The Importance of Quantitation: Mass Balances, Bioenergetics, and the Money of Life

Mum, why does the bread dough flow over and cause a mess, even before it is in the oven?

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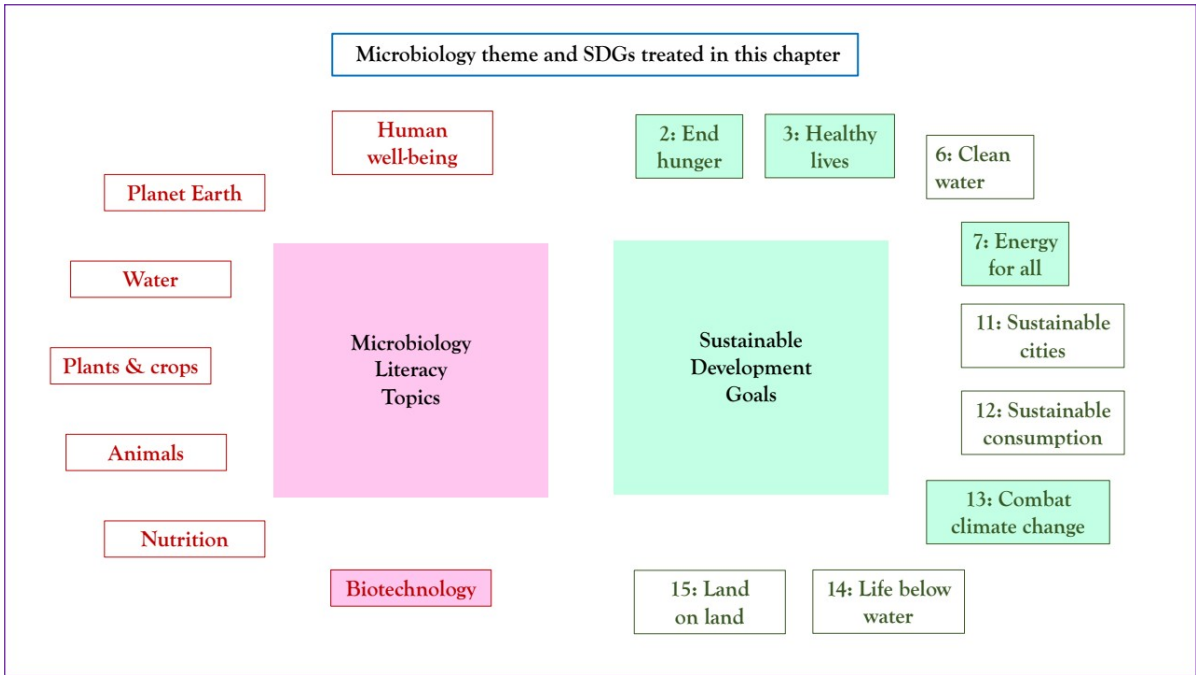
The Importance of Quantitation

Storyline

Microbial life is intrinsically coupled to the transformation of substrates to products and the simultaneous generation of metabolic energy. Assessment of microbial transformation processes requires a clean quantitative analysis of substrates and products to derive a balanced process equation. This equation allows also to quantify the energy released in the process and with this, the amount of cell material that can be formed by microbial growth. Examples are given with aerobic glucose oxidation and with fermentations forming yoghurt, sauerkraut, silage, beer, wine, and bread. Especially the formation of gaseous products exemplifies the power that is released in microbial metabolism. Quantitative aspects of microbial activities are especially important in commercial applications of microbes. Microbiological production of simple organic acids (lactic acid, citric acid), of microbial biomass (yeast), and of pharmaceuticals (vitamins, antibiotics), involves strictly controlled processes whose success depends on exact amounts of (often expensive) substrates provided in huge quantities, requiring exact predictions on the basis of reliable calculations.

The Microbiology and Societal Context

The microbiology: Respiration; fermentation; energy/ATP generation; electron acceptors, fermented foods and beverages; microbial cooperativity; methane; microbial greenhouse gas production. *Sustainability issues:* hunger, health; energy, climate change.



1. ***Microbiology is biochemistry in action.*** After our wedding, my wife and I invited my lab crew to a little party in our apartment, with onion cake and „Federweisser", a half-fermented young grape wine that is sold in early fall and is still in active fermentation, still a little sweet but already with some alcohol to it. We did not finish it off entirely; one of the plastic containers was still half full after the guests left, and my wife screwed it tight and put it out on the balcony. Next morning, we heard from our fellow tenants below that their terrace had been covered with some sticky reddish liquid smelling like wine. The plastic container lay as an exploded wreck on our balcony. We became very good friends with those fellow tenants below.

Ralph Wolfe, one of the leading spirits in microbiology in the later 1900s, used to say „Microbiology is biochemistry in action". What he meant was that the activity of microbial biochemistry can often be observed easily with the naked eye, without complex analytical machinery.

2. ***Microbial metabolism operates in terms of chemistry and biochemistry.*** Microbial metabolic activities, as biological processes in general, catalyze biochemical reactions that can be described in the quantitative terminology of chemistry. Thus, the aerobic oxidation of glucose, as many microbes and also higher animals and we ourselves catalyze it, follows a simple equation that every biologist should know:

$$C_6H_{12}O_6 + 6\ O_2 \rightarrow 6\ CO_2 + 6\ H_2O \qquad \text{(eq. 1)}$$

This reaction tells us that complete oxidation of one mol of glucose to CO_2 requires 6 mol of O_2, and that 6 mol of CO_2 and 6 mol of water is formed in this process. In the opposite direction, this reaction describes the net process of photosynthesis, i.e., the formation of plant cell material (primarily sugars) from CO_2, with simultaneous production of O_2.

3. ***Microbial metabolism creates profound changes in our world.*** In summer, photosynthesis by algae in the upper water layers of small lakes produces O_2 and organic matter, i.e., algal cells. A major part of the algal biomass sinks to the lower water body that does not mix with the surface water due to thermal stratification (i.e. because cool liquids tend to sink and warm liquids tend to rise, surface warming of static water bodies in summer creates a warm surface layer which does not mix with cooler lower layers: they become stratified in non-mixing layers. And not only do the water layers not mix, the materials present in them do not vertically mix either).

Aerobic degradation of the algal organic matter by small animals and microbes according to eq. 1 (if we take the sugar molecule as a representative of biomass) will consume O_2 in the lower water body. Since the solubility of O_2 in water is only about 10 mg or 300 µmol per litre at 10°C at air saturation, water has a very limited O_2 storage capacity and, as a consequence, O_2 resources in the deeper waters soon expire, with serious consequences for fish and other animals. This problem is enhanced if the productivity, i. e. the intensity of photosynthesis in the upper layer, and organic matter degradation in the lower layers of the lake, is enhanced by the ingress of nutrients/fertilizer from farming operations, especially phosphate (i.e. eutrophication). Thus, biological activities create entirely different life conditions in such a lake, an oxygen-oversaturated upper part and an oxygen-deprived or entirely anoxic lower water body, rendering it uninhabitable for higher life forms.

4. ***Microbial metabolism is all about energy changes and ATP formation.*** A chemical process as described in eq. 1 is also associated with a change of the energy contents of the

reacting components, as substrates are converted to products. In biochemical processes, we look at the change in the so-called Gibbs' free energy, which is the freely available energy of a system (and includes the change (Δ) in enthalpy and entropy; $\Delta G = \Delta H - T\Delta S$). ΔG values of formation of biological reactants can be looked up in tables (e. g., Thauer et al., 1977; Amend and Shock, 2001). These values usually refer to 1 molar aqueous solutions of dissolved compounds, gases at 1 atm pressure, and a temperature of 25°C (Gibbs` free energies of formation under „standard conditions", assigned as ΔG_f).

For equation 1, we can calculate the difference between the standard energies of formation between the substrates and products for standard conditions as ΔG_0 = -2870 kilo Joules (kJ) per mol. The negative value tells us that the equilibrium of the reaction is on the right side and that the reaction is exergonic, i.e., that free energy is released by the process. The opposite would be true with a positive ΔG value.

The energy released in aerobic respiration is mainly converted into ATP (Fig. 1). Synthesis of ATP from ADP and inorganic phosphate (P_i) is an endergonic reaction that requires energy:

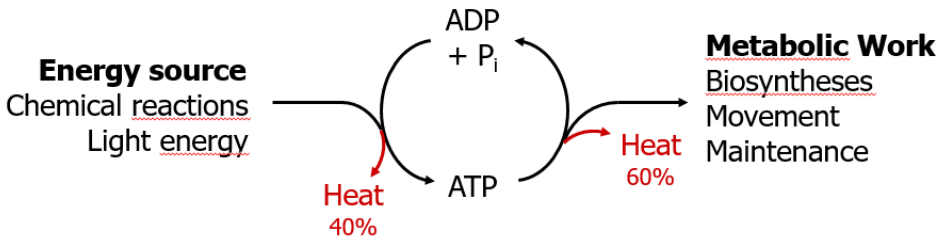
$$ADP + P_i \rightarrow ATP + H_2O \qquad \Delta G_0 = +32 \text{ kJ per mol} \qquad \text{(eq.2)}$$

Since the reactants inside the cell are not present at 1 M but at substantially lower concentrations, we have to calculate the „real" ΔG from ΔG_0 in eq. 2, via the simplified Nernst equation $\Delta G = \Delta G_0 + RT \ln K$, in which R is the general gas constant, T the absolute temperature and K the ratio of activities (actual concentrations/pressures normalized to standard concentrations/pressures) of products over substrates. For most calculations describing processes close to standard temperature (25°C) this equation can be further simplified to

$$\Delta G = \Delta G_0 + 5.7 \lg K \text{ kJ per mol, or } \Delta G = \Delta G_0 + 5.7 \, lg \frac{[Products]}{[Substrates]} kJ \, per \, mol \quad \text{(eq.3)}$$

in which lg K is the decadic logarithm of the ratio of product over substrate activities.

Fig. 1



With realistic concentrations of the reactants in the living cell (ATP = 10 mM, ADP = 1 mM, P_i = 10 mM; values determined with happily growing *Escherichia coli* cells, see Thauer et al., 1977), the ΔG_0 value of ATP synthesis (eq. 2) under physiological conditions shifts to ΔG = +49 kJ per mol.

If we further consider that every metabolic process contains irreversible steps in which part of the available energy is converted to heat, we have to add a further amount of energy to the cost of ATP synthesis, resulting in a total expenditure of 60-70 kJ per mol ATP (Thauer et al., 1977; Schink, 1997).

In aerobic respiration, the high energy yield (-2870 kJ per mol; eq. 1) can produce at maximum 38 ATP per mol glucose (see biochemistry textbooks). Dividing 2870 kJ by 38 yields about 75 kJ per mol ATP, meaning that we get rather close to the theoretical minimum value for ATP synthesis as derived above, and that ATP synthesis in aerobic respiration is rather efficient. I should add that not all aerobic bacteria exhibit the same efficiency in ATP synthesis in their respiratory chain, and that their total ATP yield can be substantially lower.

The heat release in all metabolic processes that was mentioned here can create a problem in large-scale processes in the microbiological industry. Large fermenters, especially those operating with aerobic processes, have to be cooled efficiently to avoid overheating! In agriculture, the heat developed in compost heaps, and the overheating of damp hay, are further examples of excessive heat release in microbial metabolic activities.

Of course, substrates and products in nature usually do not appear in 1 M concentrations. However, most often far lower concentrations on both sides of the reaction equation equalize out to similar values, thus, the calculation of the energy change under standard conditions is at least a realistic first approach to a quantification of the energetics of a microbially catalyzed process. We also have to realize that the concentrations go into the Nernst equation at the logarithmic scale, so minor concentration differences do not really count.

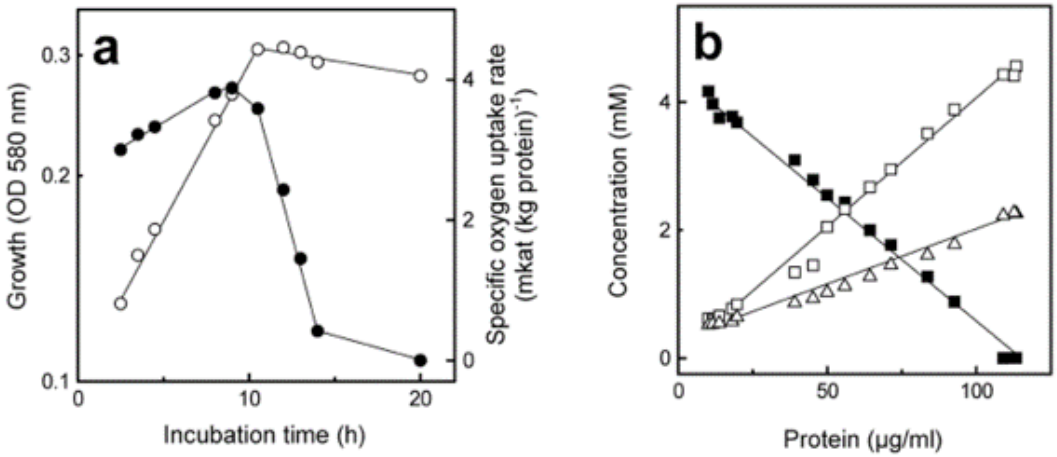
5. ***Microbial growth is determined by generation of ATP - the energy currency.*** The energy that enters the living cell either as chemical energy (as above) or as light energy (with phototrophic organisms) is converted into ATP at rather high efficiency (60%, see above; Fig. 1). ATP serves as general energy currency for the work to be done by the cell, i.e., biosyntheses (growth), transport processes across the membranes, and maintenance expenditures. In growing cells, biosyntheses make up the lion's share of these. The correlation between substrate degradation and biomass formation can be described by an empirical factor, the growth yield (Y). If the amount of ATP that is formed in the degradation of a specific substrate is known, the growth yield can be related to the formed ATP. ATP turnover and cell matter formation are linked through the ATP-related growth yield (Y_{ATP}). This factor has been determined experimentally with many metabolically different bacteria to be about 10 g dry cell mass per mol ATP. Of course, this is not a constant value but depends on the quality of the substrate supplied: synthesis of cell material from sugars requires less energy expenditure than cell matter synthesis from acetate or from CO_2. Determination of growth yields with novel, unusual substrates allows via the Y_{ATP} an estimate on the amount of ATP formed, e. g., in a novel degradation pathway. Of course, a prerequisite of such calculations is that the substrate in question is really the energy-yielding substrate, and that it is also the growth-limiting factor – and not, e.g., the accumulation of toxic reaction products. The situation is again different if cultures are limited by their nitrogen or phosphorus source, which typically are not the energy-limiting substrates.

A chemical reaction describing a microbial process as in eq. 1 should – first of all – be complete, meaning that all compounds, elements, electrons and protons coming in on the left side are accounted for on the right side. In aerobic processes this is not easy to ensure: In a bacterial culture that is shaken under air, growth is followed via turbidity measurements (in a liquid culture, the liquid becomes more turbid as more microbes are produced), and once that does not increase any more we consider growth to be complete, probably because the provided substrate has been used up completely. The formed biomass measured as turbidity is often plotted on a semi-logarithmic scale against time; the specific oxygen uptake rate reaches a

maximum to the end of the logarithmic growth phase and drops soon afterwards (Fig. 2 a; Schleheck and Cook, 2003).

In specific cases in which also the fate of further chemical elements is of interest, a correlation of biomass with transformation of other parameters is quantified in a linearized plot which shows substrate decrease and product increase as a function of biomass growth. An example is shown in Fig. 2 b: In this case, the growth substrate is saccharin which contains seven carbon atoms and one each of sulfur and nitrogen. A major part of the nitrogen ends up in the cell biomass, together with part of the carbon atoms, whereas the sulfur is released as sulfate in a nearly one-by one stoichiometry because the biomass contains only a small amount (about 1%) of sulfur. Such a plot allows to check whether our accounting of products is really complete; of course, the consumed O_2 and the produced CO_2 and H_2O are usually not accounted for.

Fig. 2



6. ***Fermentations: lactic acid and joghurt.*** In contrast to aerobic metabolic processes, anaerobic processes are typically carried out in closed vessels that exclude access of air. This makes the balancing of metabolic processes easy because nothing sneaks in and nothing escapes uncontrolled. Let's look at the classical lactic acid fermentation:

$C_6H_{12}O_6 \rightarrow 2\ CH_3CHOHCOO^- + 2\ H^+ \quad \Delta G_0 = -118$ kJ per mol

Since by definition the ΔG_0 refers to molar concentrations of all reactants, this would mean that also the proton concentration is 1 M and with this the pH is zero. Because this is rather unrealistic for most biological processes it has become a convention to include the proton with its concentration at pH = 7.0 at 10^{-7} M, which gives it a ΔG_f value of -39.9 kJ per mol (5.7 x -7 kJ per mol; see eq. 3). All calculations with this proton concentration are assigned with ΔG_0' rather than ΔG_0. With this, the free energy change of lactic acid fermentation at pH=7.0 shifts to

$C_6H_{12}O_6 \rightarrow 2\ CH_3CHOHCOO^- + 2\ H^+ \quad \Delta G_0' = -198$ kJ per mol (eq. 4)

Lactic acid bacteria convert glucose through the glycolysis pathway to two pyruvates that are subsequently reduced to two lactate molecules. Through this pathway, the hexose (6-carbon) glucose is initially activated to glucose-6-phosphate and further to fructose 1,6-bisphosphate. Later, after cleavage into two triose (3-carbon) phosphates, ATP is synthesized in the glyceraldehyde-3-phosphate dehydrogenase and the pyruvate kinase reaction. Since two

triose phosphate molecules run through the lower part of this pathway, four ATP are synthesized in this part, but two are invested at the beginning in sugar activation. Thus, two ATPs are the net yield derived from conversion of glucose to two lactates. The energy released in this process (eq. 4) easily allows synthesis of two ATP (2 x 70 kJ per mol glucose). There is even some energy left, and we have to reconsider whether our concept of running this process at neutral pH is realistic. Yes, the pH of the milk at the start of yoghurt making is close to neutral, but during the process it shifts to pH = 4-5; the dissociation constant pK (a measure of acidity) of the produced lactic acid is 3.8. At pH = 4.0, the energy release of lactic acid fermentation would still be (-198 + 5.7 x 2 x 3 kJ per mol) = -164 kJ per mol, thus, the overall fermentation process and the associated synthesis of 2 ATP per glucose would not be impeded. Lactic acid bacteria like slightly acidic environments; through production of the comparably strong lactic acid, they inhibit microbial competitors that would otherwise enjoy the rich offer of nutrients in the milk as well. This strategy is exploited by mankind to preserve foods for long-time storage, such as various kinds of sour milk, sauerkraut, kimchi (in Korea), sour beans, silage etc.

Looking at the concentrations of our reactants, the conditions of yoghurt production are not too far off from standard conditions: cow's milk has a total sugar content of about 50 g per l, i. e., 0.25 M hexose, and the lactic acid content of yoghurt after complete fermentation is 5-7%, i. e., 0.5 M.

7. ***Fermentations are dismutations.*** Lactic acid fermentation is a standard example of a simple fermentation. What are fermentations? A good definition says: fermentations are dismutations or disproportionations of carbon compounds. Dismutations (or disproportionations) are chemical processes in which part of a substrate is oxidized and another part is reduced, thus equalizing the overall electron balance. In the sugar molecule, nearly all carbon atoms carry a H and an OH substituent, i. e., they are on average at the redox state zero. In the lactate molecule, only the central carbon is still at this state whereas in the carboxylic group the carbon is at +3, and in the methyl group it is at -3, thus, the carbon has undergone a molecule-internal dismutation that provided the energy assigned in eq. 4.

8. ***Fermentations: alcohol.*** Let's look at another, even more popular fermentation, the alcoholic fermentation:

$C_6H_{12}O_6 \rightarrow 2\ CH_3CH_2OH + 2\ CO_2 \quad \Delta G_0' = -235$ kJ per mol (eq. 5)

Here, we form two different products of different oxidation states (-4 and +4). The biochemical pathway is largely the same as above, i. e. glycolysis to two pyruvate molecules. Pyruvate is decarboxylated to acetaldehyde and subsequently reduced to ethanol. The difference in the free energy change compared to lactic acid fermentation is -37 kJ per mol, corresponding to the energy released in the decarboxylation (twice) of pyruvate. Again, we are dealing with nearly standard conditions: A typical „full" beer contains about 5% (v/v) ethanol which is about 1.3 M ethanol, wines have alcohol contents of 10-18% v/v, i.e., 2.7 – 5 M.

Another example of alcoholic fermentation is the fermentation of bread (see the introductory figure of fermenting bread dough). The added yeast converts part of the added sugar to ethanol and CO_2 which causes the typical bubbly structure of fermented bread types; the ethanol evaporates and causes further bubbles during the baking process.

Also alcoholic fermentation forms only 2 ATP per hexose; a major amount of energy (-235 + 2 x 70 kJ = -95 kJ per mol) is lost as heat. Thus, the equilibrium of the fermentation reaction, including the ATP formation, is far to the right (K = 16.7). This would mean that –

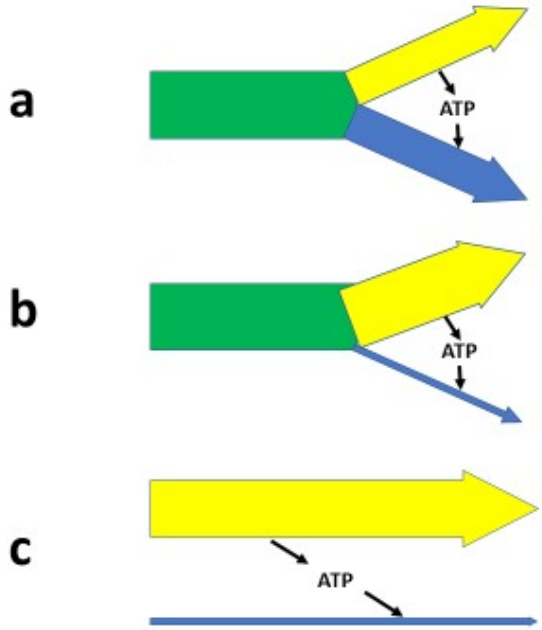
with sufficient substrate supply – the products (two ethanol, two CO_2) could accumulate to 10^4 M concentration and 10^4 atm pressure before the products would thermodynamically inhibit the fermentation process. It is not surprising, therefore, that the fermenting wine in my introductory story blasted the plastic container to annihilation, even if the leftover sugar content was probably only in the range of 0.5 M. Especially fermentations that produce gases show the power of microbial biochemistry in a most impressive manner!

The alcoholic fermentation is rarely ever inhibited thermodynamically by the accumulating products. Rather, the accumulating alcohol (an organic solvent at 1 – 5 M concentration!) becomes toxic for the microbes doing the job because it attacks and partly dissolves the cytoplasmic membranes. This toxic alcohol inhibits the wine fermentation in high-quality wines to leave some remnant flavour-carrying sugar content; wines of lower initial sugar content are either fermented until no appreciable sugar content remains, or the fermentation is stopped by addition of sulfite or by filter sterilization. Yeasts are less susceptible to alcoholic damage than bacteria, in part because of their lower surface-to-volume ratio and because their cytoplasmic membrane is less susceptible to depolarization than that of prokaryotic cells. Yeasts can therefore withstand higher alcohol levels (up to 18% v/v) than bacteria (e.g., *Zymomonas mobilis*, max. 9-10% v/v).

9. ***Fermentations versus Respirations.*** Due to the rather different energy yields of aerobic respiration and anaerobic fermentation (eq. 1 vs. eq. 4), the ratios of energy-yielding (dissimilatory) and biosynthetic (assimilatory) metabolism are rather different (Fig. 3). Whereas in aerobic respiration of sugars and other simple organic compounds usually about 50% of the substrate is oxidized to CO_2 to provide the necessary energy that is needed to assimilate the other half of the substrate into cell material, in fermentations this ratio shifts to about 90:10 because their energy yields are far lower and therefore less substrate can be converted to cell biomass (Fig. 3 a, b).

With many anaerobes, and also with so-called lithotrophic aerobes that oxidize inorganic substrates, the substrate (combination) for energy metabolism and that for cell matter synthesis may even be essentially different (Fig. 3 c): many methanogenic anaerobes oxidize H_2 with CO_2 to form methane (CH_4) for energy generation, but use acetate in combination with CO_2 for cell matter synthesis. The same is true, e. g., for aerobic lithotrophs such as aerobic sulfur oxidizers that oxidize hydrogen sulfide to sulfate while reducing CO_2 to cell matter.

Fig. 3

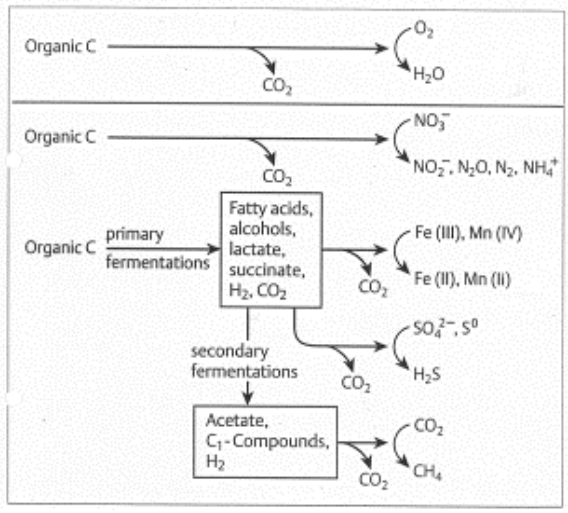


10. Anaerobic respirations.

Beyond aerobic respiration and fermentations as defined above, there are also other respirative types of energy metabolism in which alternative compounds act as electron acceptors for oxidation of organic (sometimes also inorganic) substrates (anaerobic respirations): Some aerobic bacteria can alternatively reduce nitrate to nitrite, nitrogen gas, or ammonia. Ferric iron oxides can be reduced to ferrous iron, sulfate to sulfide, CO_2 to acetate or methane. The sequence of these alternative processes, that are carried out by specialized microbes in every single case (Fig. 4), is determined by the redox potential of the corresponding electron-accepting partial reactions and with this by the reaction energetics of the overall redox reactions: aerobic respiration yields the largest amount of energy, followed by nitrate reduction etc., while methane formation at the end yields the least amount of energy. Again, exact assessments of energy yields need to be based on complete substrate degradation and product formation analyses.

Fig. 4

Sequence of redox processes coupled to mineralisation of organic matter



Redox potentials of electron acceptor systems

Major carriers	E_0' (mV)
O_2/H_2O	+ 810
NO_3^-/N_2	+ 751
NO_3^-/NO_2^-	+ 430
NO_3^-/NH_4^+	+ 363
MnO_2/Mn^{2+}	+ 390
$FeOOH/Fe^{2+}$	+ 150
SO_4^{2-}/H_2S	- 218
S^0/H_2S	-240
CO_2/CH_4	- 244
$2\ H^+/H_2$	- 414
$CO_2/<CH_2O>$	- 434

11. ***What is finally the limiting factor in the microbial transformation of a substrate?*** The energy yield of aerobic respiration of glucose (eq. 1) drives at maximum the synthesis of 38 ATP. This costs in total 38 x 70 kJ = 2660 kJ per mol glucose. The leftover free energy (-2870 + 2660 kJ= -210 kJ) is lost as heat and shifts the reaction to the right side ($K=10^{36}$!). This could lower the glucose concentration on the left side to less than 10^{-36} M which corresponds to less than 1 sugar molecule in the huge Lake Constance on our doorstep with 55 billion m^3 of water. It is obvious that this low concentration will never be reached; the microbes would not find their substrate anymore. The uptake efficiency of a microbe is determined by the substrate affinity of its substrate uptake systems, which often have half-saturation constants in the sub-nanomolar to nanomolar (10^{-10} - 10^{-9} M) range. Below this concentration, substrate uptake is kinetically limited; the organism in question does not "see" its substrate anymore. Thus, aerobic substrate oxidation is typically not limited by reaction energetics but by substrate uptake kinetics.

12. ***Exploitation of minimal energy generation opportunities by cooperation between microbes: production of the greenhouse gas methane.*** The situation is different in fermentative degradation of organic matter to CH_4 and CO_2 as final products which is catalyzed by a complex network of cooperating microorganisms, e. g. in lake sediments or in biogas reactors. Here the various reaction intermediates accumulate in the complex feeding chain of methanogenic communities to concentrations (10^{-6} - 10^{-5} M) that allow just minimal energy shares for the partner organisms involved, in the range of fractions of an ATP equivalent, and these are concentrations that we find in methanogenic environments, such as lake sediment or sewage digestors (Montag and Schink, 2018). Thus, in contrast to aerobic metabolism, anaerobic and especially fermentative metabolic activities are often limited by their reaction energetics.

Relevance for Sustainable Development Goals and Grand Challenges

Although the focus of the Topic Framework is quantitation of microbial metabolism, the examples used, namely respiration and fermentation, are central to a number of SDGs, including:

- **Goal 2. End hunger, achieve food security.** Fermentations provide greater diversity of food materials (some with important cultural value), extend food material shelf lives, and increase their nutritional value. They are thus key to food security and feeding the world.
- **Goal 3. Ensure healthy lives and promote well-being.** Disease due to contaminated food (pathogenic microbes, their toxins, etc.) is a significant problem worldwide. Fermenting food materials creates conditions that inhibit the growth of pathogens and hence reduces food-caused disease. Moreover, it provides additional nutrients that may be lacking or insufficient in the starting material and whose insufficiency negatively impacts health.
- **Goal 7. Ensure Access to affordable, reliable and sustainable energy.** An important source of energy, particularly local, small-scale energy generation, is methane (biogas), produced by fermentation of diverse wastes of food animals and crop plants, and of communal sewage.
- **Goal 13. Climate change.** Methane is a major greenhouse gas and is produced in signficant quantities by ruminant food animals through microbial fermentation of grasses in the rumen. A reduction in the consumption of ruminant meat, as well as measures to reduce methane production by food ruminants, will be essential to reducing emissions of this source of greenhouse gas.

Potential Implications for Decisions

1. ***Individual***
   - **a.** Considering the health benefits of fermented foods, should I increase them in my diet?
   - b. Should I eat more or less meat, especially of ruminants?

2. ***Community policies***
   - **a.** Regulating and managing eutrophication of local water bodies as a consequence of fertiliser use on farms, gardens and public spaces.
   - ***b.*** Education campaigns to inform the public of the consequences of fertiliser use.

3. ***National policies relating to fermentations***
   - **a.** Healthcare economics of fermentation reduction of food-borne illness
   - **b.** Cultural value of local and regional speciality fermented foods
   - **c.** Policies relating to greenhouse gas emissions

Pupil Participation

1. ***Class discussion of the issues associated with fermentation***

2. ***Pupil stakeholder awareness***
    a. Fermentation has positive and negative consequences for the SDGs. Which of these are most important to you personally/as a class?
    b. Can you think of anything that might be done to reduce the negative consequences, especially in the food supply chain?
    c. Can you think of anything that might be done to increase the positive consequences, especially in your diet?
    d. Can you think of anything you might personally do to reduce the environmental footprint of your diet?

3. ***Exercises***
    a. The fermentation of biomass to methane and CO_2 is a perfect example of carbon dismutation: $C_6H_{12}O_6 \rightarrow 3\ CO_2 + 3\ CH_4$ ΔG_0‘ = -420 kJ per mol; the carbon goes from the redox state 0 to +4 and -4. How much ATP can be formed in the overall process that is carried out by at least three different groups of organisms?
    b. To preserve a minimum of remnant sugar content in the fermentation of a poor wine must, would it make sense to stop the fermentation by pressurising the fermentation barrels with CO_2?
    c. Why is lactic acid fermentation used for preservation of food?
    d. Why is the dough for bread or cake making stored for a while with the yeast in it before it goes into the oven?

The Evidence Base, Further Reading and Teaching Aids

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Glossary

Aerobic: a metabolism using molecular oxygen as an electron acceptor

Anaerobic: a metabolism that is independent of molecular oxygen

Oxidation: a process in which a chemical compound releases electrons

Reduction: a process in which a chemical compound receives electrons

Fermentation: a metabolism in which substrates are disproportionated (dismutated) to more oxidized and more reduced products

Respiration: A type of energy metabolism that uses an external oxidant such as oxygen as electron acceptor

Gibbs' free energy: the free energy change of a chemcal reaction that is available for metabolic use

Enthalpy: a measure of the amount of heat that is relased or taken up in a chemical process

Entropy: the part of free energy change that is determned by the degree of disorder of a system; it is the most important part of energy changes in biochemcal processes

Exergonic: a process releasing energy

Endergonic: a process consuming energy

Nernst equation: describes energy changes in chemical processes as a function of temperature and the actual concentrations and pressures of the reactants

ATP: Adenosine triphosphate, the most important energy carrier in the cell. Its hydrolysis to ADP + P_i releases a defined amount of energy that can be used e.g. for biosyntheses

Growth Yield: the amount of cell material formed from a defined amount of substrate

Glycolysis: the most widespread pathway of sugar degradation in microbes, plants and animals

Lithotrophic: a type of energy metabolism using inorganic electron donors

Anaerobic respiration: a type of energy metabolism in oxidized compounds different from molecular oxygen are used as electron acceptors (e.g., nitrate, sulfate, Fe(III))

Feeding chain: a cooperative system in which metabolically different organisms supply each other with substrates (without being eaten themselves, as in a food chain)