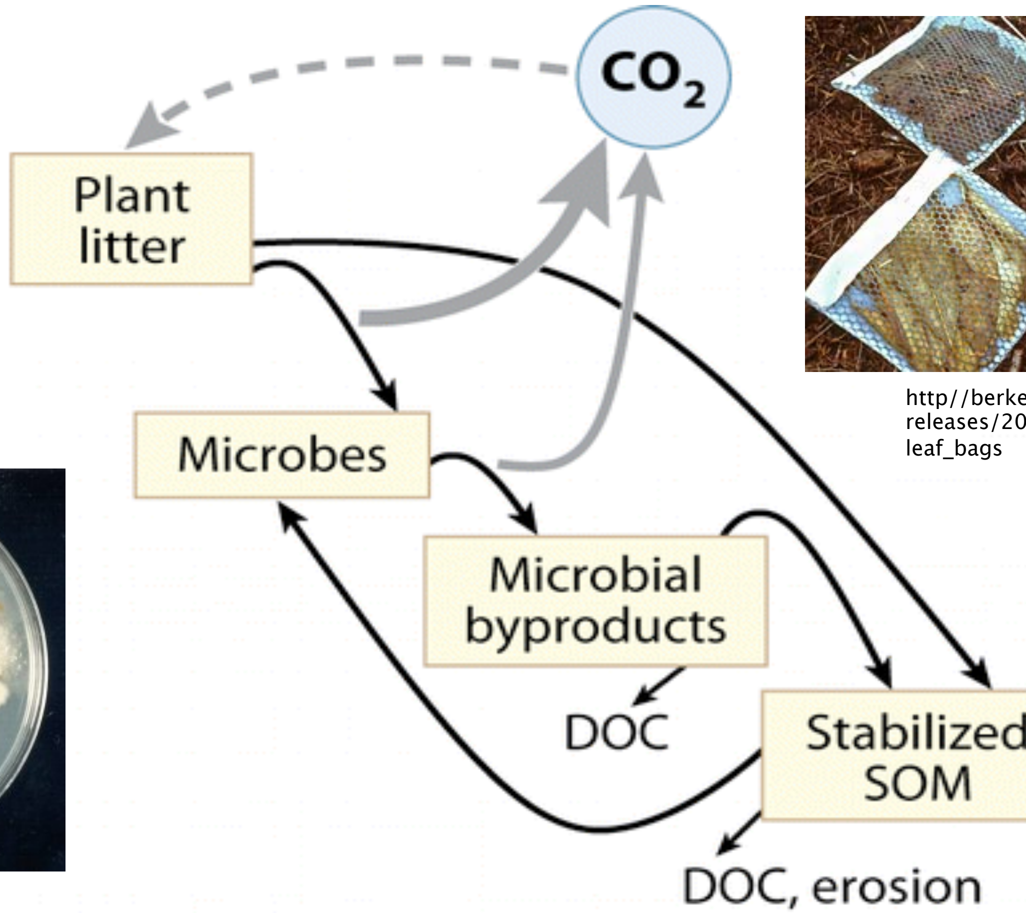
ii. fungal cell walls/arthropods

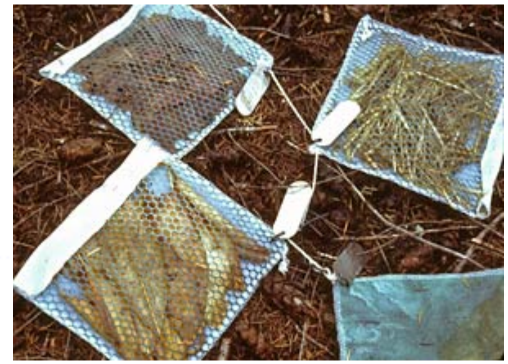
chitin

http//berkeley.edu/news/media/releases/2007/01/images/leaf_bags

TERRESTRIAL HETEROTROPHY & DECOMPOSITION

William S. Currie

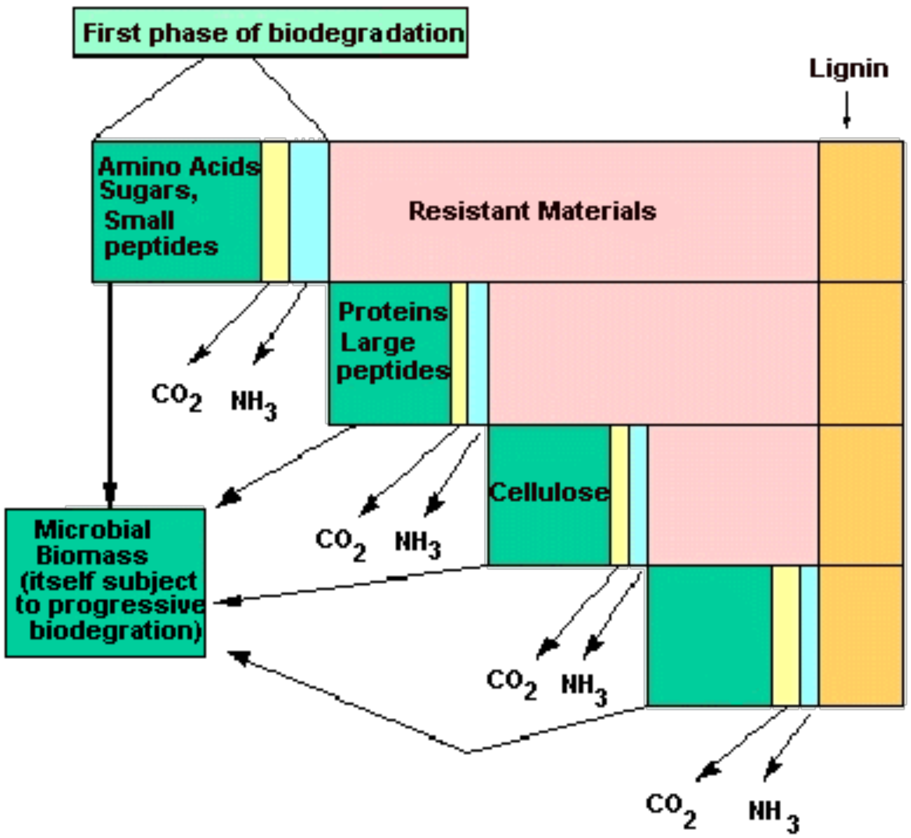




http//berkeley.edu/news/media/releases/2007/01/images/leaf_bags

AR Trumbore S. 2009.
Annu. Rev. Earth Planet. Sci. 37:47–66

Decomposition of plant materials in soil:



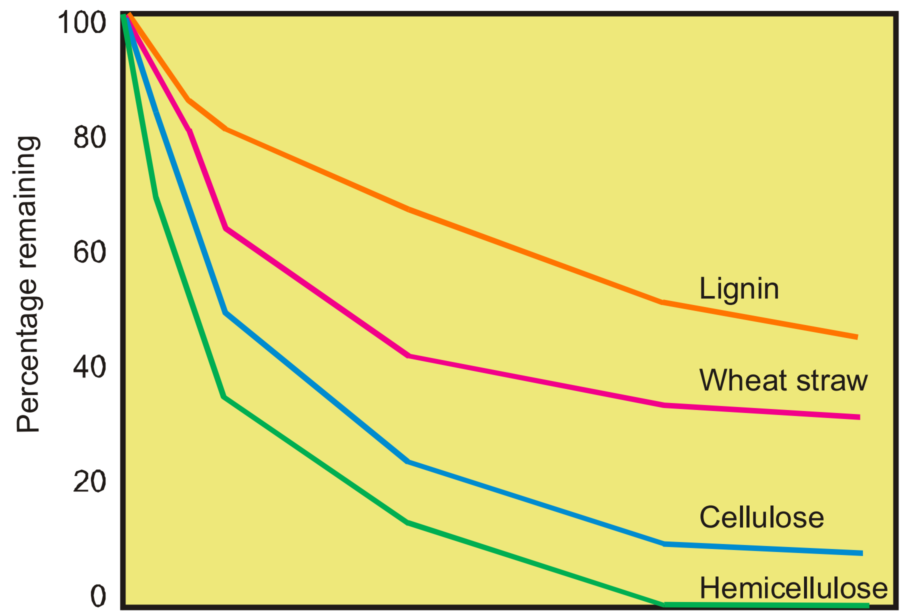
Not all fractions of SOM are degraded at the same rate.

Depends on:

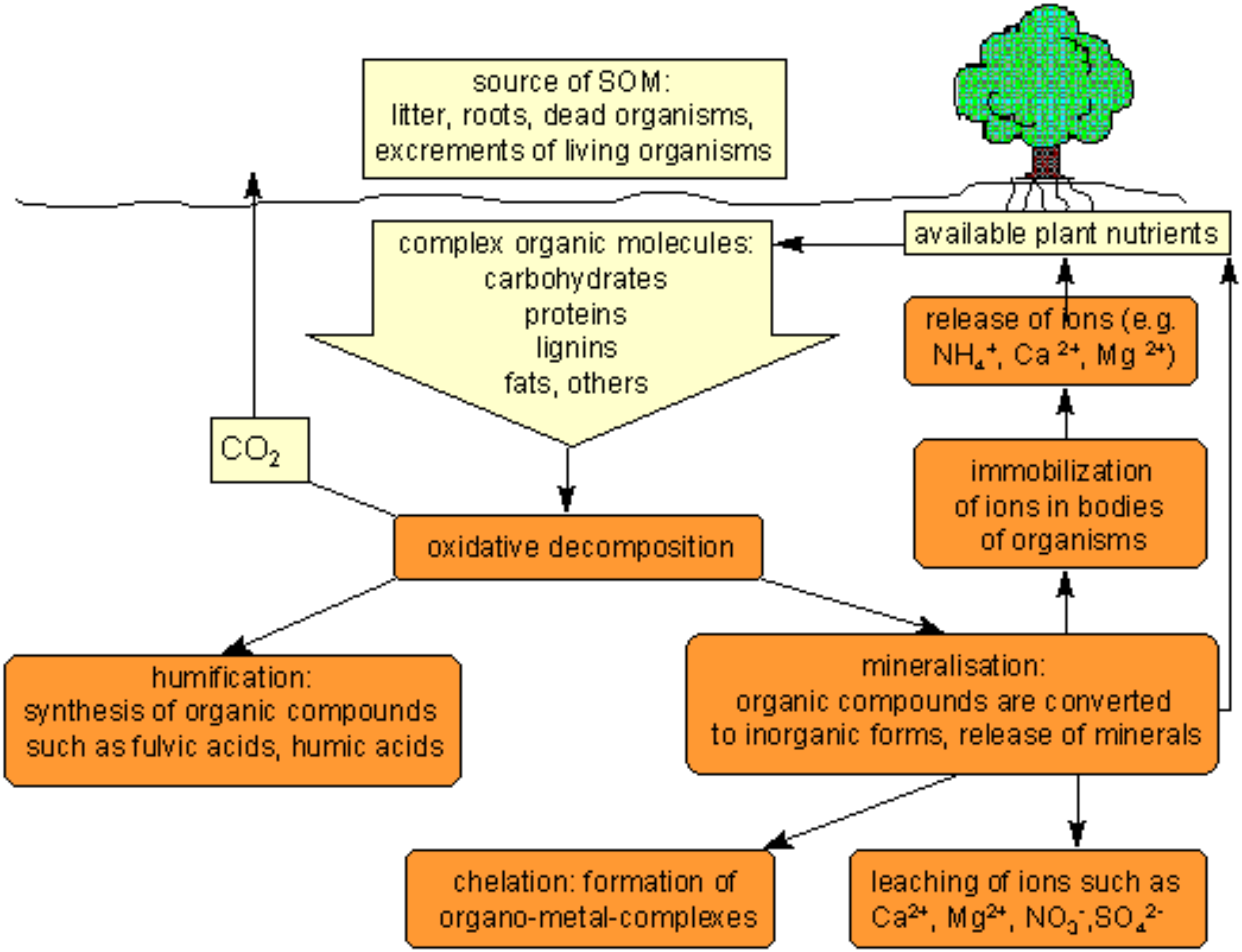
- **energy available from consumption of each**
- **the diversity (etc) of microbes performing each step**
- **breakdown of recalcitrant stuff can be "primed" by juicier C**

- **For more complex polymers i.e. lignin a variety of oxidizing enzymes are used.**

- **Lignin due to its complexity is generally degraded much more slowly than cellulose or hemicellulose.**



What sorts of other things does soil C structure impact?



source of SOM:
litter, roots, dead organisms,
excrements of living organisms
complex organic molecules:
carbohydrates
proteins
lignins
fats, others
CO_2
available plant nutrients
release of ions (e.g. NH_4^+, Ca^{2+}, Mg^{2+})
immobilization of ions in bodies of organisms
oxidative decomposition
humification:
synthesis of organic compounds such as fulvic acids, humic acids
mineralisation:
organic compounds are converted to inorganic forms, release of minerals
chelation: formation of organo-metal-complexes
leaching of ions such as Ca^{2+}, Mg^{2+}, NO_3^-, SO_4^{2-}

Aerobic vs. anaerobic heterotrophy?

The Basic Aerobic Reaction is:

$$C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_20$$

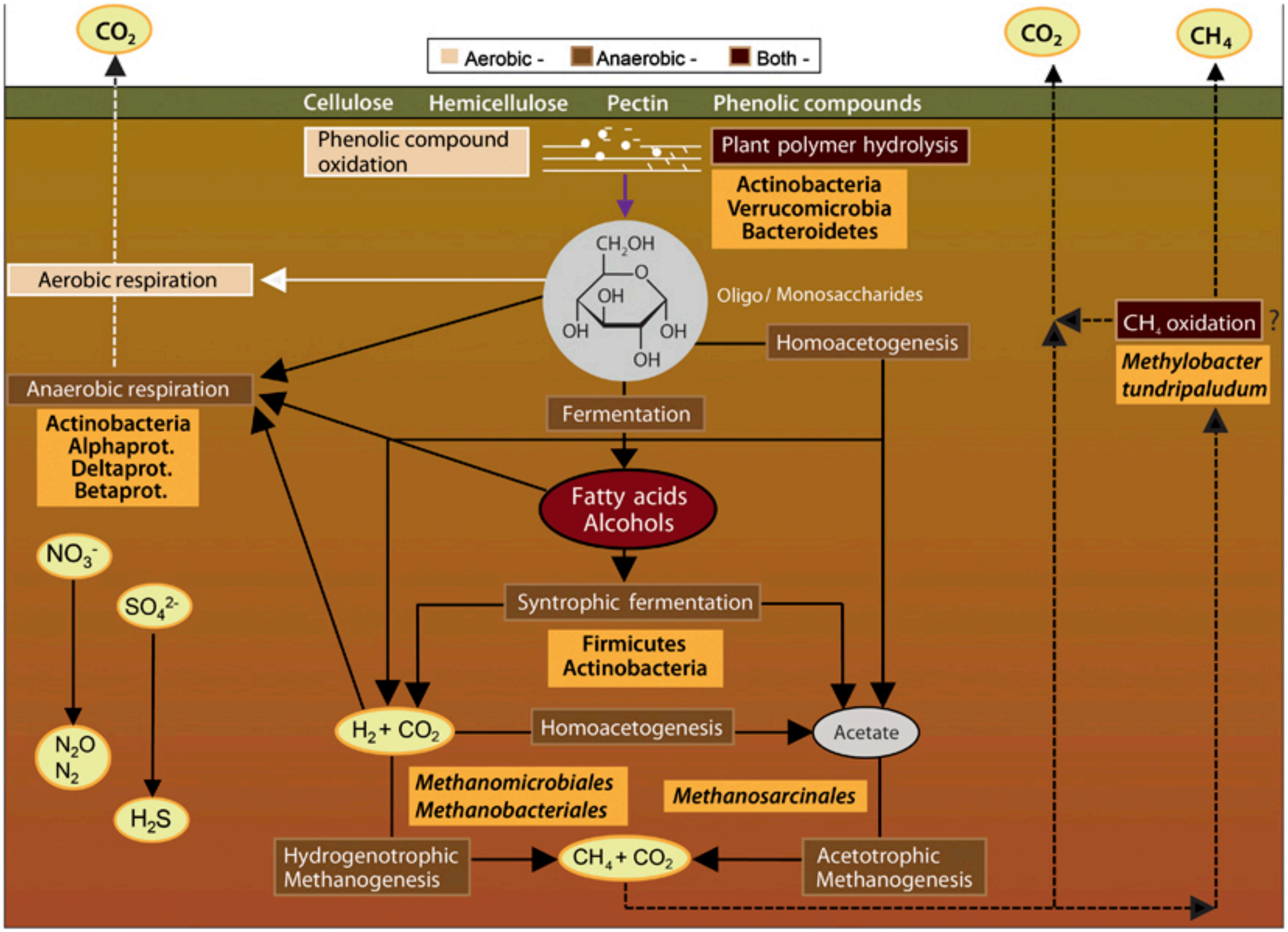
Anaerobic End Products from Glucose

Possible Anaerobic Fermentations of Glucose

Acetate	$C_6H_{12}O_6 \rightarrow 3CH_3COO^- + 3H^+$
Propionate, acetate, H_2	$C_6H_{12}O_6 \rightarrow CH_3CH_2COO^- + CH_3COO^- + 2H^+ + CO_2 + H_2$
Butyric, H_2	$C_6H_{12}O_6 \rightarrow CH_3CH_2CH_2COOH + 2CO_2 + 2H_2$
Ethanol	$C_6H_{12}O_6 \rightarrow 2CH_3CH_2OH + 2CO_2$
Lactate	$C_6H_{12}O_6 \rightarrow 2CH_3CH(OH)COO^- + 2H^+$
Methanol	$C_6H_{12}O_6 + 2H_20 \rightarrow 4CH_3OH + 2CO_2$
Methane	$C_6H_{12}O_6 \rightarrow 3CH_4 + 3CO_2$

http://www.magicsoil.com/MSREV2/oxygen_realities_in_compost.htm

Actual *in situ* decomposition is a mosaic of aerobic & anaerobic processes.



"Schematic overview of the main degradation pathways of plant polymers in the high-Arctic peatlands of Svalbard. The pathways are divided into three categories; aerobic (beige), anaerobic (light brown) and processes occurring under both conditions (dark brown). Key microbial taxa for the different degradation steps are presented (orange boxes). The figure is adapted from Figure 1 in (Conrad, 1999)."

Tveit et al 2012 ISME J

Decomposition is spatially and temporally complex

-> Changes over micrometers <-

<u>A 1-cm^3 aggregate may contain:</u>

- aerobic and anaerobic regions;
- clay, silt, and sand particles;
- plant matter in various stages of decomposition;
- a variety of invertebrates, each with its own likely-unique associated microbiota.

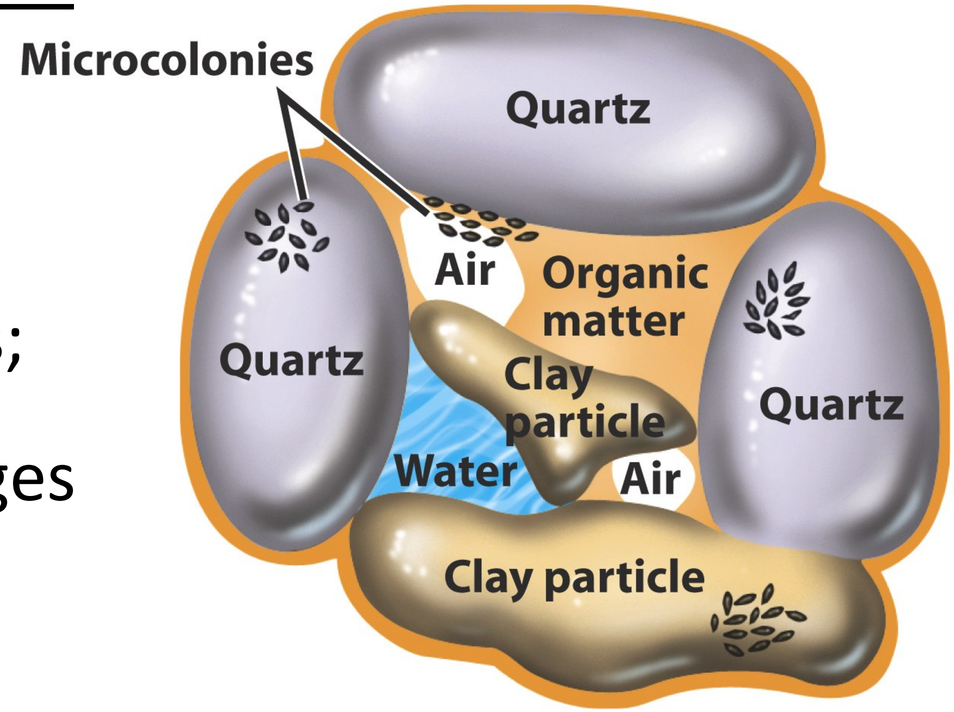
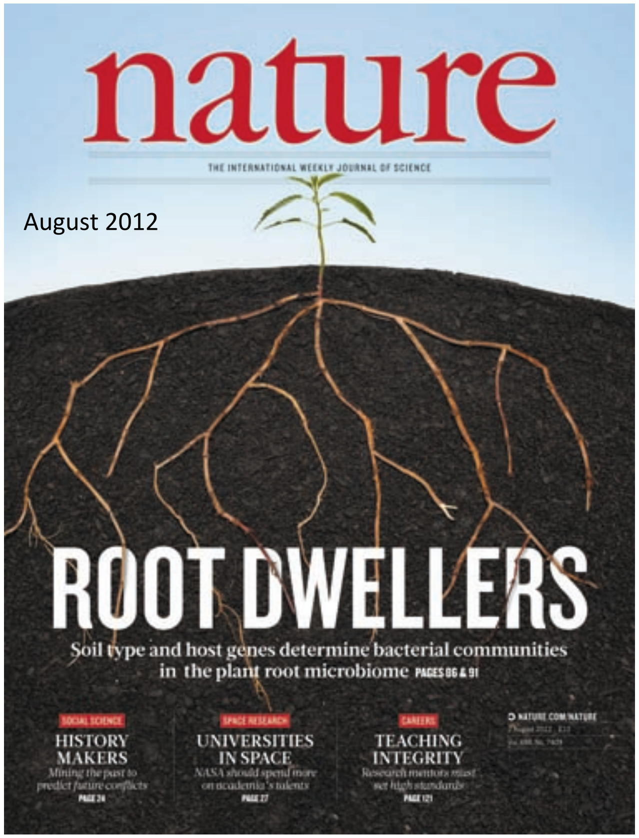
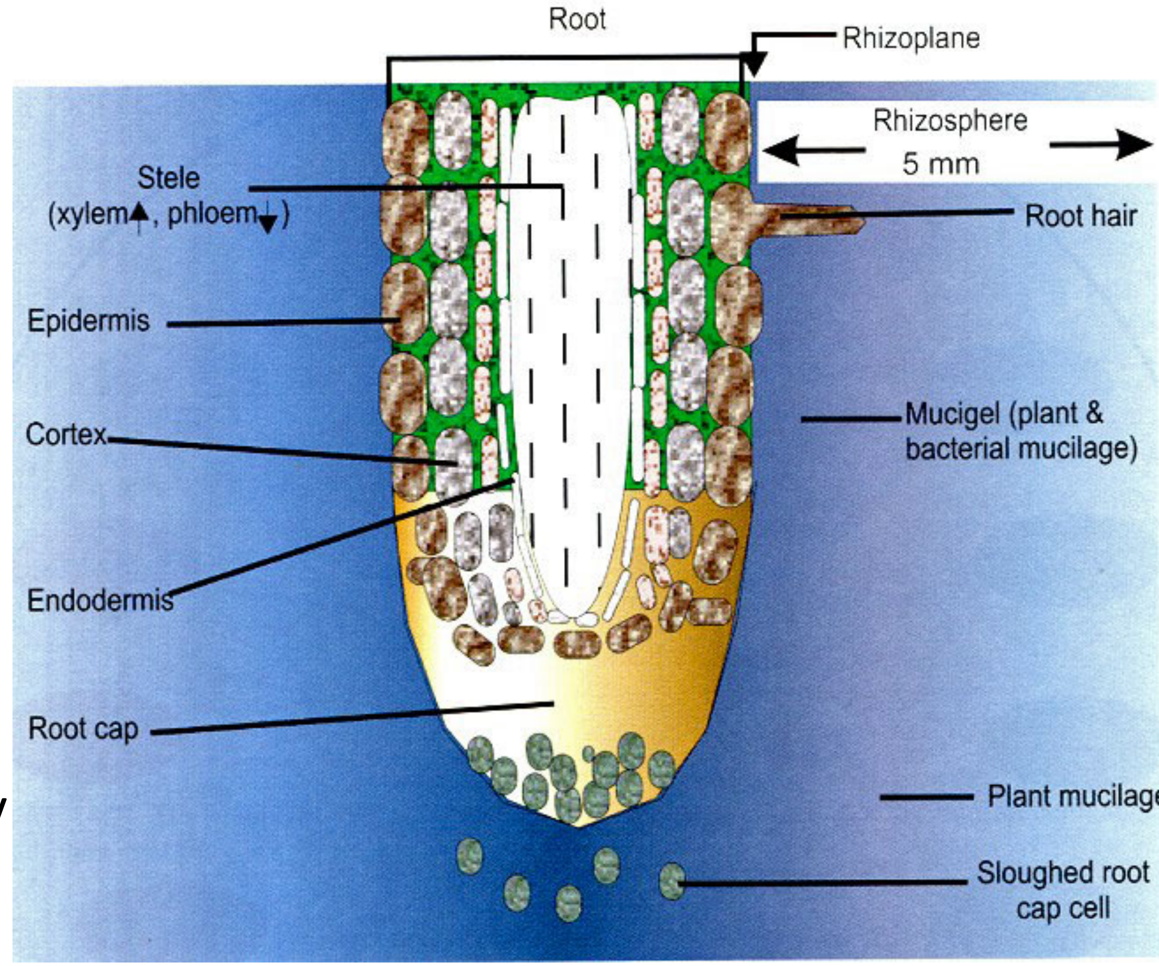


Figure 19-7 Brock Biology of Microorganisms 11/e



Oases in the soil: the Rhizosphere

"Rhizosphere" is the soil surrounding roots.



http://www.morning-earth.org/Graphic-E/BIOSPHERE/PLANTIMAGE/RHIZOSPHERE/rhizographic7.jpg

- It's like an oasis in the desert of the bulk soil
- Plants are leaky: Root exudates provide high quality C source for heterotrophs
- Rhizosphere can include N_2-fixing bacteria (more after spring break)

Special type of rhizosphere community: mycorrhizae

• Mycorrhizae (Greek for *fungus roots*) is a symbiotic (occasionally weakly pathogenic) association between a fungus and the roots of SOME plants, often includes many (uncharacterized) bacterial symbionts too.

• Mycorrhizae help scavenge nutrients from surrounding soil in exchange for a share of plant carbon.

• *Can allow plant survival in harsh and arid habitats.*

Roots of plants infected with mycorrhizae (right) vs. without (left)

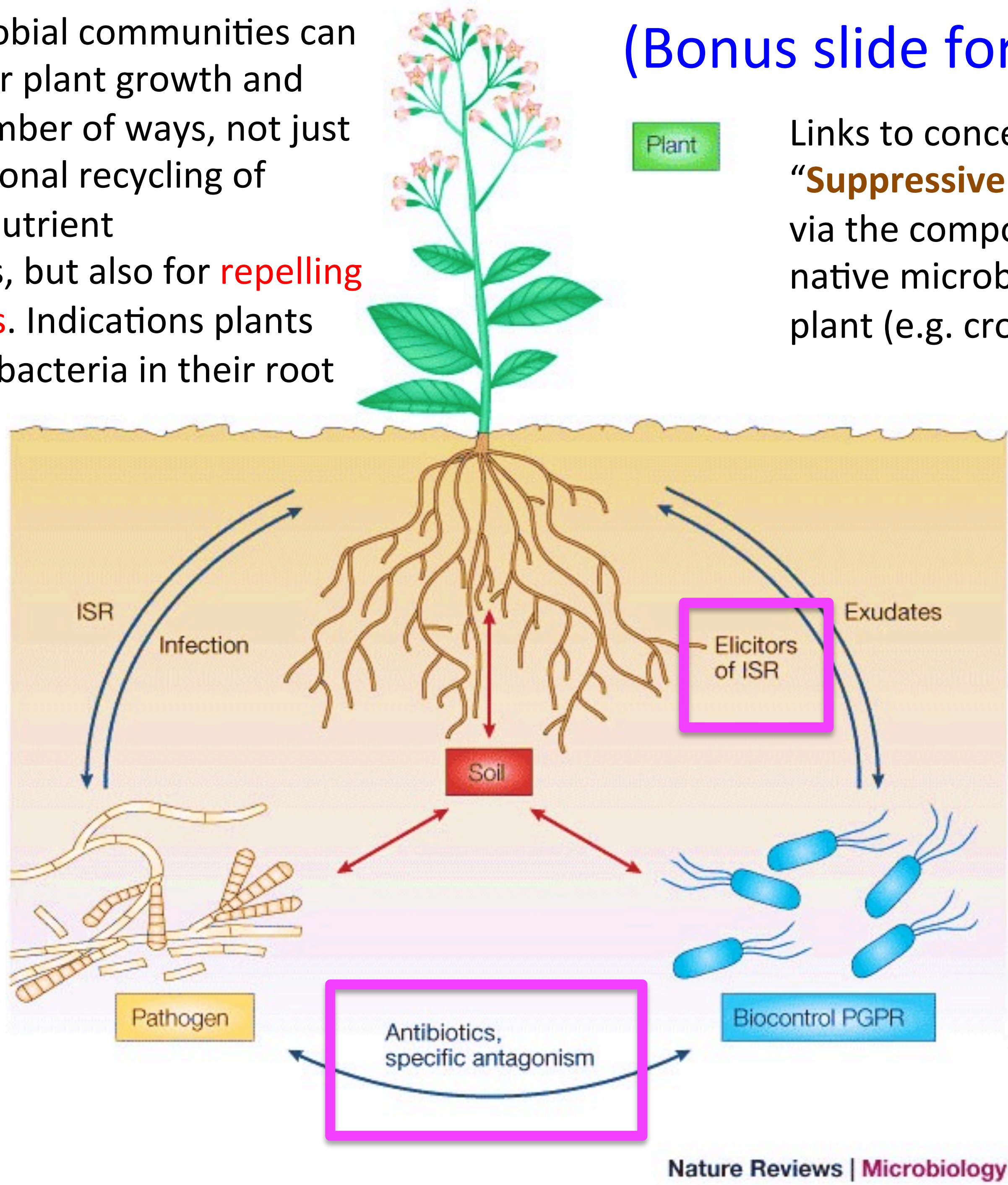
Rhizosphere = more than just mycorrhizae!! Plants without mycorrhizae <u>still have rhizosphere microbial communities</u>!

And those microbial communities can be important for plant growth and survival in a number of ways, not just via decompositional recycling of nutrients, and nutrient transformations, but also for repelling plant pathogens. Indications plants farm beneficial bacteria in their root zone…

(Bonus slide for home)

Links to concept of disease "**Suppressive Soils**", which via the composition of their native microbiota suppress plant (e.g. crop) pathogens…

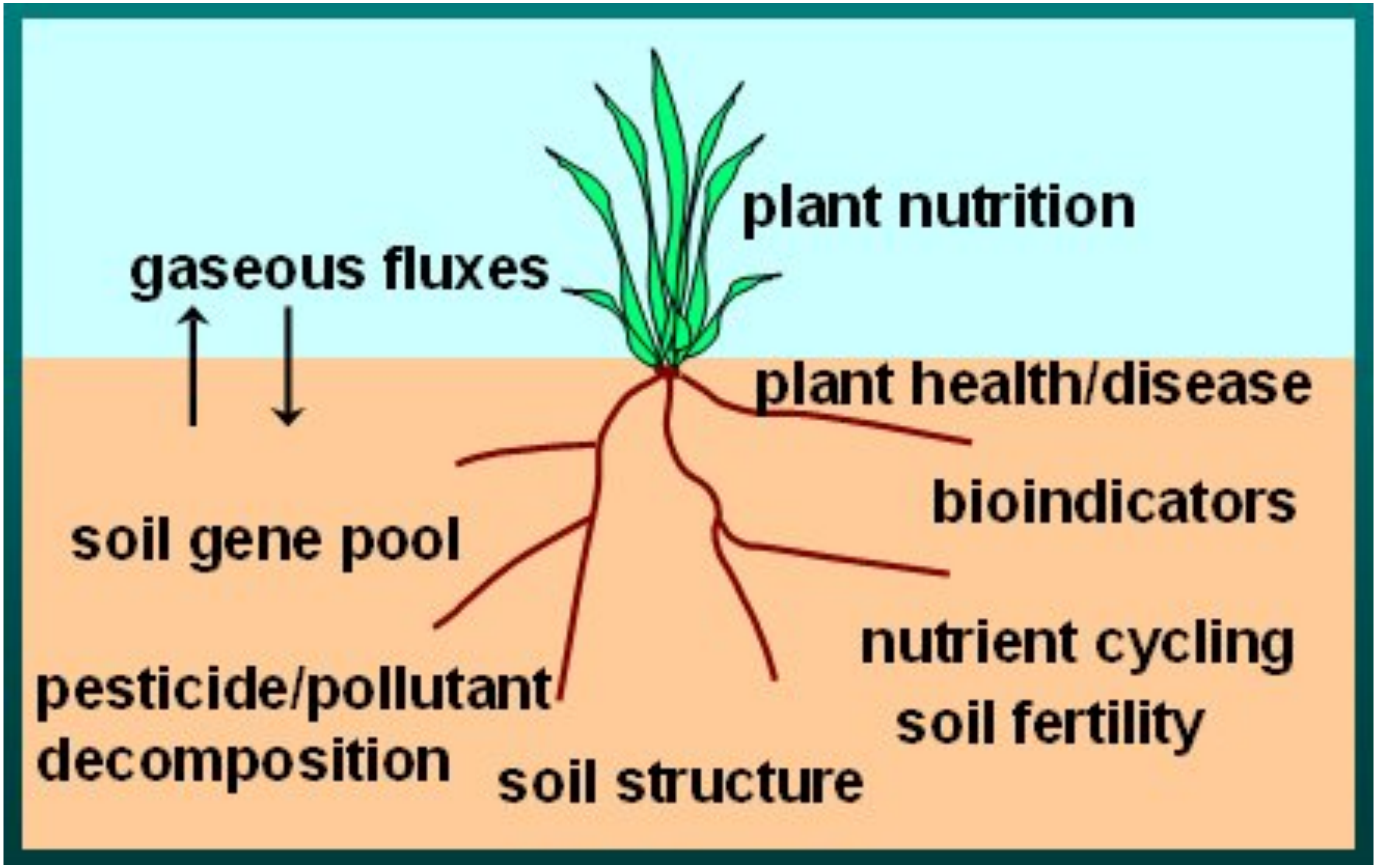
ISR = induced systematic resistance (to infection)



PGPR = Plant Growth Promoting Rhizobacteria

Haas & Défago. 2005. Nature Reviews Microbiology

(Bonus slide for home: Diverse impacts of rhizosphere microbiota)



http://www.rothamsted.ac.uk/ppi/rhizo2/images/Picture1.jpg

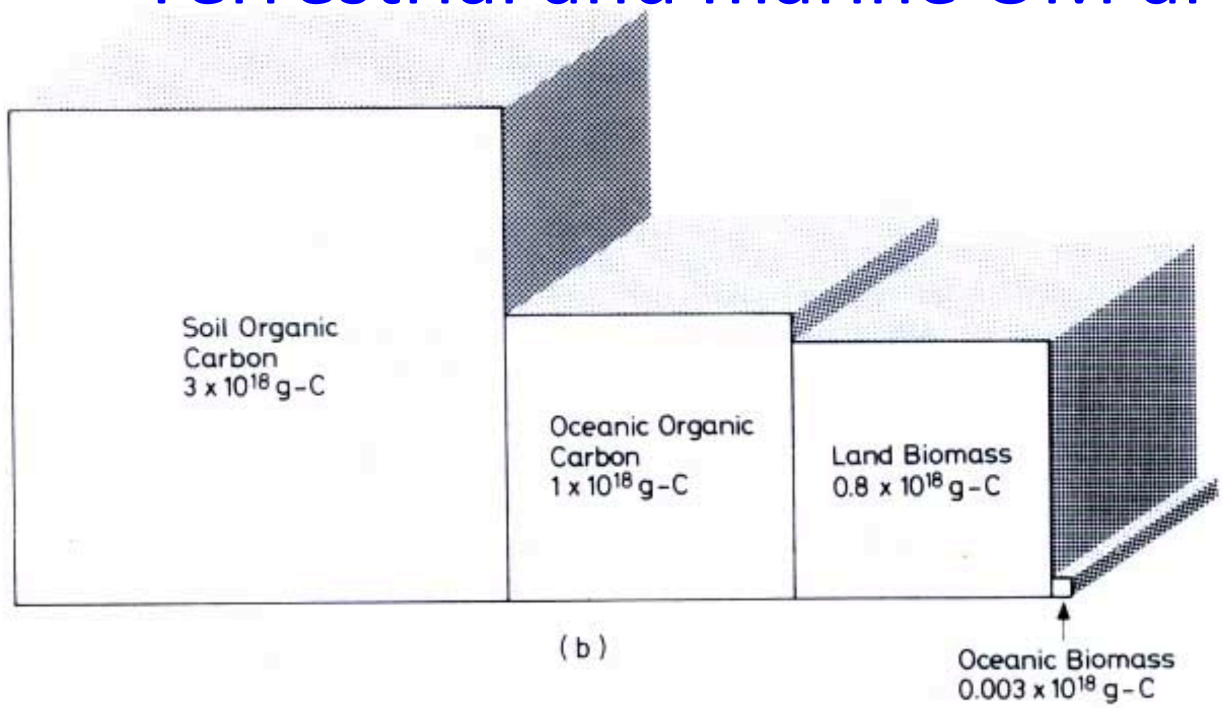
Rhizosphere = area of VERY active research

Aquatic Microbial Heterotrophy

Same basic idea, right? Yeah, but with differences..

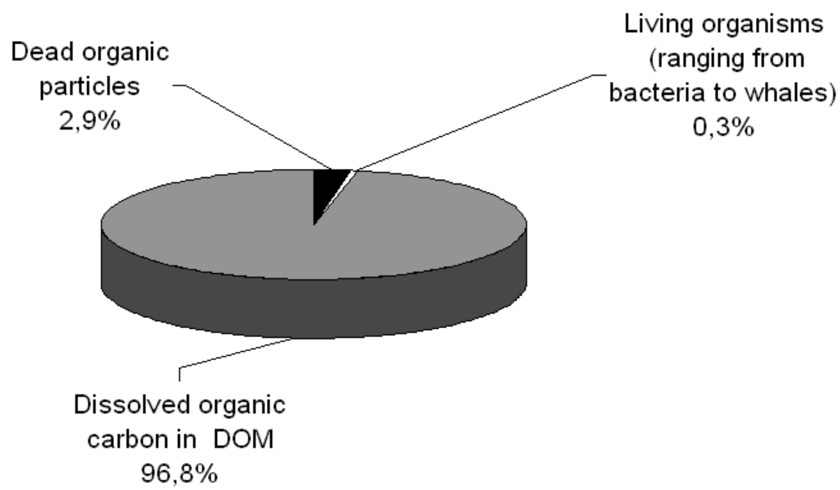
Terrestrial and marine OM are different

http://www.scopenvironment.org/downloadpubs/scope13/chapter11.html



Less OM in ocean than on land (here ~¼)

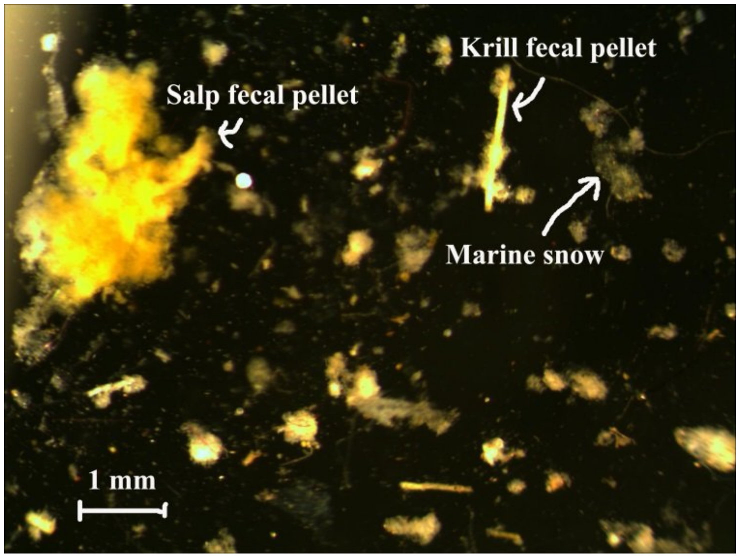
Distribution of organic carbon in the oceans



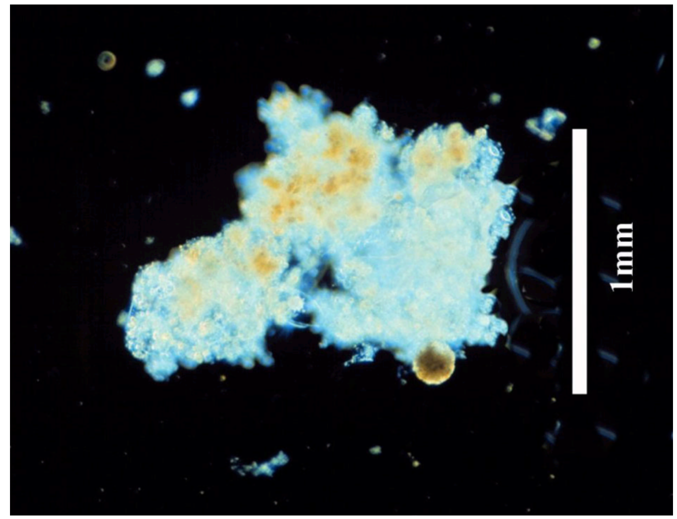
http://www.galathea3.dk/dk/Menu/Forskning/Opløst+organisk+stof/Materiale/DOM+1

Marine OM is dominated by dissolved fraction, BUT POC is what's highly reactive *(as also assumed in Ingalls et al 2006)*

The marine snow (aka sinking POC) zoo



http://downtothetwilightzone.noc.ac.uk/2013_06_01_archive.html

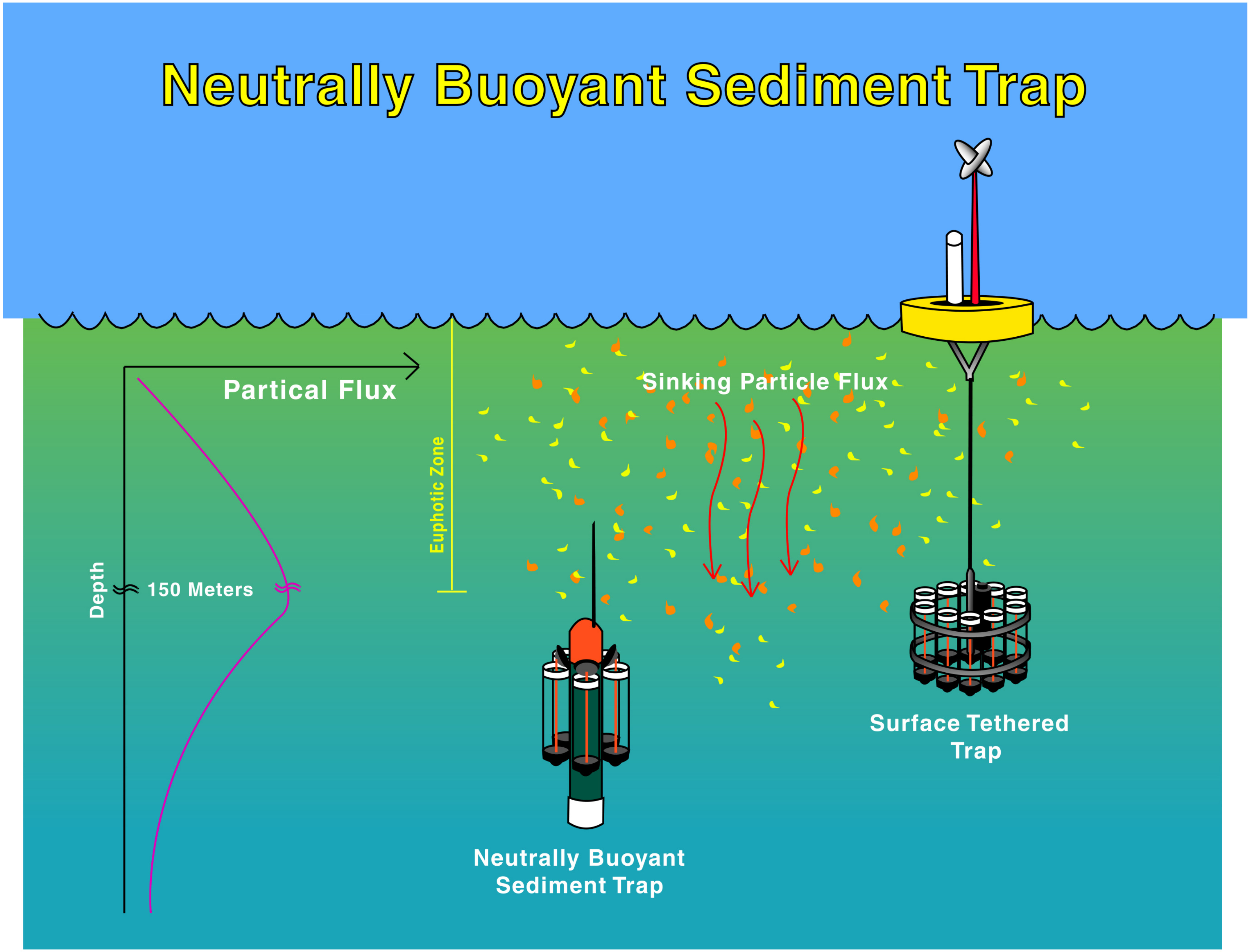


http://downtothetwilightzone.noc.ac.uk/2013/06/14-on-marine-snow-and-copepod-poo.html

http://news.sciencemag.org/sites/default/files/styles/thumb_article_l/public/article_images/sn-marinegerms.jpg

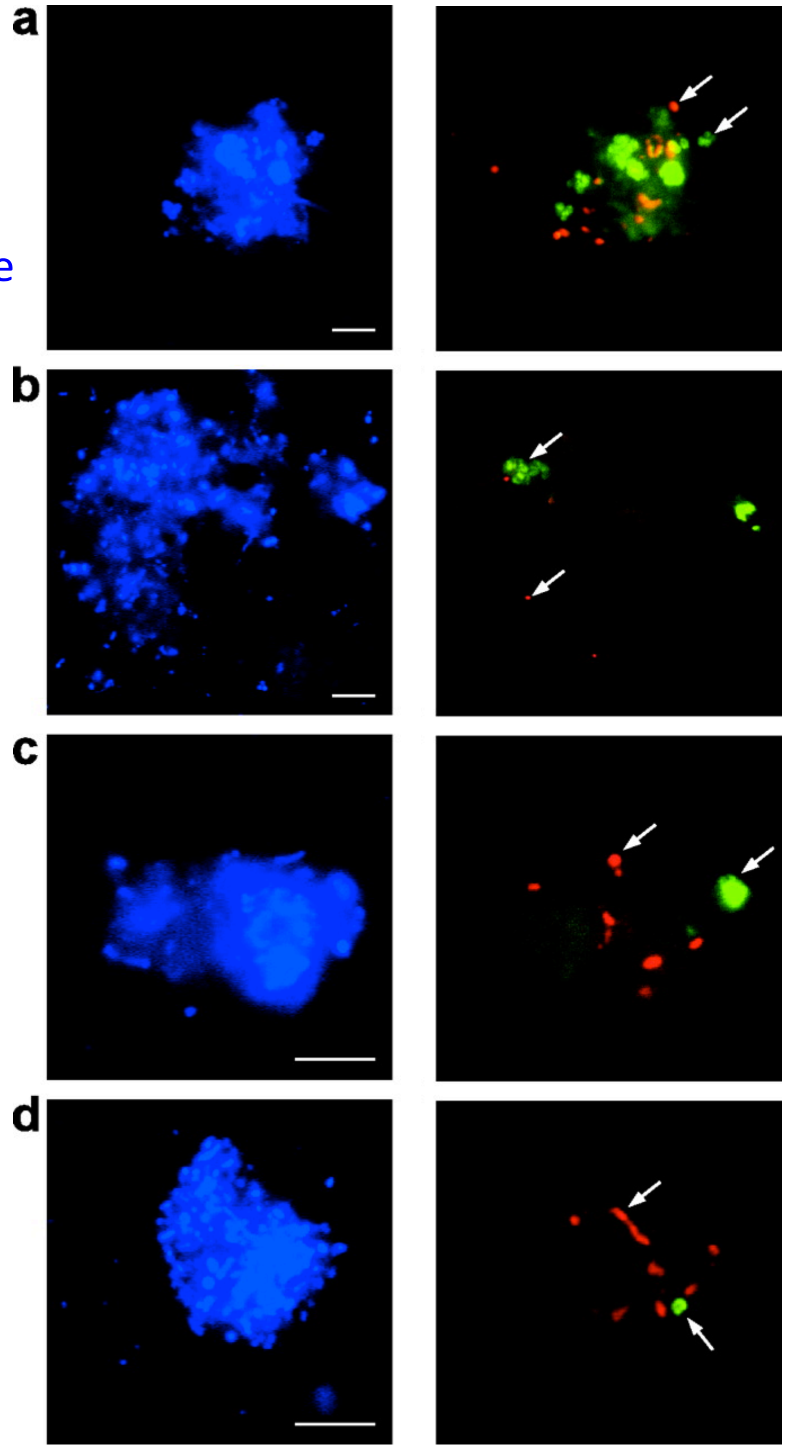
http://www.whoi.edu/cms/images/lstokey/2005/1/v40n2-honjo2en_4950.jpg

William S. Currie

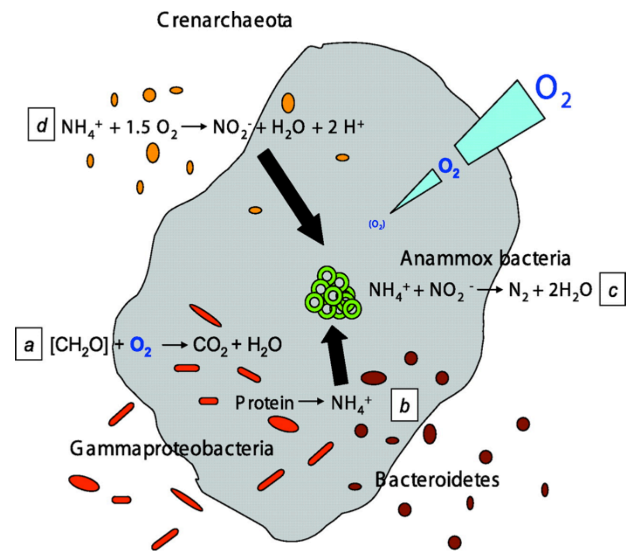


http://cafethorium.whoi.edu/website/projects/NBST_full_size.jpg

Sinking particles are teeming with microbes… *(DAPI-stained epifluor. micrographs)*



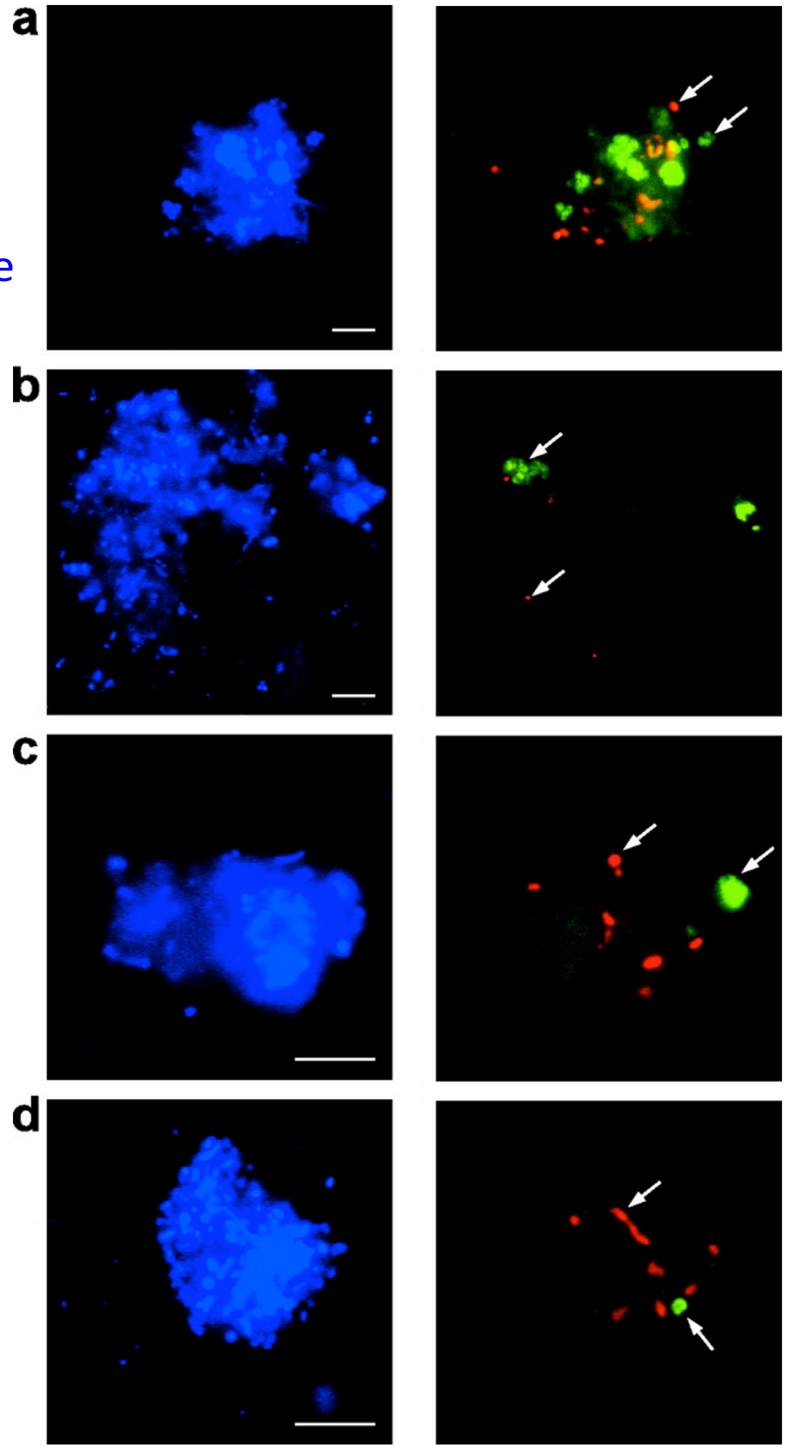
…that can be identified and localized by FISH *(green= annamox bacteria, red= other bacteria)*



…reminding us that O_2-stripping by heterotrophic decomposition can be vital at not only macro scales (Dead Zones) but micro scales (these particles) for creating conditions for anaerobic activities, including chemoautotrophy…

Woebken et al 2007. *AEM*

Sinking particles are teeming with microbes… *(DAPI-stained epifluor. micrographs)*



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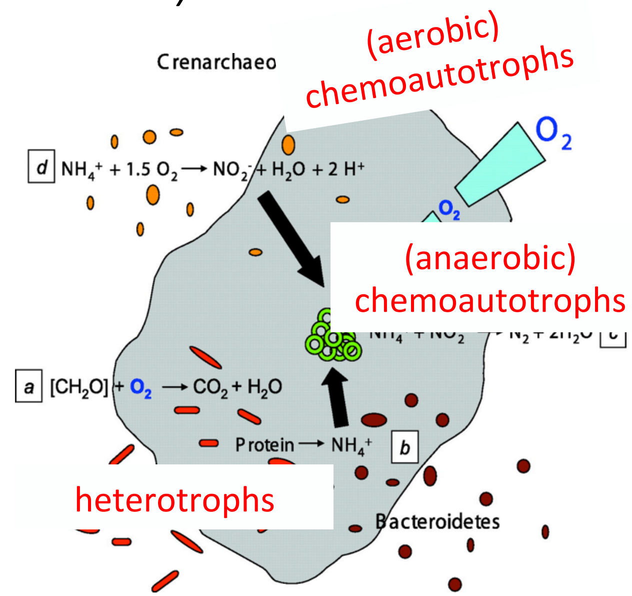
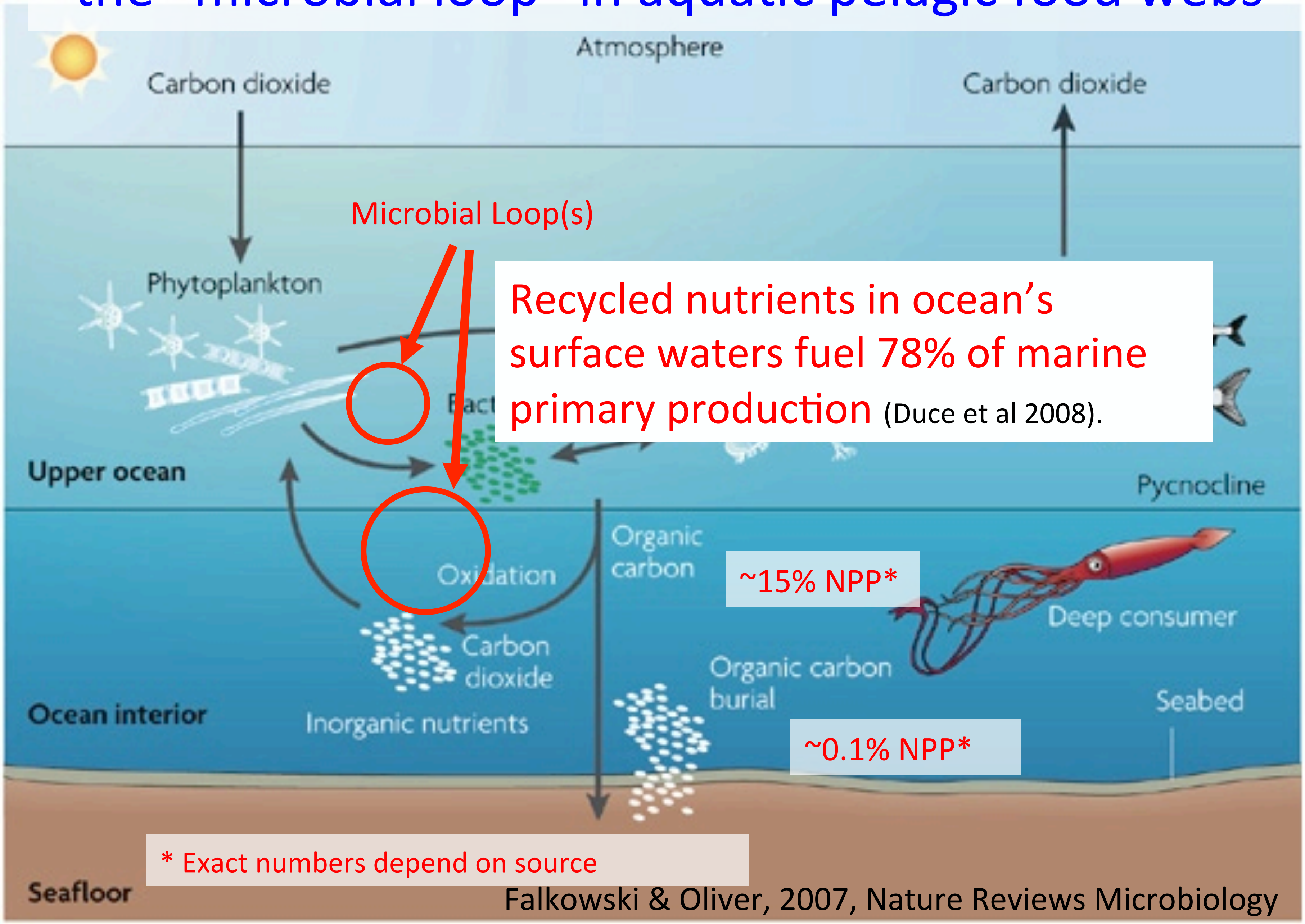


…reminding us that O_2-stripping by heterotrophic decomposition can be vital at not only macro scales (Dead Zones) but micro scales (these particles) for creating conditions for anaerobic activities, including chemoautotrophy…

Woebken et al 2007. *AEM*

One consequence of aquatic heterotrophy: the "microbial loop" in aquatic pelagic food webs

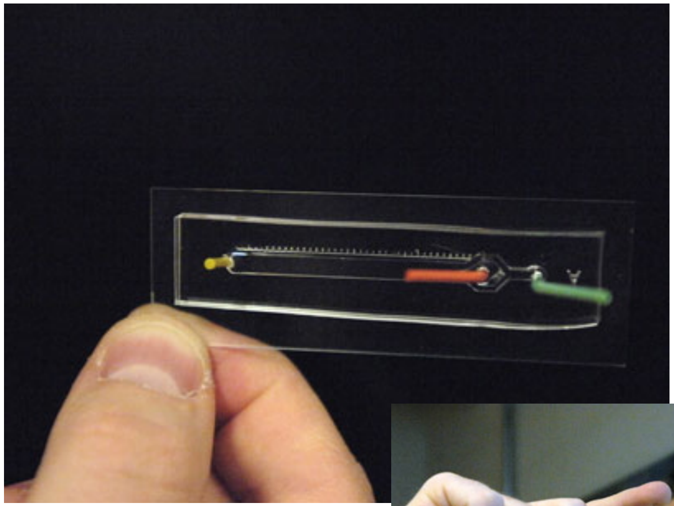


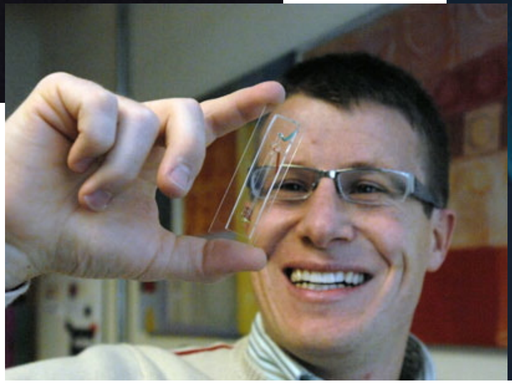
Recycled nutrients in ocean's surface waters fuel 78% of marine primary production (Duce et al 2008).

* Exact numbers depend on source

Falkowski & Oliver, 2007, Nature Reviews Microbiology

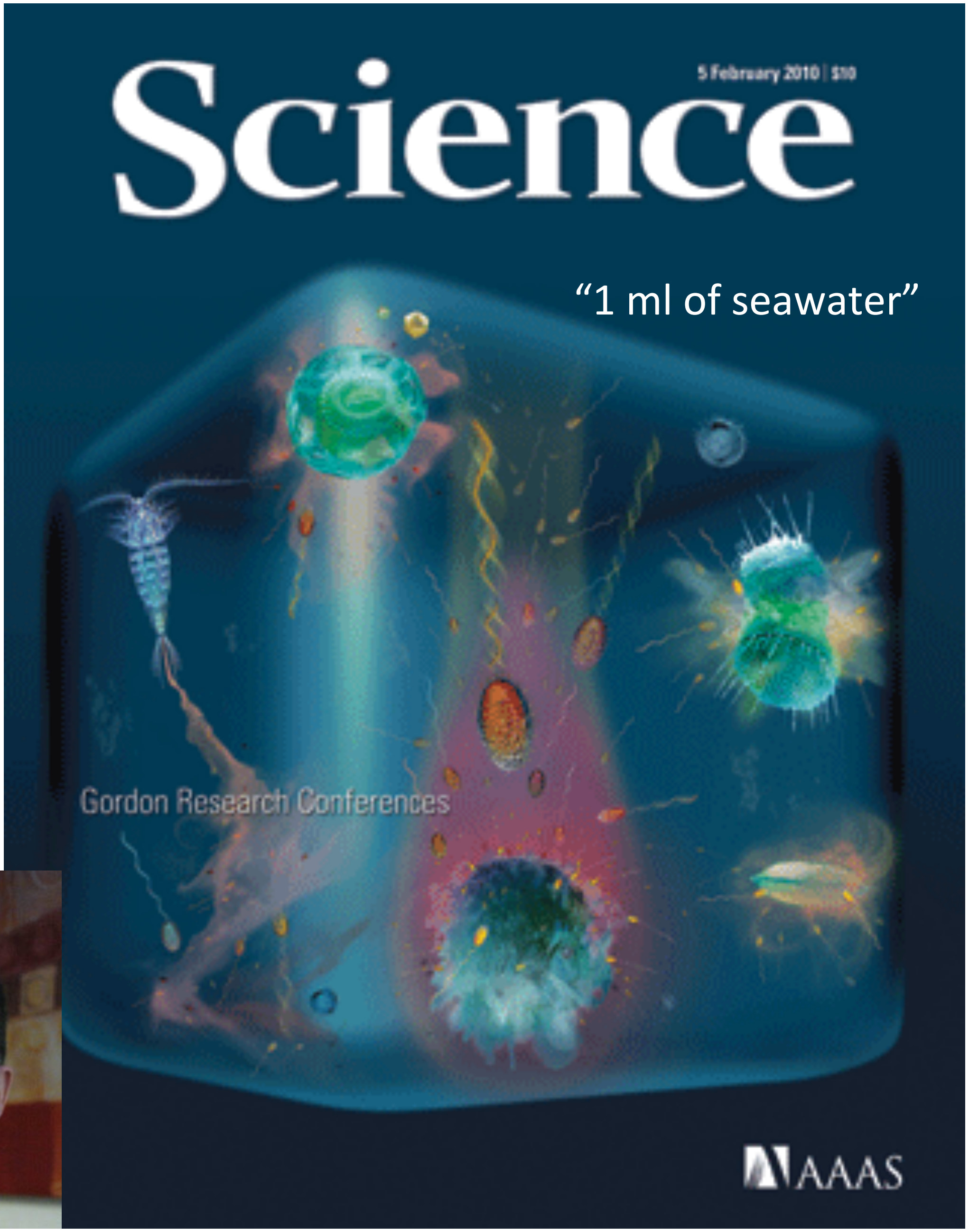
Another consequence (a tad off-topic): microbes race after sinking particles to jump on





Microfluidics to examine microbial scavenging behavior!

http://www.i-micronews.com/upload/Micronews/images/mini-eco-2-enlarged.jpg



Stocker et al Cover of Science Feb 2010

To recap MARINE microbial heterotrophy

- Heterotrophy includes predation and decomposition, microbes and viruses
- "The microbial loop" is the cyclic remineralization of carbon and nutrients in the upper pelagic zone; these recycled nutrients fuel a huge amount of the primary production
- In oceans, the imbalance between production (+ terr. C input) and respiration **defines the amount of C exported into the deep sea**, where it has the potential to be buried and sequestered from the atmosphere.
- e.g. in oceans, <0.1% of NPP reaches the sediment and gets buried (Falkowski & Oliver, 2007, Nature Rev. Micro.)

Side Q: are fungi important decomposers in the oceans?

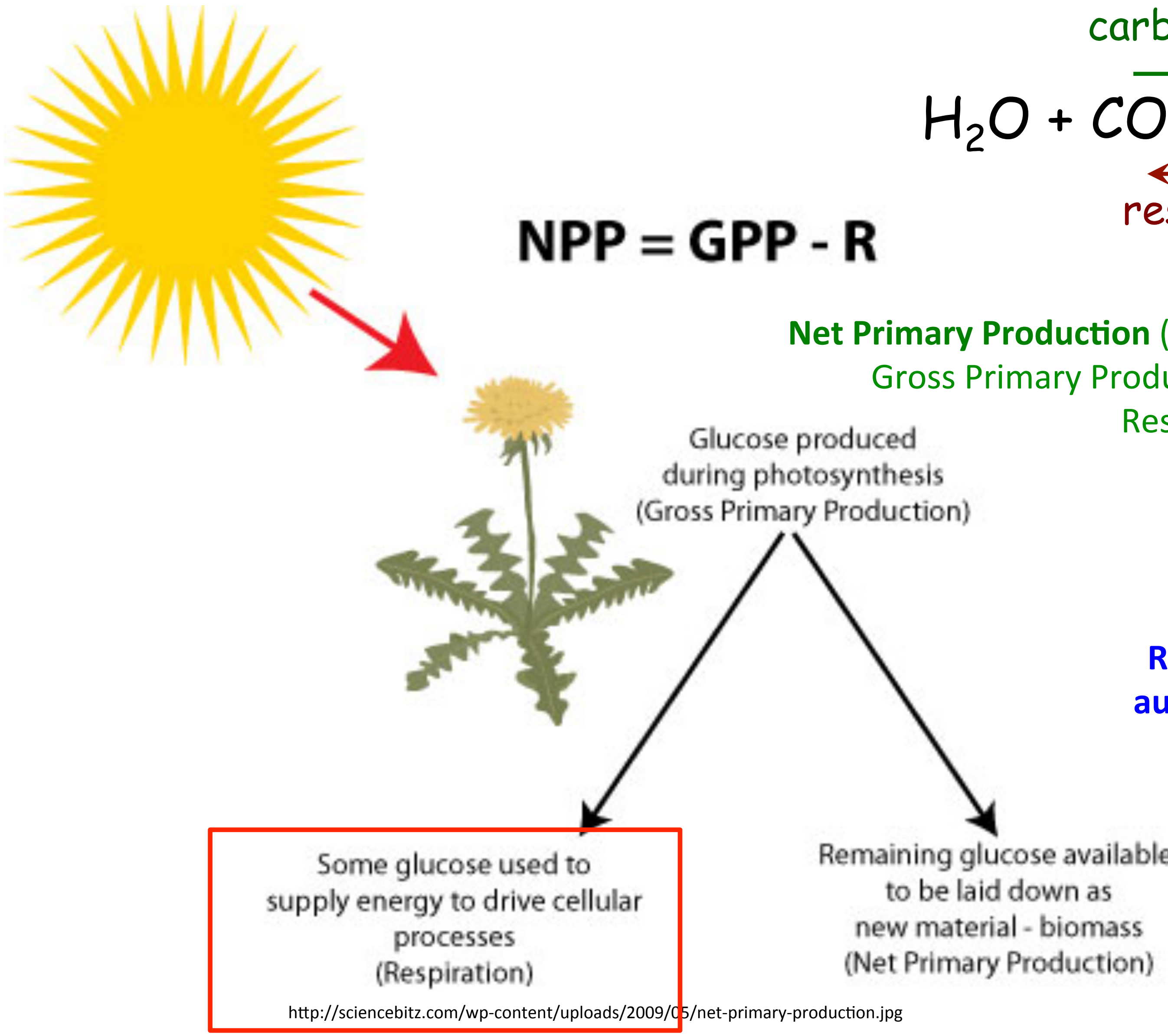
Respiration: helping constrain NPP,

which defines the fixed C available in a system to do stuff…

carbon fixation

$$H_2O + CO_2 \leftrightarrow CH_2O + O_2$$

respiration



http://sciencebitz.com/wp-content/uploads/2009/05/net-primary-production.jpg

Net Primary Production (CO_2 fixed) =
Gross Primary Production (CO_2 fixed) –
Respiration (CO_2 respired)

Respiration is done by both autotrophs (shown here) <u>and heterotrophs</u>

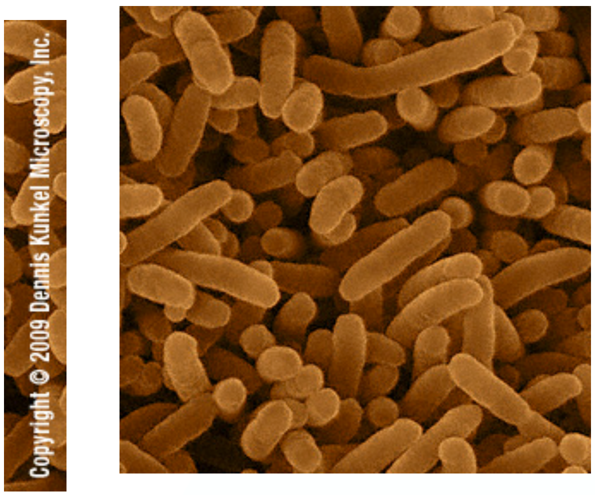
Respiration: helping constrain NPP,

which defines the fixed C available in a system to do stuff…

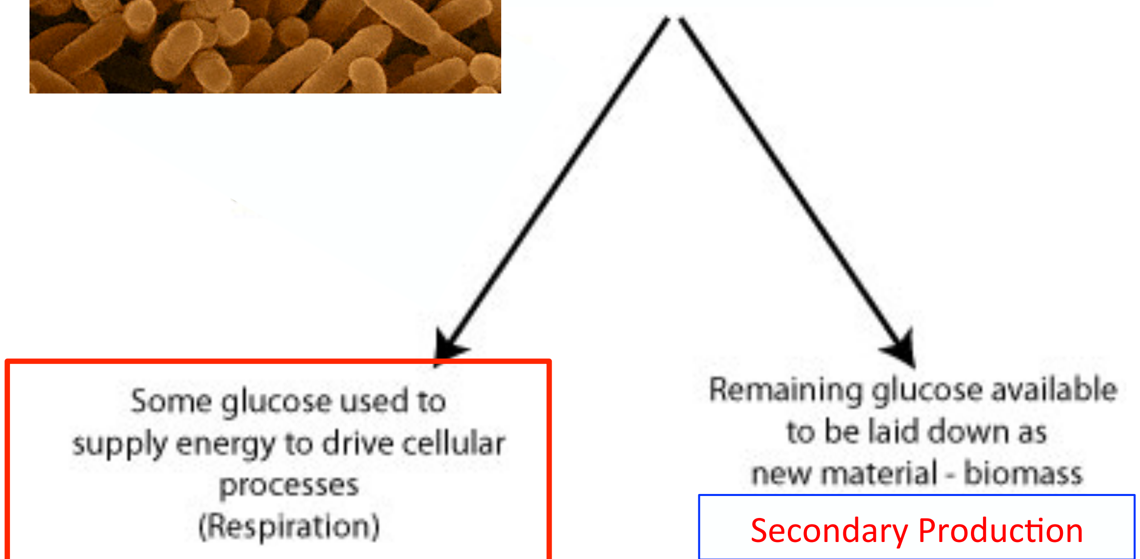
carbon fixation →

$$H_2O + CO_2 \leftrightarrow CH_2O + O_2$$

← respiration

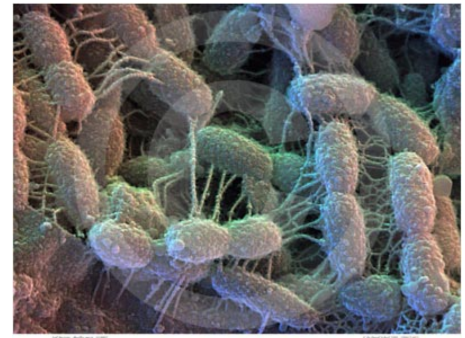


Glucose derived from
HETEROTROPHY



http://sciencebitz.com/wp-content/uploads/2009/05/net-primary-production.jpg

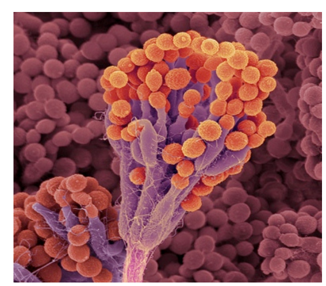
Microbial decomposition impacts climate, in at least 2 ways


www.bioquest.org

Soil bacteria

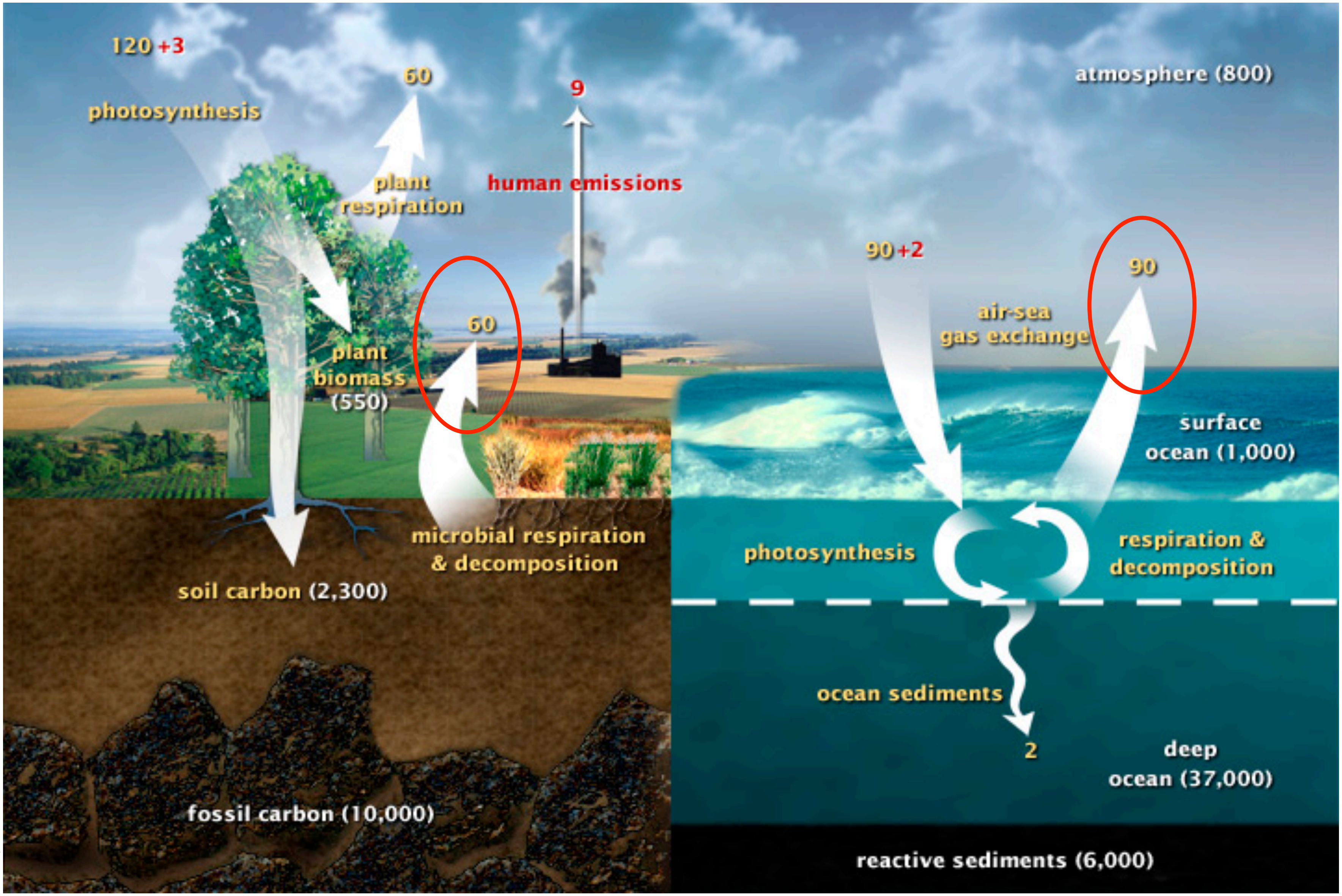
1. *Respiration = measurable output of life's breakdown of organic matter (thus both autotrophic and heterotrophic respiration.)*

- CO_2 is returned to the atmosphere by respiration of all life, plus anthropogenic activities
- Soil respiration is the largest natural source of CO_2 released to the atmosphere. (based on IPCC – slightly different in next figure)
- Marine respiration isn't far behind.
- Both much larger annually than human addition of CO_2 to atmosphere.


forces.si.edu

Soil fungus

Terrestrial and marine *respiration*



dynamicscience.com.au

Values in yellow are natural, values in red are anthropogenic.
Values are in GtC (reservoir) or GtC/yr (flux)

2. Terrestrial and marine *respiration* helps define ecosystem carbon storage, and therefore climate....

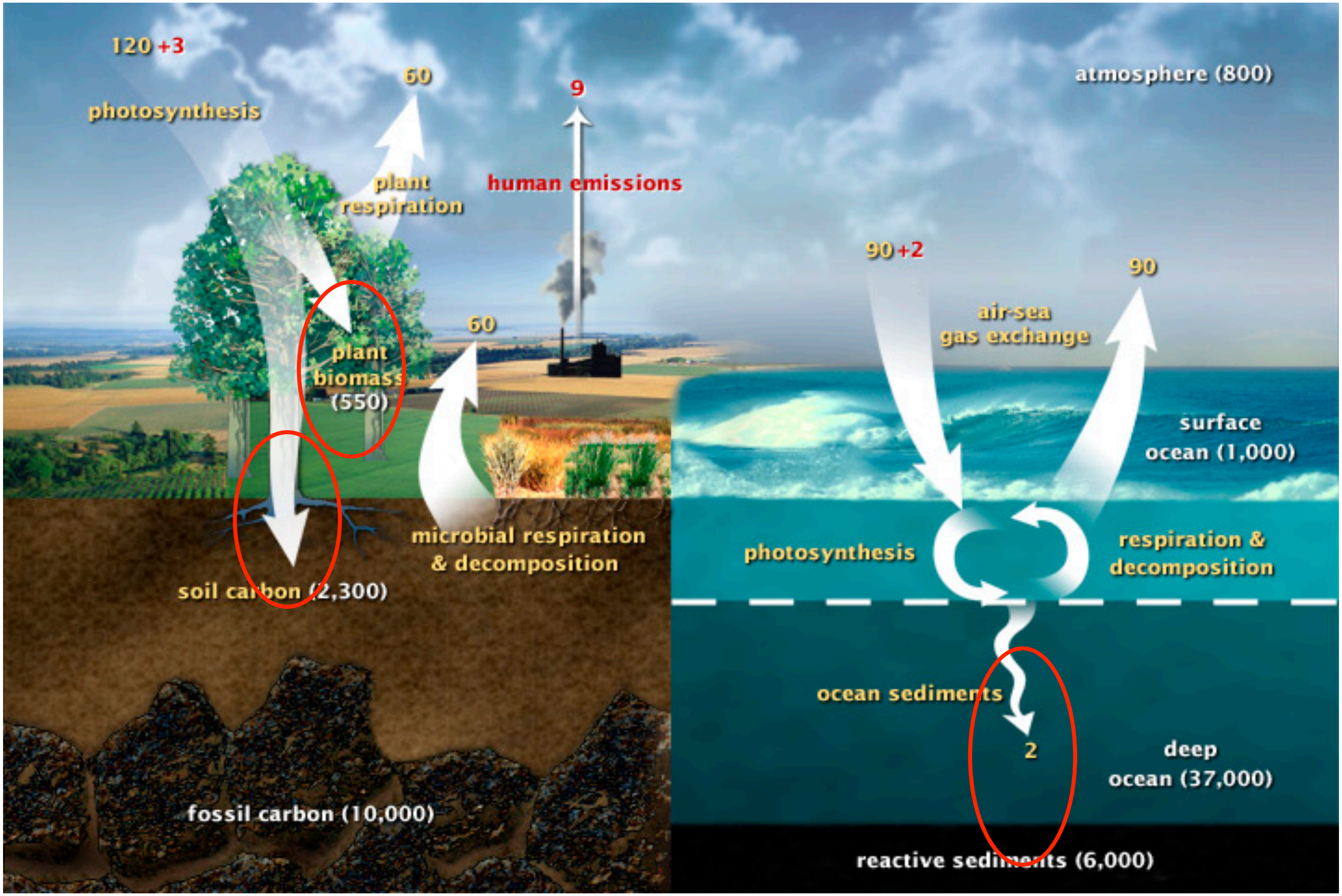
In soils, the annual imbalance between plant photosynthesis and (plant + microbial) respiration defines **NEP = Net Ecosystem Production = CO_2 taken up by an ecosystem.** (On land a chunk of this tends to stay put for a bit, and some portion may get buried/immoblized in soil for longer period).

Net Primary Production (CO_2 fixed) =
Gross Primary Production (CO_2 fixed) – Respiration (CO_2 respired)

In oceans, the imbalance between production (+ terr. C input) and respiration **defines the amount of C exported into the deep sea**, where it has the potential to be buried and sequestered from the atmosphere.

C export to deep sea =
Gross *upper H2O column* Primary Production (CO_2 fixed) –
upper H2O column Respiration (CO_2 respired)

Terrestrial and marine *respiration*



dynamicscience.com.au

Values in yellow are natural, values in red are anthropogenic.
Values are in GtC (reservoir) or GtC/yr (flux)

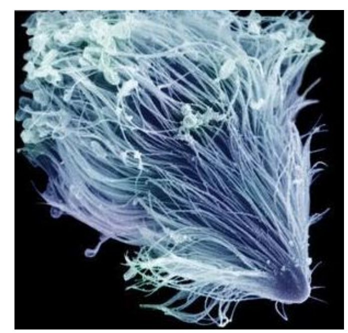
Variants on heterotrophy basics (a): Microbial decomposition is a major process not only in soils & water, but in guts

Rumen protist *Ophryoscolex*

www.morning-earth.org/Graphic-E/Biosphere/Bios-Microbe-Image/M-PCophryoscolex

- Ruminants. Hard-to-degrade cellulosic plant materials require microbial enzymes – gut is like a microbial bioreactor… (and makes CH_4)

- Termites. Surviving off gnawing wood: termite guts are filled with a rich community of symbiotic microbes (and make CH_4)



forces.si.edu

Termite protist

- Etc… Basically all multi-cellular heterotrophs – including us… (your very own – likely unique to you! – commensal gut bacteria)

OPEN ACCESS Freely available online PLoS BIOLOGY

Development of the Human Infant Intestinal Microbiota

Chana Palmer[1], Elisabeth M. Bik[2], Daniel B. DiGiulio[3,4], David A. Relman[2,3,4], Patrick O. Brown[5,6*]

Variants on heterotrophy basics (b): Non-canonical heterotrophy

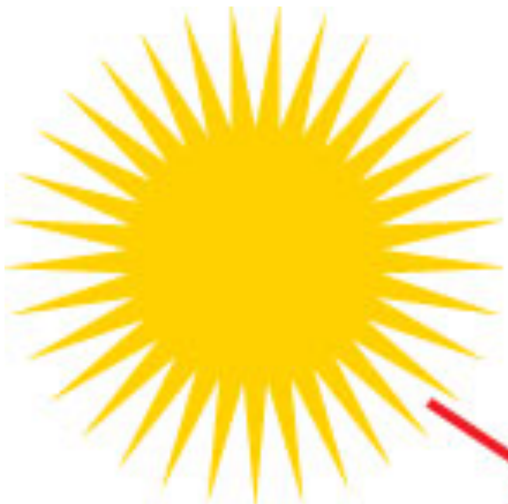
Resourceful heterotrophs make the most of light in the coastal ocean

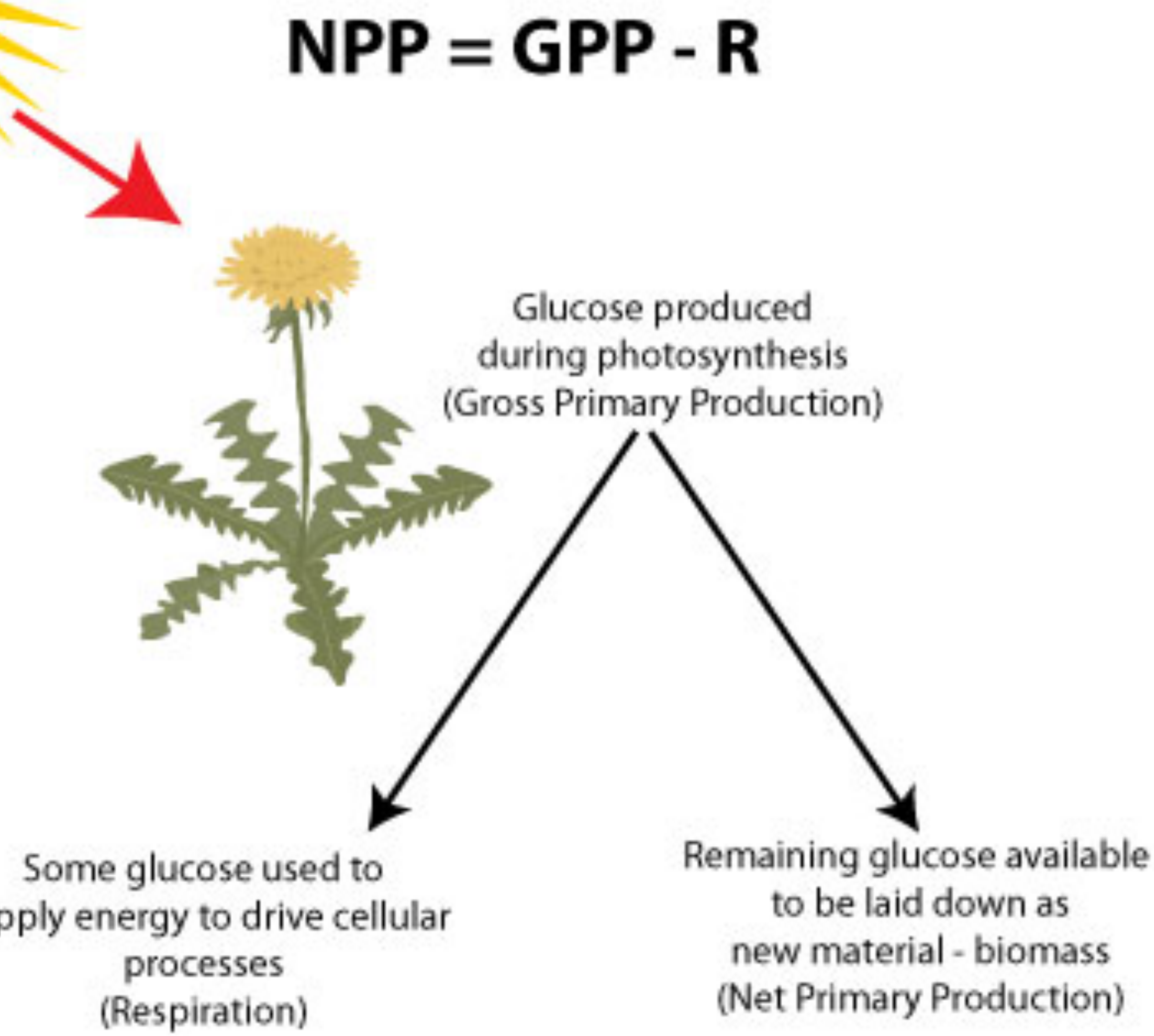
Mary Ann Moran and William L. Miller

Abstract | The carbon cycle in the coastal ocean is affected by how heterotrophic marine bacterioplankton obtain their energy. Although it was previously thought that these organisms relied on the organic carbon in seawater for all of their energy needs, several recent discoveries now suggest that pelagic bacteria can depart from a strictly heterotrophic lifestyle by obtaining energy through unconventional mechanisms that are linked to the penetration of sunlight into surface waters. These newly discovered mechanisms involve the harvesting of energy, either directly from light or indirectly from inorganic compounds that are formed when dissolved organic carbon absorbs light. In coastal systems, these mixed metabolic strategies have implications for how efficiently organic carbon is retained in the marine food web and how climatically important gases are exchanged between the ocean and the atmosphere.

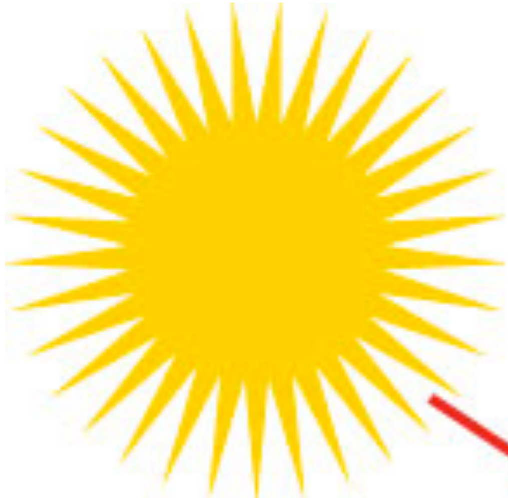
Still using organic carbon as their carbon source – so still true heterotrophs – but getting additional energy from the sun or from inorganic chemical bonds.

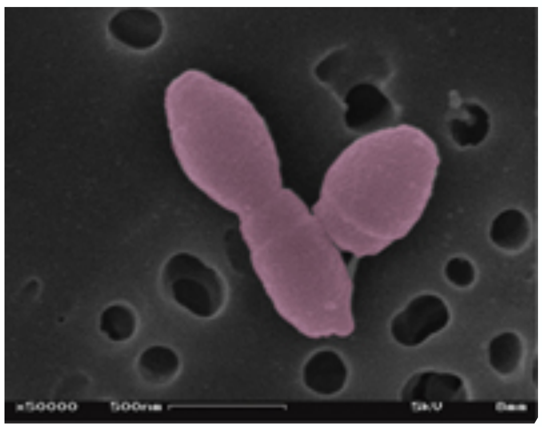
Net Primary Production (CO_2 fixed) =
Gross Primary Production (CO_2 fixed) –
Respiration (CO_2 respired)





http://sciencebitz.com/wp-content/uploads/2009/05/net-primary-production.jpg





Glucose derived from HETEROTROPHY

Some glucose used to supply energy to drive cellular processes (Respiration)

Remaining glucose available to be laid down as new material - biomass (Net Primary Production)

http://sciencebitz.com/wp-content/uploads/2009/05/net-primary-production.jpg

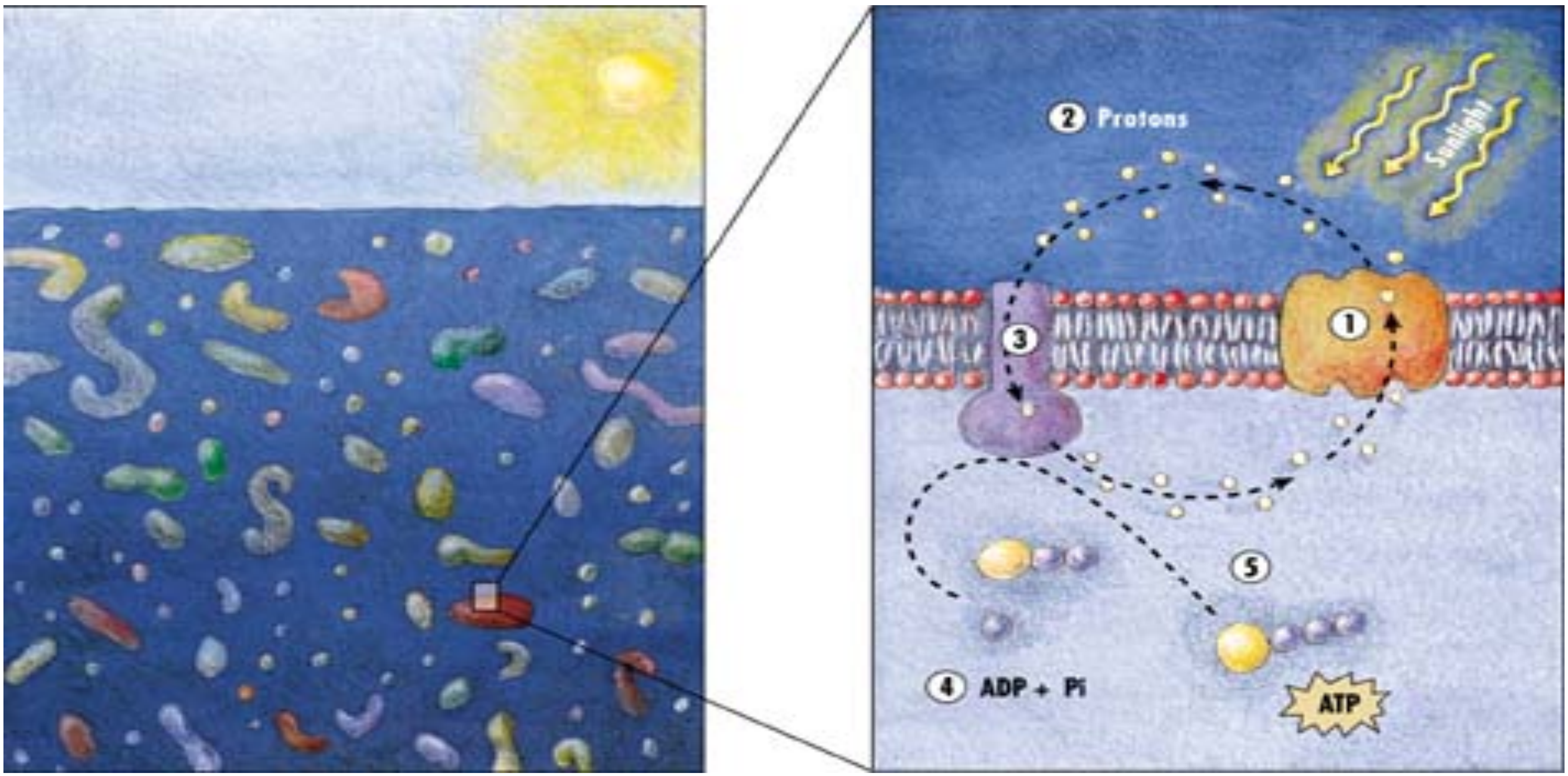
So it's *kinda* like if we could wear solar collectors to power our iPhones (except that we're not currently powering them from our guts) *(so OK, more like we could directly power our brains with them)*

Example Discovery: A new type of phototrophy…

Proteorhodopsin phototrophy in the ocean

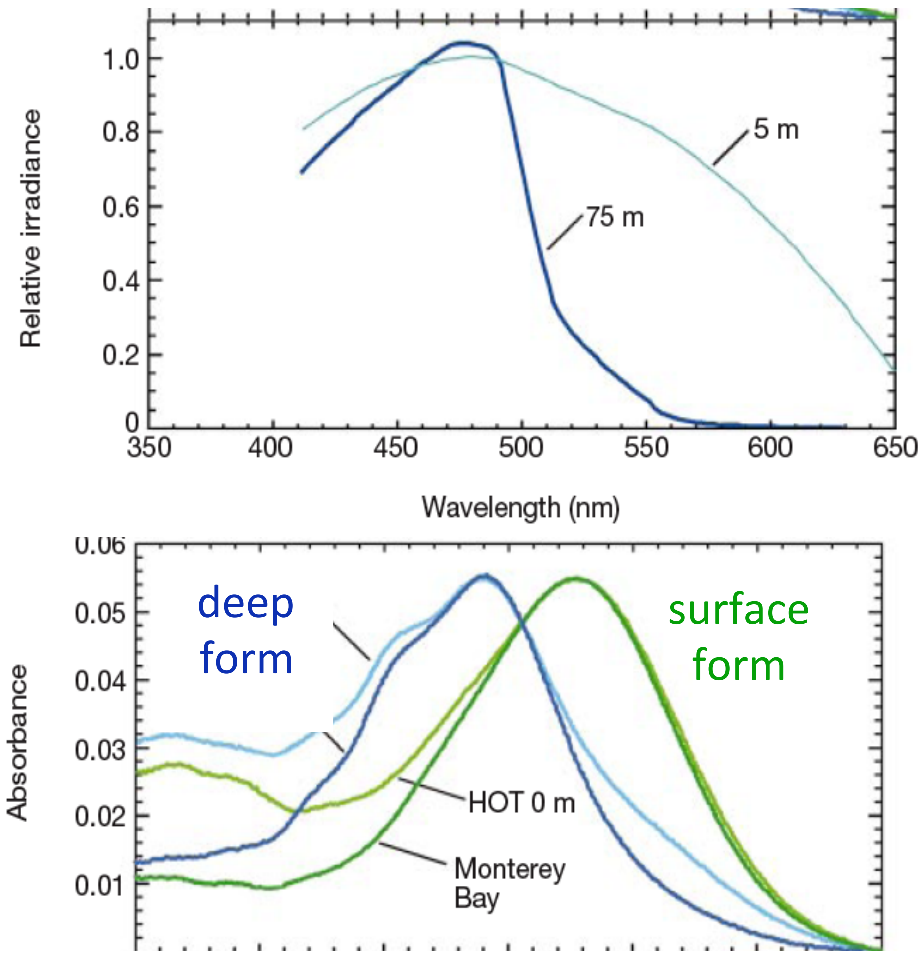
Oded Béjà*†, Elena N. Spudich†‡, John L. Spudich‡, Marion Leclerc* & Edward F. DeLong*

Nature. 2001 + 2006 + others…
It's a light-driven proton pump meaning it can make ATP



http://www.mbari.org/twenty/images/proteo.jpg

Proteorhodpsin shows "spectral tuning" to habitat just like photosynthetic pigments…

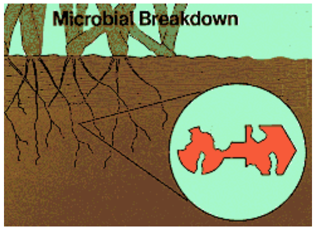


- The gene encoding proteorhodopsin is present in a remarkable 13-80% of marine surface bacteria and archaea (DeLong and Béjà, 2010)

- ubiquity partially due to extensive horizontal gene transfer

So WHEN is using sunlight energy useful to heterotrophs? And are they really still heterotrophs?

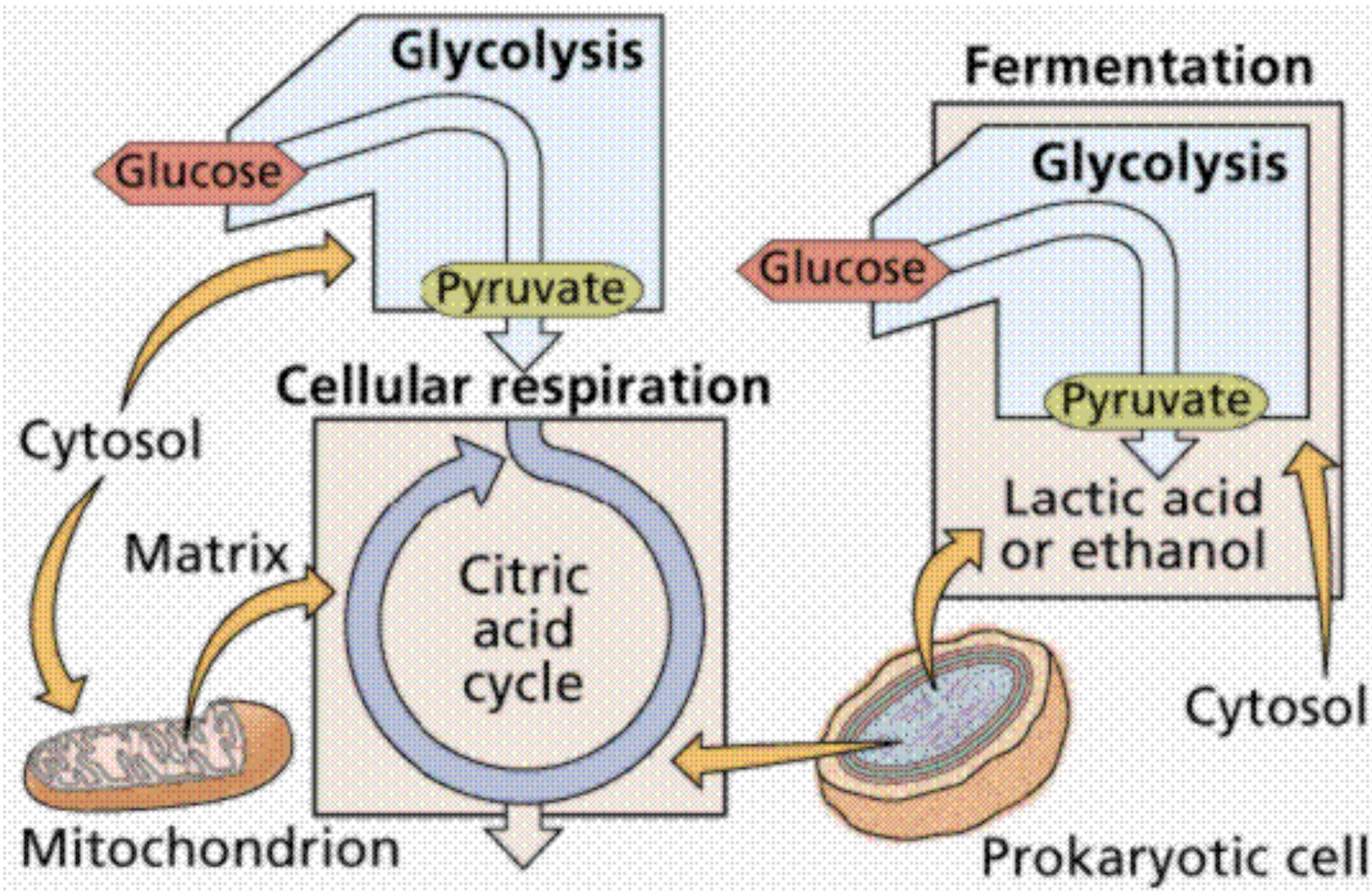
Summary of microbial heterotrophy



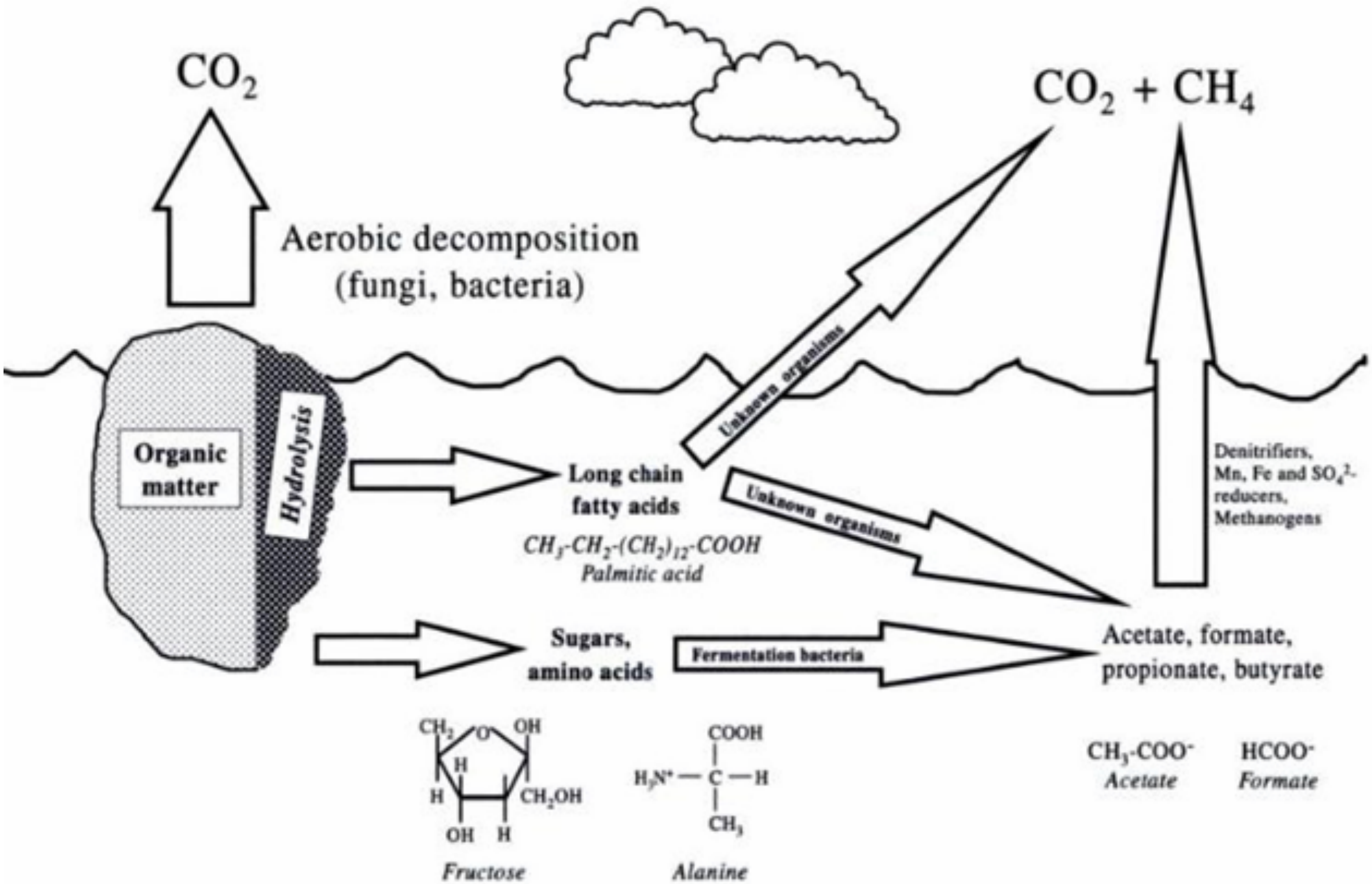
- microbes are master degraders
- releases nutrients
- organic matter breakdown quantified by respiration
- controls ecosystem C storage (imbalance between PP & respiration)
- decomposition is the major avenue of carbon loss from ecosystems, & is dominated by microbes
- <u>metazoan heterotrophy enabled by symbiotic microbial decomposition in guts</u>
- biogeochemically important twists on heterotrophy where energy is supplemented from other sources.

BONUS SLIDES

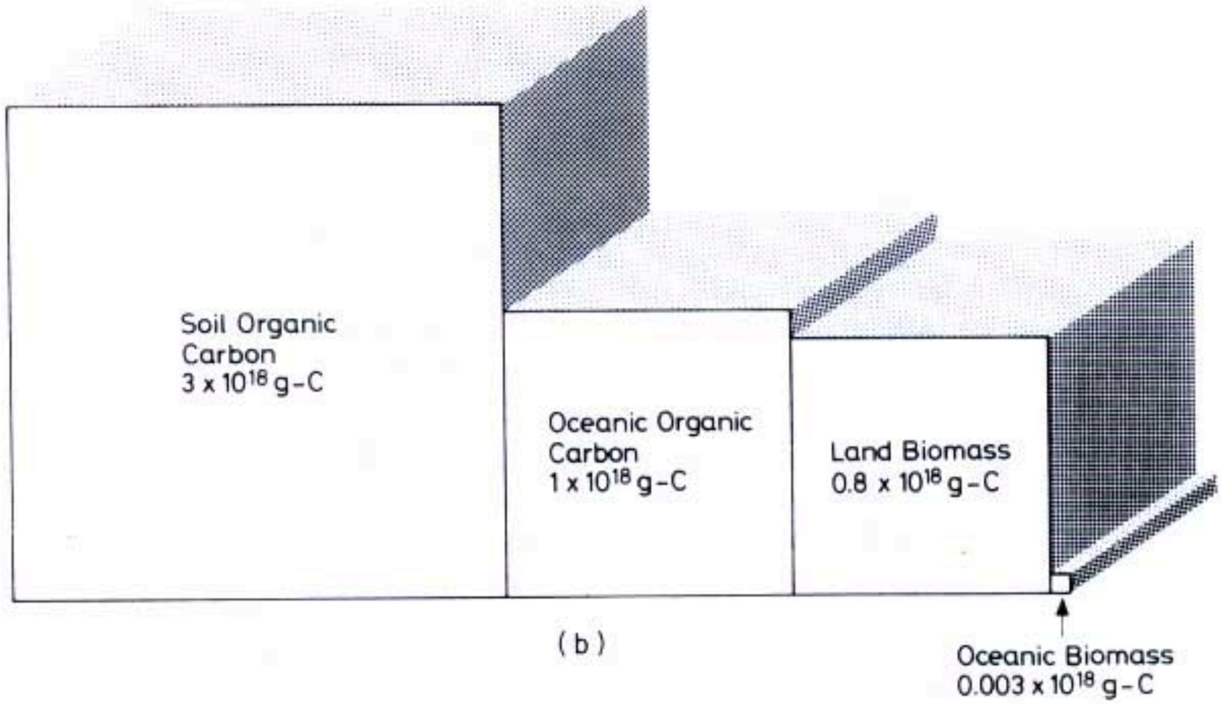
Aerobic vs. anaerobic breakdown of organic matter



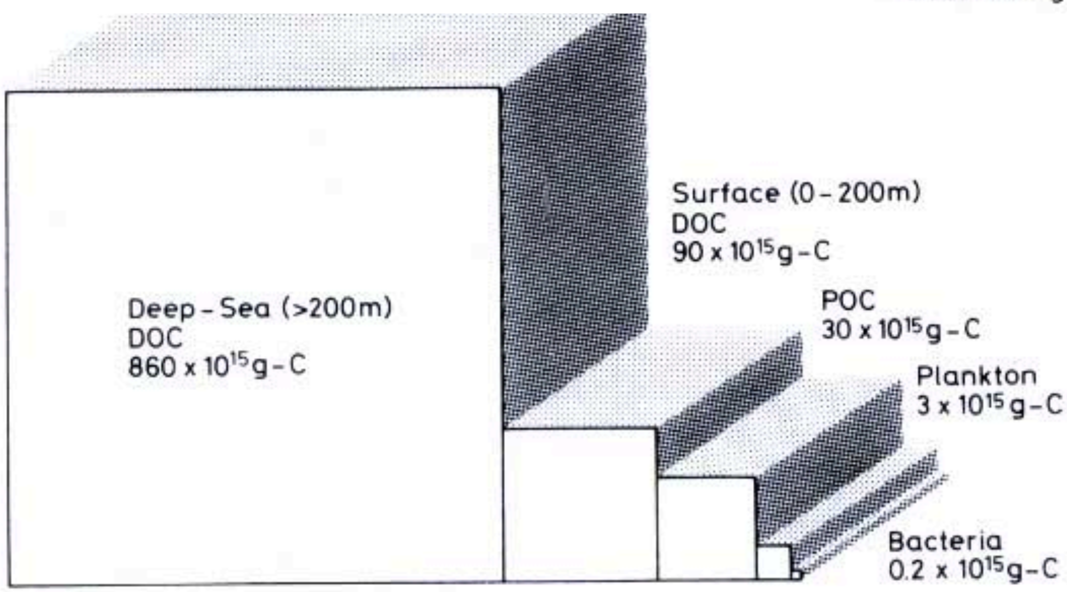
http://www.emc.maricopa.edu/faculty/farabee/biobk/energpath1.gif



http://microbewiki.kenyon.edu/index.php/File:Anaerobic_decomposition.png



(b)



(a)

http://www.scopenvironment.org/downloadpubs/scope13/chapter11.html

Table 11.1 Inputs, reservoirs and losses of organic material in the sea (modified from Williams, 1975)

Reservoirs	
DOC (assuming 700 μg C/1)	1×10^{18} g C
POC (assuming 20 μg C/1)	3×10^{16} g C
Plankton	3×10^{15} g C
Annual inputs	
Net primary productivity (assuming 100 g C fixed m^2 year)	3.6×10^{16} g C
Rain (assuming 1 mg C/1)	2.2×10^{14} g C
River (assuming 5 mg C/1)	1.8×10^{14} g C
Possible annual inputs into the dissolved fraction	
Phytoplankton excretions (10% of production)	3.6×10^{15} g C
Resistant material from phytoplankton (5% of production)	1.8×10^{15} g C
Annual losses by sedimentation	
Nearshore	2.7×10^{12} g C
Pelagic	9.2×10^{13} g C
Organic carbon accumulated in marine sediment per 10^8 years	1.1×10^{22} g C

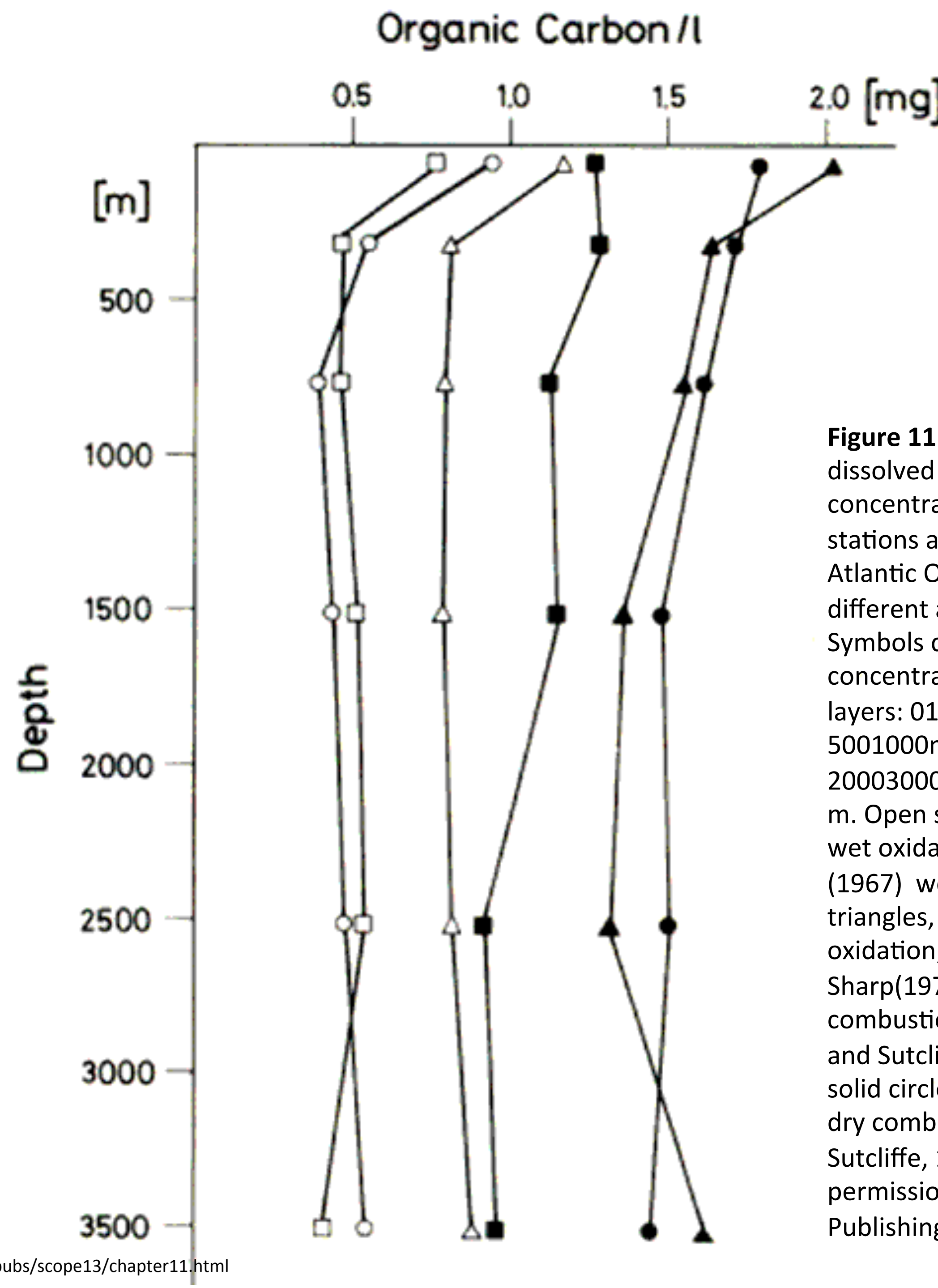


Figure 11.2 A comparison of dissolved or total organic carbon concentrations reported at various stations and dates in the Northwest Atlantic Ocean by authors using different analytical methods. Symbols designate the average concentration within successive layers: 0100m, 100500m, 5001000m, 10002000m, 20003000m, and deeper than 3000 m. Open squares, Duursma (1965) wet oxidation; open circles, Menzel (1967) wet oxidation; open triangles, Sharp (1973a) wet oxidation; solid squares, Sharp(1973b) wet high temperature combustion; solid triangles, Gordon and Sutcliffe(1973) dry combustion; solid circle,Skopintsev *et al.* (1966) dry combustion. (After Gordon and Sutcliffe, 1973. Reproduced by permission of Elsevier Scientific Publishing Co.)

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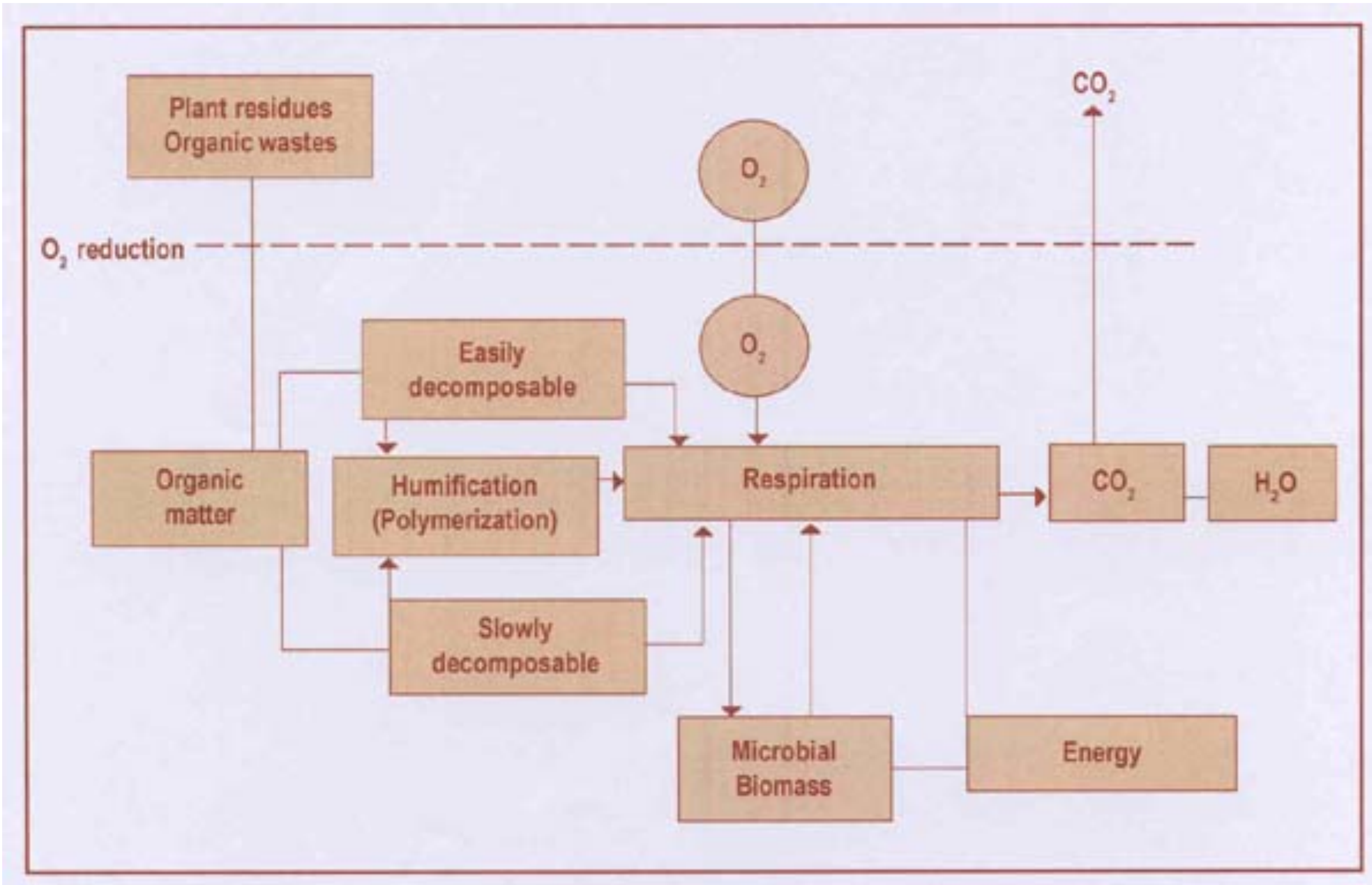
Marine respiration

- marine respiration = ~20% autotrophic (~phytoplanton) and 80% heterotrophic (microbes + metazoans) (e.g. del Giorgio & Duarte 2002 Nature)
- of heterotrophic respiration, metazoans account for <1% up to 50% depending on the region, productivity, depth, etc. (del Giorgio & Duarte 2002 Nature).



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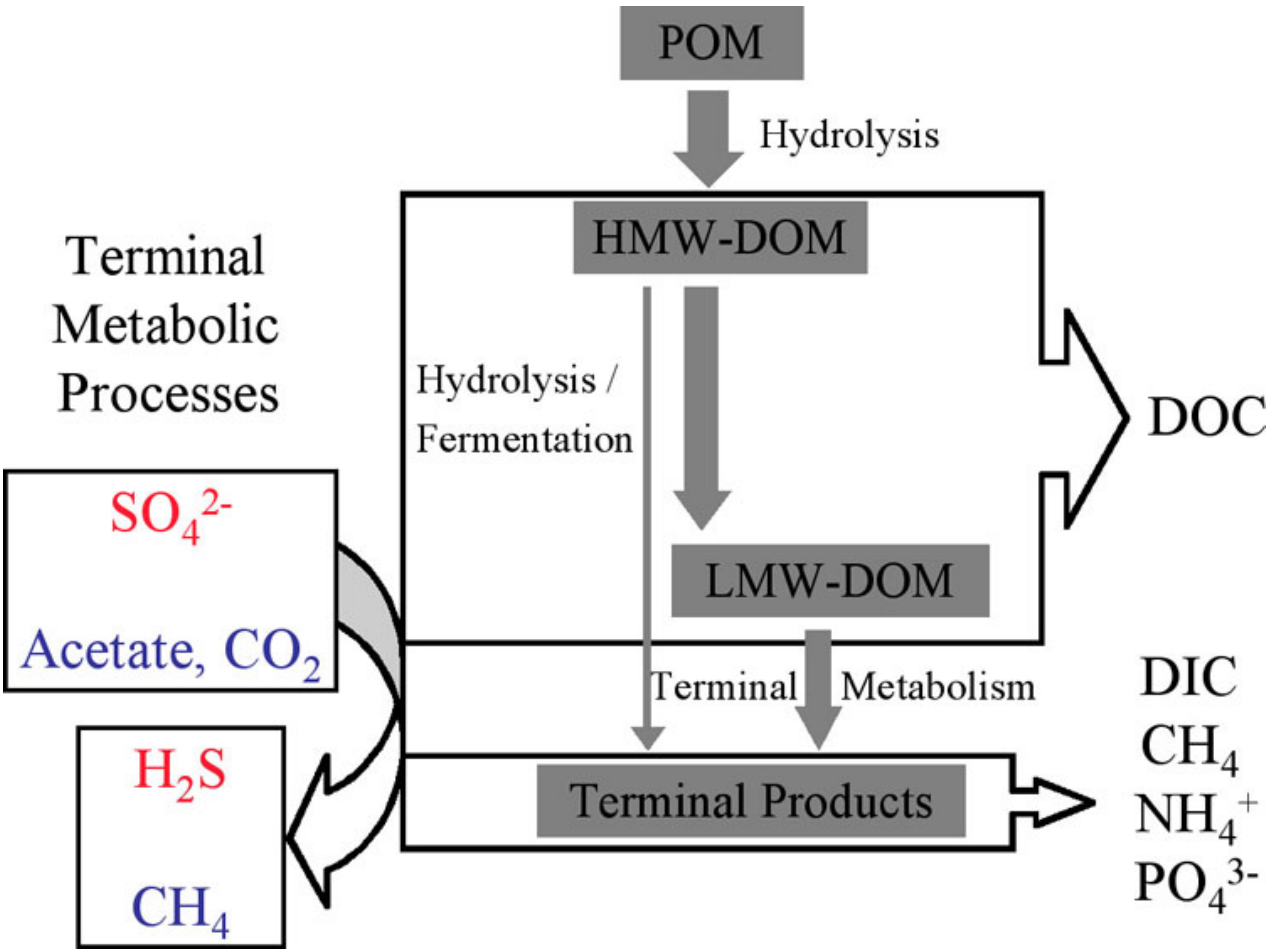

http://joyeresearchgroup.uga.edu/research/surficial-extreme-environments/polar-salt-lakes/microbially-mediated-anaerobic-carbon-cycling