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Research Article

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Optimal energy dissipation in growing microorganisms and rectification columns

Abstract: This paper proposes a new point of view in analyzing the optimal Gibbs energy dissipation in growing microorganisms. Small Gibbs energy dissipation in growth would be of biological advantage because less resource is consumed and the biomass yield on these resources could be maximized. It is however not so clear why microorganisms still dissipate considerable amounts of Gibbs energy while growing. Distillation columns are used as a simple qualitative model system in order to gain a qualitative understanding of the question. In both growing microorganisms and continuously operated distillation columns, small energy dissipation values result in small process driving forces and therefore in tentatively slow operation. In microorganisms this entails relatively higher maintenance energy requirements, increasing thereby the resource cost for growth and decreasing the biomass yield. In distillation columns, it results in higher capital and maintenance cost, thereby increasing overall process costs. A simple model is proposed to calculate the biomass yield as a function of Gibbs energy dissipation. It shows that this function goes through a maximum because of maintenance requirements at small dissipations. Experimental data confirm that growing microorganisms dissipate an amount of Gibbs energy that is associated with this maximum.

Keywords: Growth of microorganisms, distillation columns, Gibbs energy dissipation, Kleiber's law, metabolism of microorganisms, thermodynamic driving force

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1 Process efficiency and energy dissipation in growing microbes and distillation columns

From a thermodynamic point of view, living organisms and technical devices have a number of similar thermodynamic characteristics. First, they both represent open systems often operating at steady state. What is more, they both are operating far from equilibrium and consequently are forced to produce entropy continuously. The thermodynamically parallel features could be illustrated by comparing growing microorganisms with, for example, continuously operating rectification columns. In both cases, useful work is produced at the expense of Gibbs energy or exergy dissipation. Rectification columns used for binary distillation separate mixtures into their constituent pure components and thus transform continuously a high entropy feed stream into two low entropy products streams (Figure 1). Taken by itself, this represents a reduction of entropy. However, it is more than compensated for by a continuous injection of heat at high temperature into the boiler at the bottom of the column. This heat can often almost integrally be recovered at the condenser at the top of the column. But while the heat must be supplied to the boiler at the high boiling temperature of the heavy component and thus represents a low-entropy feed stream, it can only be recovered at the low boiling point of the light component, thus producing a large entropy product stream. Therefore, entropy is continuously generated even when allowing for the entropy reduction resulting from the de-mixing of the distillation feed mixture. An equivalent statement says that distillation continuously dissipates energy despite the fact that it produces materials of high chemical potential from a low chemical potential mixture.

Growing microorganisms may often also be imagined to be at steady state (Figure 2). They constantly produce low entropy material in the form of new biomass from high entropy nutrition, because they have

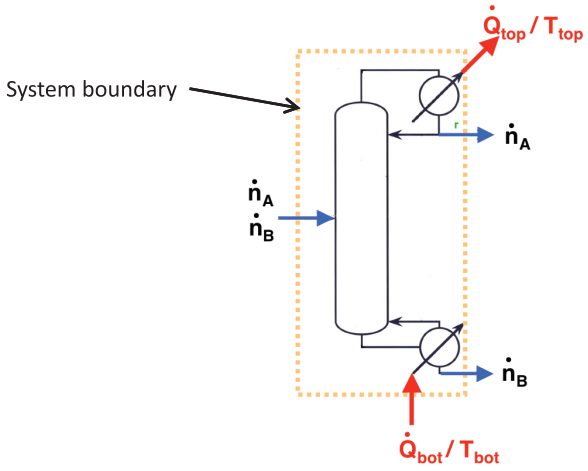

Figure 1. Sketch of a simple binary continuous rectification column separating a mixture of A and B in almost pure A and almost pure B.

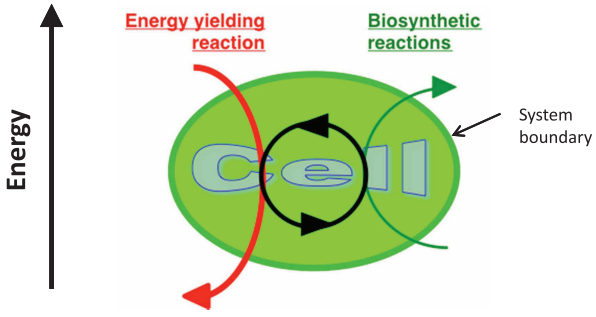

Figure 2. Sketch of a growing cell. The biosynthetic reactions (anabolism) transform simple molecules into highly complex structures, whereas the energy-yielding reaction (catabolism) degrades simple, yet relatively energetic molecules into energy poor debris and thus provides the driving force for anabolism.

to synthesize material in a highly organized and macro-molecular form from quite simple food molecules. This so-called anabolic reaction represents again a continuous reduction of entropy, or a generation of Gibbs energy. This is more than compensated for not by high temperature heat consumption, but by a so-called catabolic reaction, which dissipates more Gibbs energy than what anabolism produces.

In aerobic growth, a complete oxidation of glucose into CO_2 and H_2O is often the catabolic or energy-yielding reaction. In anaerobic fermentation, molecules such as glucose or another energy source are split into smaller molecules such as CO_2 and ethanol (ethanolic fermentation), or lactic acid (lactic acid fermentation) or other substances.

In bioprocess engineering such considerations are important in order to predict the so-called biomass yield $Y_{X/S}$ (see Ref. [1]). This coefficient, defined by Eq. (1), indicates the amount of fresh biomass, expressed in g of dry matter or in C-moles that can be grown per g or C-mol of the main nutritional substrate (often glucose) consumed.

$$Y_{X/S} \equiv \frac{\Delta m_X}{\Delta m_S} = \frac{\dot{m}_X}{\dot{m}_S}. \tag{1}$$

The inverse of $Y_{X/S}$ represents the "cost" of growth, expressed as the amount of substrate consumed per unit of fresh biomass synthesized.

The biomass yield may roughly be predicted from a Gibbs energy balance such as Eq. (2) if one knows $\Delta_{an}G$, the Gibbs energy change of the anabolic growth reaction, which usually is positive or close to zero; $\Delta_{cat}G$, the Gibbs energy change of the catabolic reaction, which must be strongly negative; and $\Delta_r G_S$, the Gibbs energy change of the overall growth reaction.

$$\Delta_r G_S = \Delta_{cat}G + Y_{X/S}\Delta_{an}G. \tag{2}$$

The exact derivation of Eq. (2) is given elsewhere [2]. The Gibbs energies of reaction for catabolism and anabolism may be estimated from the known stoichiometries of these reactions and from the standard Gibbs energies of formation of the involved molecular compounds. In principle, the concentrations and the activity

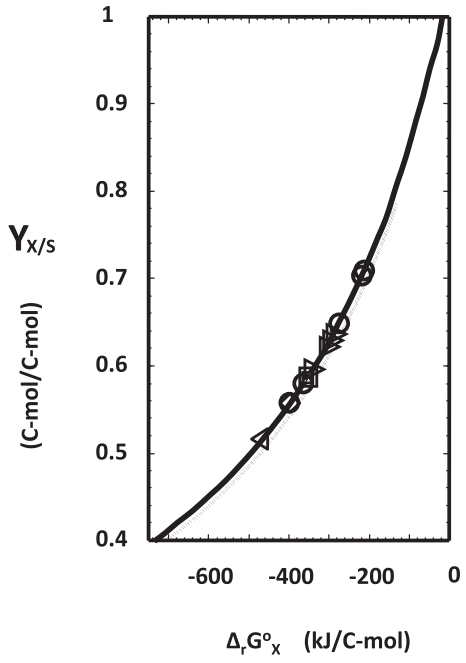

Figure 3. Solid line: relationship between the overall Gibbs energy dissipation, or the Gibbs energy of reaction $\Delta_r G_X$ and the biomass yield for aerobic growth as calculated from a variant of Eq. (2). Markers: observed biomass yields for *K. marxianus* (○), *C. utilis* (□), *S. cerevisiae* (▽), *C. pseudotropicalis* (◇), *E. coli* (△).

coefficients of the involved chemical compounds would have to be accounted for in such calculations. However, the standard Gibbs energies are often so large compared to the concentration-dependent terms that the latter may be neglected in an approximate estimation. The Gibbs energy change of the overall reaction $\Delta_r G_S$, on the other hand, is a priori unknown.

An optimal situation would exist if the catabolic reaction would just release the amount of Gibbs energy needed by the anabolic growth reaction, so that the negative $\Delta_{\text{cat}} G$ term and the positive $Y_{X/S}\Delta_{\text{an}} G$ term on the right side in Eq. (2) just compensate. $\Delta_r G_S$ would then become zero. Setting $\Delta_r G_S$ to zero in Eq. (2) and solving it for $Y_{X/S}$ will yield the highest biomass yield that is allowed by the Second Law of Thermodynamics. However, growth would then constitute an equilibrium reaction, which does not dissipate any Gibbs energy, and therefore would proceed at zero rate.

In order for growth to occur at a finite rate, a thermodynamic driving force must exist in the form of a Gibbs energy dissipation such that $\Delta_r G_S < 0$. This means that less anabolism occurs for a given amount of catabolism (see Figure 2) and that the biomass yield $Y_{X/S}$ in Eq. (2) must be smaller than the theoretical maximal value. The amount of Gibbs energy $\Delta_r G_S$ that is not invested in biomass synthesis but dissipated is equivalent to what is sometimes called "lost work" in an engineering context.

Substituting different negative $\Delta_r G_S$ values into Eq. (2) and solving for $Y_{X/S}$ results in growth yield predictions as a function of Gibbs energy dissipation. Such a prediction is plotted in Figure 3, but the Gibbs energy change of the overall reaction was not expressed per C-mole of carbon and energy substrate consumed as in Eq. (2), but per C-mole of dry biomass grown ($\Delta_r G_X$). The relationship between $\Delta_r G_X$ and the growth yield is non-linear [2]:

$$\Delta_r G_X = \frac{1}{Y_{X/S}} \Delta_{\text{cat}} G + \Delta_{\text{an}} G. \tag{3}$$

The example illustrated by Figure 3 is aerobic growth on glucose [3]. The highest yield of about 1 C-mole of dry biomass per C-mole of glucose is reached for $\Delta_r G_X = 0$, whereas at more negative values of $\Delta_r G_X$ progressively lower $Y_{X/S}$ is predicted. On the other hand, however, one could expect faster growth for more negative $\Delta_r G$ values, because a larger thermodynamic driving force exists.

The markers on the line show the Gibbs energy dissipations of various microbial strains grown in the laboratory [3]. They also were calculated from Eq. (3) used for computing the line in Figure 3, on the basis of experimental biomass yields. They show that aerobic microorganisms dissipate anywhere from −450 to −200 kJ/mol in order to grow fast enough.

Catabolism	$\Delta_r G_X$ [kJ/C-mol]	Biomass yield [C-mol/C-mol]
Aerobic respiration	≈ -350	0.5–0.7
Ethanol fermentation	≈ -250	0.1–0.13
Homolactic fermentation	≈ -400	0.07–0.1
Acetotrophic methanogenesis	≈ -500	0.04
Autotrophic methanogenesis	≈ -700	0.015–0.02

Table 1. Typical biomass yields for various microbial growth systems and Gibbs energy dissipation estimated from a variant of Eq. (2) [4].

The calculations represented in Figure 3 were repeated for a number of anaerobic growth systems (Table 1) [3]. These included three fermentation systems (ethanolic, homolactic, acetotrophic methanogenesis) and one case of anaerobic respiration (autotrophic methanogenesis). In these growth systems, the Gibbs energy changes of the catabolic reactions $\Delta_{cat}G$ are much less negative than the ones in aerobic respiration and result in considerably smaller biomass yields. Substituting the measured biomass yields into Eq. (3) showed however that the Gibbs energy dissipations fall into a similar range as for aerobic growth [4] (Table 1). An exception are autotrophic methanogens, which for some reason dissipate as much as –700 kJ/C-mol of Gibbs energy [5].

The relation between the biomass yield and Gibbs energy of reaction $\Delta_r G_x$ in Table 1 is well understood because it reflects Eq. (3). However, one might be tempted to ask what controls the magnitude of $\Delta_r G_X$ and thus also the biomass yield of the strain. The Gibbs energy dissipations $\Delta_r G_X$ for a very large number of growth experiments have been correlated empirically to the physical properties of the carbon source for growth by Heijnen and Van Dijken [6], thus tentatively explaining the differences between various microbial systems. However, a reason for the general magnitudes of these values has not been proposed. Why would these microorganisms not reduce their $\Delta_r G_X$ and thus increase $Y_{X/S}$? Growth would clearly be slower, but the microorganisms existing since billions of years ought to have time for slow growth.

It is the aim of this paper to develop an answer to this question by examining qualitatively the dissipation in continuous rectification columns and by exploring whether any reason for an "optimal" dissipation in such devices might hint at an analogous one that could explain the Gibbs energy dissipation in microbial growth.

2 Qualitative comparison with rectification columns

In binary rectification columns, boiling liquid descends from plate to plate and is repeatedly contacted with raising vapor. The effects of the plates may be visualized on a so-called McCabe–Thiele diagram, which plots the mole fraction of the lighter compound in the vapor (y_A) versus the mole fraction of the same lighter compound in the liquid (x_A, Figure 4).

The straight lines, termed operating lines, represent the actual relationship between the two concentrations, whereas the curved "equilibrium" line represents the relationship for the two phases at thermodynamic equilibrium. The vertical distances represent therefore the tendency that exists for the vapor phase to increase its content of light component, or, in other words, the existing driving force for mass transfer. According to distillation theory, the plates needed for a given separation may be stepped off as shown in Figure 4 [7].

What makes distillation columns an interesting object for understanding the optimal Gibbs energy dissipation is not only the fact that one may see the driving forces directly on a McCabe–Thiele diagram, but that in addition the Gibbs energy dissipation may be varied when designing the device by changing the so-called boil-up ratio. The liquid exiting from the bottom plate is partially evaporated in the boiler. The resulting vapor stream is sent back into the column, whereas the fraction remaining liquid constitutes the product stream consisting of almost pure heavy component. The boil-up ratio indicates the fraction that will be re-boiled and recycled back into the column.

If a column is designed with a high boil-up ratio (Figure 4a), the operation will consume a large amount of heat. The Gibbs energy (or exergy) dissipation will be large, and the distillation will be expensive. Relatively few plates will be needed because one distills using a large driving force.

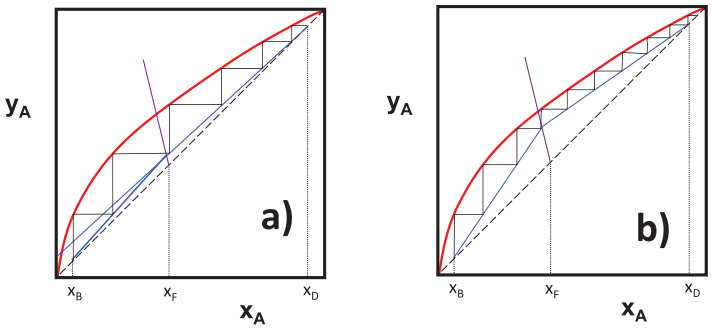

Figure 4. McCabe–Thiele diagram for a continuous binary separation using (a) a high, and (b) a low boil-up ratio. A high boil-up ratio consumes a large amount of energy but necessitates only few distillation plates, whereas a low boil-up ratio limits the energy consumption and thus needs a column with more plates in order to compensate for the fact that it operates with lower mass transfer driving forces. Both designs will separate a feed containing a mole fraction of light component of x_F into a distillate with a light component fraction of x_D and a bottom product with a light component content of x_B.

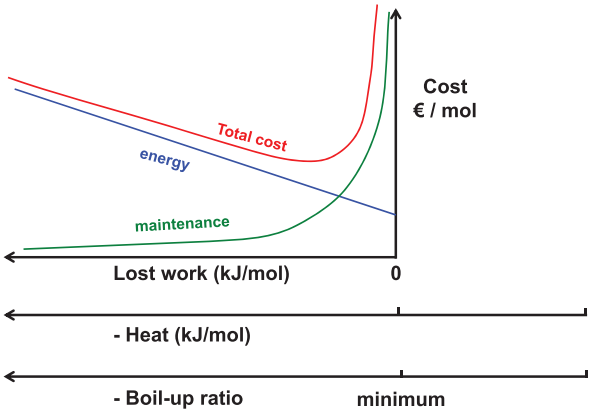

Figure 5. Distillation costs as a function of boil-up ratio. Large boil-up ratios correspond to a high heat consumption and to a large amount of lost work (to the left of the diagram). Lost work may be minimized if an equilibrium situation occurs in the column. This minimizes energy cost but drives maintenance and capital cost toward infinity.

Figure 4b shows a design using a lesser boil-up ratio (see Refs. [7, 8]). Clearly, this set-up will be more efficient because it dissipates less exergy and is thus cheaper. However, the price is lower mass transfer driving forces and consequently slower distillation, which must be compensated for by increasing the plate numbers.

An absolute minimum for energy dissipation could be reached by reducing the boil-up ratio to the point where the straight operating and the curved equilibrium lines touch at some point. This would entail thermodynamic equilibrium on the respective plates with zero mass transfer rates. In order to achieve the desired distillation nevertheless, one would need an infinite number of plates. Thus, operating costs would be minimal but capital and maintenance costs would tend toward infinity. Because of that, designers of real distillation equipment do not approach this minimum boil-up ratio too closely.

Figure 5 is a qualitative plot of the costs as a function of the boil-up ratio. In order to emphasize the analogy to the Gibbs energy dissipation in microbial growth, higher boil-up ratios, representing higher heat consumption and thus higher energy dissipation or more lost work, are plotted toward the left.

A distillation column design with a high boil-up ratio such as illustrated in Figure 4a would appear on the left of Figure 5. It is seen to generate large operating costs because of the high energy consumption. As the boil-up ratio and thus the heat duty is lowered, the energy costs do decrease, but at a certain point the capital and maintenance costs due to the ever increasing number of plates increase so steeply that the total cost of distillation goes through a minimum and then starts to increase as well. In the case of distillation columns, it is therefore easy to see how this minimum defines the optimal boil-up ratio, and that distillation columns ought to be designed for that. Instead of approaching a minimal boil-up ratio too closely, one must accept the energy dissipation at the optimal point.

3 Optimal Gibbs energy dissipation in growing microorganisms

Just as in distillation columns, maintenance is also an issue for such structures as microbial cells. Proteins will be thermally denatured after a certain time of service, membranes will become leaky, and DNA accumulates errors. There are natural repair mechanisms that constantly rectify these errors, but they consume energy. The practically observed biomass yields therefore do not only depend on the energy substrate consumption needed to provide the energy for growth, but some substrate is also catabolized for providing maintenance energy:

$$Y_{X/S} = \frac{\dot{m}_X}{\dot{m}_{S,\text{growth}} + \dot{m}_{S,\text{maint}}}. \tag{4}$$

While a lower Gibbs energy dissipation would decrease both the rate of fresh biomass synthesis and the rate of substrate consumption for pure growth, the substrate consumption for maintenance energy would not be reduced because the rate of denaturation would stay constant. Indeed, Tijhuis, Van Loosdrecht, and Heijnen [9] have examined a large body of literature data on maintenance requirement and have recalculated it in terms of the maintenance Gibbs energy dissipation $\dot{g}_{\text{maint}}$. They found that all data could be satisfactorily represented with a standard deviation of 40% by the following empirical equation:

$$\dot{g}_{\text{maint}} = 4.5\ \text{kJ C-mol}^{-1}\ \text{h}^{-1} \cdot \exp\left\{\frac{-69\ \text{kJ/mol}}{R}\left(\frac{1}{T} - \frac{1}{298\ \text{K}}\right)\right\}. \tag{5}$$

Obviously denaturation of microbial constituents is only influenced by temperature and has an activation energy of 69 kJ/mol. If therefore growth slows down too much, the substrate consumption for maintenance $\dot{m}_{S,\text{maint}}$ will become the dominant factor in Eq. (4) and the biomass yield will decrease.

The cost of growth, corresponding to the inverse of $Y_{X/S}$, thus must be the sum of two factors as shown by this modified form of the famous Herbert–Pirt equation:

$$\frac{1}{Y_{X/S}} = \frac{1}{Y_{X/S}^{\text{growth}}} + \frac{\dot{g}_{\text{maint}}}{\Delta_{\text{cat}}G \cdot \mu}. \tag{6}$$

$Y_{X/S}^{\text{growth}}$ represents the ideal biomass yield for pure growth without maintenance. It is this coefficient that ought to be substituted into Eqs. (2) and (3) when calculating $\Delta_r G_S$ or $\Delta_r G_X$. The latter expression can therefore be used to express $Y_{X/S}^{\text{growth}}$ as a function of $\Delta_r G_X$. Substituting this into Eq. (6) yields the first right-hand term of Eq. (7).

The symbol μ in Eq. (6) denotes the specific growth rate in h^{-1}. According to non-equilibrium thermodynamics, μ depends on the driving force for growth, $\Delta_r G_X$, and may be assumed proportional to it ($\mu \approx L \cdot \Delta_r G_X$). As a result, Eq. (6) becomes

$$\frac{1}{Y_{X/S}} = \frac{\Delta_r G_X - \Delta_{\text{an}}G}{\Delta_{\text{cat}}G} + \frac{\dot{g}_{\text{maint}}}{\Delta_{\text{cat}}G \cdot L \cdot \Delta_r G_X}. \tag{7}$$

The left-hand side of Eq. (7) may be interpreted as the overall cost of growth in terms of C-moles of energy substrate consumed per C-mole of dry biomass formed. The first right-hand term represents $1/Y_{X/S}^{\text{growth}}$, the substrate cost for pure growth, whereas the second right-hand term indicates the additional substrate consumption for maintenance per C-mole of dry biomass.

Equation (7) was plotted in Figure 6 using the real data for aerobic growth. The only adjustable parameter was L. One single value of $L = 0.5 \cdot 10^{-3}$ C-mol $\text{kJ}^{-1}\ \text{h}^{-1}$ was used for all five different growth systems in Table 1. As may be seen, the cost structure for growth in microbes follows quite closely the qualitative curves for distillation. The optimum Gibbs energy dissipation is found as the minimum of $1/Y_{X/S}$.

Figure 7 shows both $Y_{X/S}^{\text{growth}}$ and the real biomass yield, allowing for maintenance, as a function of Gibbs energy dissipation. Whereas $Y_{X/S}^{\text{growth}}$ reaches a value close to unity when $\Delta_r G_X$ tends toward zero, the real biomass yield goes through a maximum at $\Delta_r G_X$ around −200 kJ/C-mol. The range of experimentally found $\Delta_r G_X$ values occurred at a region where maintenance requirements just start to make a serious difference between the ideal and the real biomass yields.

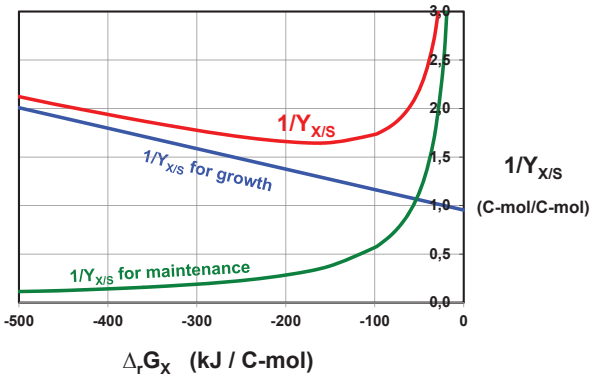

Figure 6. The substrate "costs" for aerobic microbial growth as a function of Gibbs energy dissipation, calculated from Eq. (7). As $\Delta_r G_X$ is lowered, the costs for pure growth $1/Y_{X/S}^{\text{growth}}$ decreases toward a minimal value of one but the maintenance costs tend toward infinity.

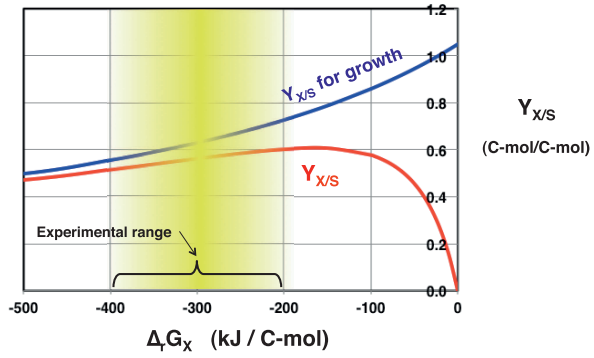

Figure 7. The biomass yield for growth only and the biomass yield including the maintenance requirements as a function of Gibbs energy dissipation. Calculated from Eq. (7) for aerobic growth. The experimentally observed data fell into the range indicated.

Similar model calculations were performed for all five growth systems mentioned in Table 1 with very similar results. A report with details on these calculations is in preparation [10]. They also explained why autotrophic methanogenesis dissipates so much more Gibbs energy than the other cases. Indeed, the methanogen strain *Methanobacterium thermoautotrophicum* used in these experiments is thermophilic and was grown at 65 °C and not at 30 °C as the other four types of microorganisms. At this temperature the maintenance Gibbs energy requirements are considerably higher and the real biomass yield started to deviate from the ideal one already at $\Delta_r G_X$ values of –800 kJ/mol. In accordance with the other examples, this large Gibbs energy dissipation was therefore the optimum for this strain, thus explaining the low growth yields.

In industrial rectification units, not only can the costs be minimized by designing the plants at an optimal boil-up ratio and thus at an optimal exergy dissipation, but the capital and maintenance costs may be further reduced by scaling the plants up, and by replacing many small columns by one very large one. Indeed, the classical text of Peters and Timmerhaus [11] states that the construction costs of plants often scale proportionally to their capacity to the 0.7th power. This is also expected to hold for maintenance costs.

The question arises whether the evolution from microorganisms to large animals has a similar background and permitted life to function with smaller driving forces and therefore to increase the efficiency of the process. Many authors have studied the increase of maintenance energy dissipation with the size of animals and other organisms [12, 13], and the results include the famous mouse-to-elephant curve by Kleiber [14]. This widely known correlation plots the heat given off by a large variety of animals as a function of their mass. As the data primarily concern the basal metabolism, it may be interpreted as an approximation of the rate of heat dissipation due to maintenance. Also, in aerobic catabolism the rate of heat dissipation is equal to the rate of Gibbs energy metabolism because for this reaction the entropy change is close to zero and $\Delta G \approx \Delta H$. Such allometric curves ought therefore to reflect the Gibbs energy dissipation rate due to maintenance in animals. Indeed, it can easily be verified that Eq. (5) for microorganisms also lies practically right on Kleiber's curve.

The fact that Kleiber and many other authors concluded that the energy dissipation is proportional to the mass of the animal to the 0.75th power, an exponent close to what was found in the chemical process industry, is intriguing and might confirm the hypothesis that larger organisms may be able to live with reduced

maintenance costs as compared to microorganisms, which allows them to dissipate less Gibbs energy and live more efficiently from an energy point of view.

4 Conclusions

Minimizing the Gibbs energy dissipation in growing microorganisms appears to be biologically advantageous because fewer resources are consumed and the process becomes thermodynamically more efficient. However, the Gibbs energy dissipation also represents the overall driving force from the point of view of non-equilibrium thermodynamics. More efficient growth processes would proceed at a slower rate. In distillation column design, a similar situation exists, and slow operation would force a designer to increase the size of the equipment, thus augmenting capital and maintenance costs. Similarly, slow growth in microbes would result in more of the biological structure degrading by thermal denaturation and would therefore increase biological maintenance requirements. As a function of Gibbs energy dissipation, biomass yields therefore must go through a maximum. Experimental data confirms that observed Gibbs energy dissipation in different types of growing microbes approximately correspond to this optimum.

List of symbols

$\Delta_r G_S$	Gibbs energy of growth reaction, kJ/C-mol of substrate consumed
$\Delta_r G_X$	Gibbs energy of growth reaction, kJ/C-mol of dry biomass grown
$\Delta_{an} G$	Gibbs energy of anabolic reaction, kJ/C-mol
$\Delta_{cat} G$	Gibbs energy of catabolic reaction, kJ/C-mol
$\dot{g}_{maint}$	Rate of Gibbs energy dissipation for maintenance, kJ h^{-1} C-mol^{-1}
$\dot{m}_S$	Rate of substrate consumption, g/h, C-mol/h
$\dot{m}_X$	Rate of biomass production, g/h, C-mol/h
μ	Specific growth rate, h^{-1}
$\dot{n}_A$	Flow rate of light component, mol/s
$\dot{n}_B$	Flow rate of heavy component, mol/s
L	Proportionality coefficient between μ and $\Delta_r G_X$, C-mol kJ^{-1} h^{-1}
$\dot{Q}_{bot}$, $\dot{Q}_{top}$	Rate of heat injection at bottom and heat recovery at top of column, respectively, W
y_A, x_A	Mole fraction of light component in the vapor and in the liquid phase, respectively
x_F, x_B, x_D	Mole fraction of light component in, respectively, the feed, the bottom product, and the top product
$Y_{X/S}$	distance growth yield, g/g, C-mol/C-mol

References

[1] von Stockar, U., Biothermodynamics of live cells: A tool for biotechnology and biochemical engineering, J. Non-Equilib. Thermodyn., 35 (2010), 415–475.

[2] von Stockar, U., Vojinović, V., Maskow, T. and Liu, J.-S., Can microbial growth yield be estimated using simple thermodynamic analogies to technical processes? Chem. Eng. Process., 47 (2008), 980–990.

[3] von Stockar, U., Maskow, T., Liu, J.-S., Marison, I. W. and Patiño, R., Thermodynamics of microbial growth and metabolism: An analysis of the current situation, J. Biotechnol., 121 (2006), 517–533.

[4] von Stockar, U. and Liu, J.-S., Does microbial life always feed on negative entropy? Thermodynamic analysis of microbial growth, Biochim. Biophys. Acta, 1412 (1999), 191–211.

[5] Schill, N., Liu, J.-S. and von Stockar, U., Thermodynamic analysis of growth of Methanobacterium thermoautotrophicum, Biotechnol. Bioeng., 64 (1999), 75–81.

[6] Heijnen, J. J. and Van Dijken, J. A., In search of thermodynamic description of biomass yields for the chemotrophic growth of micro-organisms, Biotechnol. Bioeng., 39 (1992), 833–858.
[7] King, C. J., Separation Processes, 2nd edn, Mc-Graw Hill, New York, 1980.
[8] Stichlmair, J. G. and Fair, J. R., Distillation, Principles and Practices, Wiley-VCH, New York, 1998.
[9] Tijhuis, L., Van Loosdrecht, M. and Heijnen, J. J., A thermodynamically based correlation for maintenance Gibbs energy requirements in aerobic and anaerobic chemotrophic growth, Biotechnol. Bioeng., 42 (1993), 509–519.
[10] von Stockar, U., Microbial biomass yields reflect an optimum between small Gibbs energy dissipation and small maintenance requirements, in preparation.
[11] Peters, M. S. and Timmerhaus, K. D., Plant Design, McGraw-Hill, New York, 1958.
[12] Brown, J. and West, G., One rate to rule them all, New Scientist, 2445 (2004), 38–41.
[13] Glazier, D. S., A unified explanation for diverse metabolic scaling in animals and plants, Biol. Rev., 85 (2010), 111–138.
[14] Kleiber, M., Body size and metabolic rate, Phys. Rev., 27 (1947), 511–541.

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