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Volume 21

Microbial Biochemistry

Edited by

J. R. Quayle, B.Sc., Ph.D., F.R.S.

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Consultant Editors' Note

The MTP *International Review of Biochemistry* was launched to provide a critical and continuing survey of progress in biochemical research. In order to embrace even barely adequately so vast a subject as "progress in biochemical research," twelve volumes were prepared. They range in subject matter from the classical preserves of biochemistry—the structure and function of macromolecules and energy transduction—through topics such as defense and recognition and cell differentiation, in which biochemical work is still a relatively new factor, to those territories that are shared by physiology and biochemistry. In dividing up so pervasive a discipline, we realized that biochemistry cannot be confined to twelve neat slices of biology, even if those slices are cut generously: every scientist who attempts to discern the molecular events that underlie the phenomena of life can legitimately parody the cry of *Le Bourgeois Gentilhomme*, "Par ma foi! Il y a plus de quarante ans que je dis de la Biochimie sans que j'en susse rien!" We therefore make no apologies for encroaching even further, in this second series, on areas in which the biochemical component has, until recently, not predominated.

However, we repeat our apology for being forced to omit again in the present collection of articles many important matters, and we also echo our hope that the authority and distinction of the contributions will compensate for our shortcomings of thematic selection. We certainly welcome criticism—we thank the many readers and reviewers who have so helpfully criticized our first series of volumes—and we solicit suggestions for future reviews.

It is a particular pleasure to thank the volume editors, the chapter authors, and the publishers for their ready cooperation in this venture. If it succeeds, the credit must go to them.

H. L. Kornberg
D. C. Phillips

Preface

Most reviews these days start with the author or editor presenting a nest of Chinese boxes to the reader and then, because of the wide-ranging title grandiloquently written on the outer case, the author in his introduction, with appropriate patter, proceeds to strip away successive cases until he is left with one that contains what he is really going to concern himself with. With the title of "Microbial Biochemistry" on the present outer case I too must extract a smaller box from within and explain to the reader the somewhat smaller print written on its lid.

The area of microbial biochemistry that forms the setting to this volume is the borderland between metabolism and energetics. With the main metabolic pathways now well charted, one of the primary thrusts in microbial biochemistry is toward a full understanding at the physicochemical level of the various mechanisms of energy transduction carried out by microbes. As the knowledge of cellular metabolism and energy transduction deepens, it becomes more feasible to calculate how much cell material should, or could, be made from a given quantity of substrate and/or energy source. This can then be compared with the values determined experimentally by the growth physiologist. The closeness of fit is a measure of the extent to which we understand the relationship between metabolism and energetics. It is therefore appropriate that the first chapter should be written by Professor Stouthamer on the search for correlation between theoretical and experimental growth yields. Readers may find it interesting to reflect on the progress that has been made since the pioneering studies of Monod, Gunsalus, Elsden, and their associates. Such correlations can only be based on the understanding of energy metabolism operating in the different modes of microbial life—aerobic, anaerobic, and photosynthetic; chapters 2, 3, and 4 describe the present state of play in these areas.

The development of the continuous culture chemostat over the last 20 years has provided an instrument to the growth physiologist as important as the spectrophotometer is to the biochemist. Much of the correlation between microbial growth behavior and biochemistry has only been made possible through applications of continuous culture technique, as will be evident throughout chapter 1. This book would therefore be incomplete without an account of some of the applications of the chemostat to microbial biochemistry. Professor Bull and Dr. Brown recount a selection of these in chapter 5 and in addition point the way to new and fascinating fields that the chemostat is now opening up. It is most important and timely that microbiologists and biochemists of all followings should be aware of the potentialities of continuous culture in mixed substrate and heterogeneous substrate systems and also of the new kinds of microbial biochemistry and population dynamics that are starting to emerge from the study of interacting microbial communities.

Chapters 1 through 5 encompass a central area lying between metabolism and energetics. Two topics have then been chosen where metabolism, energetics, and technological potential are combined. The first of these topics is dealt with in chapter 6 by Dr. Dalton, who describes the different modes of utilization of inorganic nitrogen by microbial cells. This is an area of great importance in growth yield studies and it abounds in hard and challenging biochemistry; the potential

prize of grafting microbial nitrogen fixation into crop plants also hovers in the distance life a Holy Grail. The second of these topics is dealt with in a composite chapter by Professor Wolfe and Dr. Higgins on the microbial biochemistry of methane. This too abounds in hard and challenging biochemistry: here lie problems of metabolism and energetics that have resisted solution for three decades. The recent recognition of the great importance of methane in both terrestrial and celestial carbon cycles, and its central position in the technologies of waste recycling and possibly biomass production, have added a new urgency to fundamental researches into its microbiology and biochemistry.

Finally, bearing in mind that this volume is one of an international review series, it may be noted that it is written by authors from five different countries.

J. R. Quayle

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The Search for Correlation Between Theoretical and Experimental Growth Yields

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With slight exaggeration one can say that the evolution of microorganisms has led to the existence of an enormous number of organisms with more or less the same cell structure but all differing in the nature of their energy-yielding mechanisms. One can distinguish differences in the number of substrates that can be used, the pathways by which these substrates are catabolized, the number of electron acceptors that can be used, the complexity of the respiratory chain, and the number of essential cellular components that can be formed from the ingredients of the growth medium. It is therefore evident that the study of the relationship between energy production and growth forms a central theme in microbiology.

During heterotrophic growth the utilization of a certain amount of substrate will give rise to the formation of a certain amount of new cell material. The yield of new cell material formed from a substrate will mainly depend on the amount of energy generated during catabolism and the amount of energy needed for the synthesis of new cell material. The purpose of yield studies in microorganisms is to find the relationship between substrate utilization, ATP generation, and the formation of new cell material. The interpretation of yield studies is easiest for microorganisms growing anaerobically, because in this case the ATP production from substrates that are degraded by known catabolic pathways can be directly calculated. Anaerobic experiments are therefore ideally suited to identifying the environmental factors that influence the relationship between energy production and growth. For growth with external hydrogen acceptors, yield studies are more difficult to interpret because in many cases the efficiency of oxidative phosphorylation is not known with certainty.

During the last few years the relationship between energy production and growth has been intensively studied. This chapter attempts to present an overall picture of this relationship integrated from the large number of papers on this subject. A fairly complete picture can be obtained about the various factors that influence molar growth yields. The evidence indicating that under some growth conditions there is a discrepancy between the rate of ATP production by catabolism and the rate at which ATP can be used for the formation of microbial cell material is presented. A speculative discussion on the various possible mechanisms that may adjust the rate of ATP production to the needs of anabolism is included. It is argued that the evolution of microorganisms has not led to mechanisms that result in an optimal growth yield under each condition of growth, but instead has led to great flexibility for growth under the maximum number of different conditions and to possibilities for rapid adaptation to changes in the environmental conditions.

THEORETICAL CALCULATIONS ON THE ATP REQUIREMENT FOR THE FORMATION OF MICROBIAL BIOMASS

Influence of the Carbon Source and Complexity of the Medium

In theoretical calculations of the ATP requirement for the formation of cell material, the macromolecular composition of the cells is taken as a base. Subsequently the ATP requirement for the formation of each cell constituent is calculated. Such calculations have been performed by Gunsalus and Shuster (1), Forrest and Walker (2), and Stouthamer (3). The last author used the detailed analysis of the cell composition of *Escherichia coli* by Morowitz (4) as a base. The ATP requirement for the formation of cell material of this composition from glucose and preformed monomers (amino acids and nucleic acid bases) and from glucose and simple inorganic salts is given in Table 1. The results show that, theoretically, 31.9 g cells can be formed per mol of ATP for growth with glucose and preformed monomers and 28.8 for growth with glucose and inorganic salts. It is remarkable that the difference between these values is relatively small, which is due to a small ATP requirement for monomer synthesis from glucose, as shown in Table 1. With other carbon sources the situation is completely different. The ATP requirement for the formation of cell material from pyruvate and preformed monomers and from pyruvate and inorganic salts is included in Table 1 for comparison. The results show that the nature of the carbon source has a strong influence on the ATP requirement for the formation of cell material. The amount of cell material formed per mol of ATP from pyruvate and inorganic salts is much smaller than the amount formed from glucose and inorganic salts. This difference is due to a larger ATP requirement for monomer formation and for transport processes during growth on pyruvate than during growth on glucose. Furthermore, during growth on

Table 1. ATP requirement for the formation of microbial cells from glucose or pyruvate in the presence or absence of amino acids and nucleic acid bases[a]

Macromolecule	Amount of macromolecule (g/100g cells)	ATP required (10^4 × mol/g cells formed) A	B	C	D
Polysaccharide	16.6				
G6P formation		10.3	10.3	61.5	61.5
Polymerization		10.3	10.3	10.3	10.3
Protein	52.4				
Amino acid formation		0	13.5	0	148
Polymerization		191.4	191.4	191.4	191.4
Lipid	9.4	1.4	1.4	27	27
RNA	15.7				
Nucleoside monophosphate formation		14.8	34.5	37	62
Polymerization		9.2	9.2	9.2	9.2
DNA	3.2				
Deoxynucleoside monophosphate formation		3.8	8.6	8	14
Polymerization		1.9	1.9	1.9	1.9
Turnover mRNA		13.9	13.9	13.9	13.9
Total		257.0	295.0	369.2	539.2
Transport of					
Carbon source		0	0	58.1	148
Amino acids		47.8	0	47.8	0
Ammonium ions		0	42.4	0	42.4
Potassium ions		1.9	1.9	1.9	1.9
Phosphate		7.7	7.7	7.7	7.7
Total ATP requirement		314.5	347.1	475.7	740.2
Gram cells per mol ATP		31.9	28.8	21.0	13.5

[a]Data from Stouthamer (3, 28, and unpublished results). Media: A) glucose, amino acids, and nucleic acid bases; B) glucose and inorganic salts; C) pyruvate, amino acids, and nucleic acid bases; D) pyruvate and inorganic salts.

pyruvate the effect of supplementation of the medium with amino acids and nucleic acid bases is much more pronounced than during growth on glucose. The results in Table 1 demonstrate that, theoretically, 21 g of cell material can be formed per mol of ATP from pyruvate and preformed monomers and 13.5 g of cell material from pyruvate and inorganic salts. The ATP requirement for the formation of cell material in a mineral salts medium with various carbon sources is given in Table 2. Again it is evident that the nature of the carbon source has a very profound influence on the ATP requirement for the formation of cell material. For growth on acetate, theoretically only 10 g of cell material can be formed per mol of ATP. For

Table 2. ATP requirement for the formation of cell material in mineral salts medium containing various carbon sources[a]

Synthesis of	ATP requirement (10^4 × mol/g cells) for growth on			
	Lactate	Malate	Acetate	CO_2
Polysaccharide	71	51	92	195
Protein	339	285	427	907
Lipid	27	25	50	172
RNA	85	70	101	212
DNA	16	13	19	
Transport	200	200	306	52
Total	738	644	995	1538
Gram cells per mol of ATP	13.4	15.4	10.0	6.5

[a]The data are simplified from Stouthamer (3) and Harder and van Dijken (5). The composition of the microbial cells is as given in Table 1.

autotrophic growth this value is only 6.5 g (5), which is due to the very large ATP requirement for monomer formation under these circumstances.

These calculations offer an explanation for two experimental observations. First, for aerobic batch cultures the Y_O values (g of dry weight per g atom oxygen taken up during growth) are smaller for growth on simple compounds than for growth on glucose (6). A Y_O value of 31.9 for growth of *Aerobacter aerogenes* on glucose (7) and a value of 3.9 for growth of *Pseudomonas oxalaticus* on formate (8) may be mentioned as extremes. In a recent review (9), $Y_{O_2}^{max}$ (g of dry weight per mol oxygen taken up, corrected for maintenance respiration) values for chemostat cultures of a number of organisms growing on various substrates have been listed. Many examples can be derived from this review that show that the $Y_{O_2}^{max}$ values for growth on simple compounds are smaller than for growth on glucose. Second, supplementation of a glucose-mineral salts medium with amino acids has scarcely an influence on the Y_O value (10). On the other hand, supplementation with amino acids strongly increases the Y_O value for cells growing on ethanol or acetate. This difference is explained by the higher ATP requirement for amino acid formation during growth on simple compounds than for formation during growth on glucose (compare Table 1). Similarly the results discussed below in "Anaerobic Chemostat Cultures" (see Table 7) show that the ATP requirement for the formation of cell material from citrate is larger than that for its formation from glucose.

ATP Requirement for Transport Processes

There are a number of uncertainties in the calculations treated in the previous section, especially in the amount of ATP required for transport processes. Glucose is transported by the phosphoenolpyruvate:sugar phospho-

transferase system, by which glucose is converted into glucose 6-phosphate during transport (11); therefore no energy requirement is present for glucose transport. In the original calculations (3) the most recent views on transport processes for other compounds were taken into account (12, 13). It was considered that ATP or an energized state of the membrane is involved in transport, as in the concept of transport by chemiosmotic processes (14). According to the chemiosmotic hypothesis the hydrolysis of 1 molecule of intracellular ATP is associated with the extrusion of two protons, by which a membrane potential is generated. Accumulation of K^+ and NH_4^+ was attributed to electrogenic porters and consequently the uptake of 2 K^+ or NH_4^+ ions is associated with the hydrolysis of 1 mol of ATP. The uptake of phosphate was thought to require 1 mol of ATP (13, 14); the uptake of malate similarly requires 1 mol of ATP. However, the amount of ATP associated with the uptake of 1 mol of amino acid was at that time not known and it was assumed that 1 mol of ATP was required for the uptake of 1 mol of amino acid or carbon source. Agreement on the mechanism of transport has since been reached and it has been accepted that transport of substrates occurs by proton symport mechanisms predicted by the chemiosmotic hypothesis (15, 16). It has become clear that β-galactosides in *E. coli* are cotransported with protons, the stoichiometry of the process being 1 proton per molecule of β-galactoside transported (17, 18, 19). Uptake of lactate and of alanine was also associated with the uptake of 1 proton per molecule transported (20). Based on these observations it seems that the amount of ATP required for transport processes during growth has been overestimated in some previous calculations. However, Ramos and Kaback (21) have recently shown that the stoichiometry between the number of protons per mol of solute transported must be dependent on the extracellular pH. Furthermore, Collins et al. (20) selected mutants of *E. coli* during growth in the chemostat with alanine as the growth-limiting carbon/energy source, in which the stoichiometry was altered to 2 or even 4 protons per mol of alanine transported. Due to these changes in the stoichiometry, the mutants are capable of accumulating substrates to higher concentration ratios than the wild type. On the other hand, some doubt has arisen about the number of protons extruded per mol of ATP hydrolyzed (22). Because of this uncertainty, the lack of data about the stoichiometry of amino acid to protons during transport for all amino acids, and the possibility that different ratios exist for one substrate in different organisms and for one organism under different experimental conditions, no revision of the original calculations has yet been performed. Therefore, the amounts of ATP required for transport processes are only estimates (and probably overestimates). For this reason they are given separately in the previous tables, which will make correction easier when more definite data for the amounts of ATP required for transport processes become available.

The data in Table 1 indicate that on theoretical grounds 15 or 27% of the total ATP requirement for the formation of cell material during growth

on mineral salts and either glucose or pyruvate, respectively, is used for transport processes.

It has been stressed before that these estimates are approximations. However, it seems a safe conclusion that the ATP requirement for transport processes during growth on glucose is much smaller than the requirement during growth on pyruvate. Recently, experimental evidence for the influence of the ATP requirement for transport processes on molar growth yields has been presented by Dijkhuizen and Harder (23). They observed molar growth yields of 3.8 g/mol and 3.4 g/mol for growth of *P. oxalaticus* with oxalate and formate, respectively. This was rather unexpected, because formate is assimilated by the ribulose diphosphate cycle and oxalate by the glycerate pathway. Therefore, the ATP requirement for the formation of cell material from formate is much higher than that from oxalate. That the molar growth yields were, nonetheless, so closely similar was explained by the assumption that the energy requirement for oxalate transport has a very great influence on the total energy budget of the organism during growth on that substrate. On the contrary, formate transport was not considered to be an active process requiring energy.

In a later section of this chapter an experimental estimate of the amount of ATP required for transport processes and membrane energization is given. The data indicate a much higher ATP requirement for membrane energization than that calculated on the assumptions mentioned above.

Influence of Cell Composition

The influence of cell composition on the ATP requirement for the formation of cell material is relatively small; in order to evaluate this, the ATP requirement for the formation of cellular macromolecules is given in Table 3. It is evident from these data that the ATP requirement for the formation of protein, RNA, and DNA is larger than the ATP requirement for the formation of polysaccharide and lipid. The composition of *A. aerogenes* differs considerably from that of *E. coli*, which was taken as the basis for

Table 3. ATP requirement for the formation of cellular macromolecules in a glucose-inorganic salts medium[a]

Macromolecule	ATP requirement (10^4 × mol/g macromolecule)
Polysaccharide	123.6
Protein	391.1
Lipid	14.8
RNA	373.2
DNA	330.0

[a] Results from Stouthamer (9). Calculated from the data in Table 1 (column B).

the calculations in the previous sections. A high protein content (75%) and a low polysaccharide content have been reported (24). On the basis of these data it can be calculated that, theoretically, about 25 g of cells per mol of ATP can be formed, a value that does not differ strongly from the value of 28.8 (Table 1, column B) calculated for the composition of *E. coli* as reported by Morowitz (4). It is well known that the composition of microbial cells is influenced by the growth rate and the growth condition (25, 26). The influence of these changes on the ATP requirement for the formation of cell material is extremely small, unless large amounts of storage material are formed.

The influence of growth conditions on the formation of energy storage compounds has been described extensively in a recent review by Dawes and Senior (27). The ATP requirement for the formation of storage materials has been treated by Stouthamer (28). When large amounts of storage materials are formed, the ATP requirement for the formation of cell material is much smaller than in the absence of the formation of storage material. For instance, 81 g of polysaccharide can be formed from glucose per mol of ATP, or 80 g of polymetaphosphate per mol of ATP. The formation of poly-β-hydroxybutyrate from glucose is even associated with net ATP formation and the formation of lipid from glucose scarcely needs ATP. It has indeed been observed that molar growth yields are higher under conditions in which storage materials are formed than under conditions in which they are not. Holme (29) has observed that glycogen deposition occurs in nitrogen-limited chemostat cultures of *E. coli*. The largest amounts of glycogen were deposited at low values of the specific growth rate. The same observations have been made for *A. aerogenes* (Stouthamer and Bettenhaussen, unpublished results). A large accumulation of glycogen coincided with a high value for the molar growth yield for glucose. These and other examples described by Herbert (25) suggest that the formation of storage compounds is largely controlled by the nitrogen content of the medium.

In oxygen-limited cultures of *Azotobacter beijerinckii* and of *Azotobacter chroococcum* the molar growth yield for glucose is much higher than in carbon-limited cultures (30, 31). This effect is explained by the observation that up to 50% of the bacterial dry weight in oxygen-limited chemostat cultures is poly-β-hydroxybutyrate. From these examples it is evident that the formation of storage materials indeed has a profound effect on the molar growth yield, which can be explained by a lower theoretical ATP requirement for formation of cell material under such conditions.

Influence of the Nitrogen Source

There is a large ATP requirement for nitrogen fixation. In cell-free extracts, utilization of 12–15 mol of ATP per mol of nitrogen fixed has been reported (32). Theoretical calculations of the amount of cell material that can be formed per mol of ATP for various assumed ATP requirements per mol of

ammonia have been published by Stouthamer (9). During nitrogen fixation the assimilation of the ammonia formed occurs by the glutamine synthetase/glutamate synthase pathway (for reviews see ref. 33 and Dalton, this volume). Assimilation of ammonia by this pathway requires 1 mol of ATP, whereas ammonia assimilation by glutamate dehydrogenase, which occurs during growth with excess ammonia, does not require ATP. This extra ATP requirement was not taken into account in the previous calculations (9). If this is done, the results described in Table 4 are obtained. During ammonia-limited growth or during growth with nitrate the assimilation of ammonia also occurs by the glutamine synthetase/glutamate synthase system. Theoretically, for ammonia-limited growth or growth with nitrate in a mineral salts medium, 23.1 g of cell material can be formed per mol of ATP, whereas 28.8 g of cell material can be formed with excess ammonia (Table 4).

It is evident that the nature of the nitrogen source in the medium has a very drastic influence on the ATP requirement for the formation of cell material. The amount of cell material that can be formed per mol of ATP is much lower during growth with molecular nitrogen than with ammonia. The experimentally observed molar growth yields are in accordance with these theoretical calculations (34, 35, 36). With growing cells of *Klebsiella pneumoniae* an ATP:N_2 ratio of 30 was observed (35), and for *Clostridium pasteurianum*, there was an ATP:N_2 ratio of about 20 (36). Similarly, in nongrowing cells of a derepressed nitrogen-fixing mutant of *K. pneumoniae* about 30 mol of ATP were required per mol of N_2 fixed (37).

Influence of the Carbon Assimilation Pathway of the Growth Substrate

The calculations given above indicate that the pathway of nitrogen assimilation has a profound influence on the ATP requirement for the formation of cell material. A similar influence is exerted by the carbon assimilation pathway. Different assimilation pathways have been found for growth with methane and methanol (5, 38, 39, Higgins and Wolfe, this volume). The

Table 4. Influence of the nitrogen source on the theoretical amount of cell material formed per mol of ATP[a]

Source	ATP requirement/mol N_2 fixed	Cell material (g)/mol ATP
NH_3		28.8
NO_3'		23.1
N_2	12	11.1
	18	8.7
	24	7.1
	30	6.0

[a] For growth with molecular nitrogen various ATP:N_2 ratios are used. The value of 12 for the ATP:N_2 ratio is the minimal ratio that is possible based on a requirement of 4 mol ATP per electron pair transferred in the nitrogenase reaction (32).

theoretical amounts of cell material formed per mol of ATP for growth with methane or methanol using the different carbon assimilation pathways are shown in Table 5. It is evident that the influence of the carbon assimilation pathway on the ATP requirement for the formation of cell material is very great. In agreement with these theoretical calculations, it has been observed that the molar growth yield for methanol varies from 15.7 to 17.3 for a number of organisms using the ribulose monophosphate cycle and from 9.8 to 13.1 for a number of organisms using the serine pathway (40).

Calculation of Aerobic Growth Yields

The calculations of the amount of ATP required for the formation of microbial cell material do not give sufficient information for the description of yield studies under aerobic growth conditions. For aerobic experiments yields are generally expressed as Y_{sub} (g of dry weight per mol of substrate consumed) and Y_{O_2} (g of dry weight per mol of oxygen consumed). Therefore it seems very useful to have a method for calculating the theoretical values for these parameters from the theoretical calculations of the ATP requirement for the formation of microbial cell material given in the previous sections. As an example, an outline for such a calculation is given in Table 6. As a starting point the elementary formula of cells is used [compare Herbert, (41)]. Then the assimilation equation can be determined. In this equation the consumption of 0.25 "H_2" is included, in which "H_2" is used to indicate that reducing equivalents (e.g., $NADH_2$) are used during the formation of biomass. From the growth equation and the theoretical molar growth yield for glucose equations can be derived for the amount of $NADH_2$ or $FADH_2$ available for oxidation and the amount of ATP formed by substrate-level phosphorylation. The total amount of ATP produced is dependent on the number of phosphorylation sites present in the respiratory chain of the organism studied. In the example given in Table 6 the calculation is given for 2 or 3 sites in the respiratory chain, respectively. By multi-

Table 5. Theoretical amount of cell material formed per mol of ATP for microorganisms using different carbon assimilation pathways for growth on methane and methanol[a]

Assimilation pathway	Cell material (g)/ mol ATP
Ribulose monophosphate cycle, fructose diphosphate aldolase variant	27.3
Ribulose monophosphate cycle, 2-keto-3-deoxy-6-phosphogluconate aldolase variant	19.4
Serine pathway	12.5
Ribulose diphosphate cycle	6.5

[a] Data from Harder and van Dijken (5).