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Utilization of Mass–Energy Balance Regularities in the Analysis of Continuous-Culture Data

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Summary

Material and energy balances for continuous-culture processes are described based on the facts that the heat of reaction per electron transferred to oxygen for a wide variety of organic molecules, the number of available electrons per carbon atom in biomass, and the weight fraction carbon in biomass are relatively constant. Energy requirements for growth and maintenance are investigated and related to the biomass energetic yield. The consistency of experimental data is examined using material and energy balances and the regularities identified above. When extracellular products are absent, the consistency of yield models containing separate terms for growth and maintenance may be investigated using organic substrate consumption, biomass production, oxygen consumption (or heat evolution), and carbon dioxide evolution rate data for a series of dilution rates. The consistency of continuous-culture data in the published literature is examined.

INTRODUCTION

Organic substrate requirements in continuous culture have frequently been divided into requirements for growth and maintenance. Pirt[1] identified some of the earlier work[2–5] and used the equation

$$1/Y_S = 1/Y_S^{\max} + m_S/\mu \tag{1}$$

in graphical form to estimate the values of the maintenance coefficient, m_S, and the true growth yield, Y_S, based on organic substrate. Values of growth yield, Y_S, and specific growth rate, μ, were determined using continuous culture at a series of dilution rates with a chemostat.

In this work the mass-energy balance method of Minkevich and Eroshin[6–23] is used to develop mass and energy balance relationships that may be used to test the consistency of experimental data

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and the accuracy of assumptions regarding the utilization of the energy in the organic substrate. These material and energy balances are developed based on the facts that the heat of reaction per electron transferred to oxygen for a wide variety of organic molecules, the number of available electrons per carbon atom in biomass, and the weight fraction carbon in biomass are relatively constant.[8,10,24-26]

Material and energy balances and their regularities may be used with experimental measurements of organic substrate consumption, biomass production, oxygen consumption, carbon dioxide evolution, heat evolution, and dilution rate to investigate the consistency of the experimental measurements. A more complete understanding of how organic substrate energy is utilized may also be obtained when material and energy balances and their regularities are applied.

THEORY

The energy in the organic substrate may be incorporated into biomass, evolved as heat, or incorporated into extracellular products. The balance equation

$$CH_mO_l + aNH_3 + bO_2 = y_cCH_pO_nN_g + zCH_rO_sN_t + cH_2O + dCO_2$$

will be used to consider the material and energy balances associated with microbial growth. In this equation CH_mO_l denotes the elemental composition of the organic substrate, $CH_pO_nN_g$ is the elemental composition of the biomass, and $CH_rO_sN_t$ describes the elemental composition of any extracellular products. This chemical balance equation is a general equation that may be used to describe both growth and maintenance. When there are no extracellular products, z (the fraction of organic substrate carbon converted to products) is equal to zero. Furthermore, when no products are formed, maintenance energy results from the oxidation of organic substrate to CO_2 and H_2O; i.e., when a, y_c, and z are equal to zero, the chemical balance equation describes pure maintenance.

In this work, the concept of reductance degree or equivalents of available electrons that may be transferred to oxygen is employed. Minkevich and Eroshin[8] define the reductance degree for organic substrate, biomass, and product, respectively, as follows:

$$\gamma_s = 4 + m - 2l$$

$$\gamma_b = 4 + p - 2n - 3g$$

$$\gamma_p = 4 + r - 2s - 3t$$

where γ is the number of equivalents of available electrons per g atom carbon based on C = 4, H = 1, O = −2, and N = −3. The valence of −3 is used for nitrogen because nitrogen in biomass and in ammonia has this reductance degree. With the values of reductance degree C = 4, H = 1, O = −2, and N = −3, there are no available electrons in CO_2, H_2O, and NH_3. Thus, a balance based on the available electrons in the above chemical equation yields

$$\gamma_s + b(-4) = y_c\gamma_b + z\gamma_p \tag{2}$$

This balance may be used together with a carbon balance for the chemical equation

$$y_c + z + d = 1.0 \tag{3}$$

to investigate growth and maintenance in continuous culture. Equation (2) may be written in the form

$$\frac{4b}{\gamma_s} + y_c\frac{\gamma_b}{\gamma_s} + z\frac{\gamma_p}{\gamma_s} = 1 \tag{4}$$

where the first term gives the fraction of available electrons transferred to oxygen, the second term gives the fraction of available electrons transferred to biomass, and the third term gives the fraction of available electrons transferred to extracellular products. Based on a large number of experiments with biomass and various organic molecules,[7,8,17,24–27] it is known that the heat evolved per equivalent of available electrons transferred to oxygen, Q_o, is approximately 27 kcal/g equiv (equivalent). If each term in eq. (2) is multiplied by Q_o, an energy balance is obtained relating the energy in the consumed organic substrate, $Q_o\gamma_s$ to the heat evolution, $4bQ_o$, energy incorporated into biomass, $y_c\gamma_bQ_o$, and energy incorporated into extracellular products, $z\gamma_pQ_o$. Equation (4) may be considered to be either an available electron balance or an energy balance.[6,7] Equation (4) may be written

$$\epsilon + \eta + \xi_p = 1 \tag{5}$$

where

$$\epsilon = 4b/\gamma_s = 4bQ_o/Q_o\gamma_s \tag{6}$$

$$\eta = y_c(\gamma_b/\gamma_s) = y_c\gamma_bQ_o/Q_o\gamma_s \tag{7}$$

$$\xi_p = z(\gamma_p/\gamma_s) = z\gamma_pQ_o/Q_o\gamma_s \tag{8}$$

Of the energy in the organic substrate, the fraction evolved as heat, ϵ, is given by eq. (6), the fraction transferred to biomass, η, is given by eq. (7), and the fraction transferred to extracellular products, ξ_p,

is given by eq. (8). Minkevich and Eroshin[8,16] refer to η as the biomass energetic yield coefficient and ξ_p as the product energetic yield coefficient.

Minkevich and Eroshin and coworkers[8,17] have investigated data in the available literature as well as the results of their experiments, and have found[17] that $Q_o = 26.95$ kcal/equiv, $\gamma_b = 4.291$, and $\sigma_b = 0.462$ and that the coefficient of variation is 4% for Q_o and γ_b and 5% for σ_b (σ_b is the weight fraction carbon in dry biomass). Since these values are relatively constant, they may be used in material and energy balance calculations.

One purpose of this paper is to use the above approach of Minkevich and Eroshin to develop consistency tests that may be used with continuous-culture experiments designed to investigate growth and maintenance requirements of a culture. Consider the case of pure maintenance where the only products are CO_2 and H_2O. In this case a, y_c, and z are zero, and eqs. (3) and (4) reduce to

$$d = 1.0 \tag{9}$$

and

$$4b/\gamma_s = 1.0 \tag{10}$$

If we define the energetic maintenance coefficient, m_e, as the rate of consumption of energy (or available electrons) in the organic substrate per unit of energy (or available electrons) in biomass/hr, other defined maintenance coefficients may be related to m_e. Conversion of units yields

$$m_c = (\gamma_b/\gamma_s)m_e \tag{11}$$

where m_c is g atoms carbon in consumed organic substrate/g atom carbon in biomass/hr. Equation (10) relates the oxygen consumption rate and organic substrate consumption rate for maintenance; i.e.,

$$m_o/m_c = b = \tfrac{1}{4}\gamma_s \tag{12}$$

where m_o is the oxygen maintenance coefficient (g mol O_2/g atom carbon in biomass/hr). Equations (11) and (12) may be combined to yield

$$m_o = \tfrac{1}{4}\gamma_b m_e \tag{13}$$

Equation (9) relates the CO_2 evolution rate and the substrate consumption rate for maintenance; i.e.,

$$m_d/m_c = 1.0 \tag{14}$$

or from eq. (11)

$$m_d = (\gamma_b/\gamma_s)m_e \tag{15}$$

where m_d is the carbon dioxide maintenance coefficient (g mol CO_2 evolved/g atom carbon in biomass/hr).

Frequently, mass units are used for biomass and organic substrate. The organic substrate maintenance coefficients, m_S (mass basis) and m_c (g atom carbon basis) are related as follows:

$$m_S = (\sigma_b/\sigma_s)m_c = (\sigma_b\gamma_b/\sigma_s\gamma_s)m_e \tag{16}$$

Equations (11)–(16) may be used together with experimental data to determine if estimated values of the maintenance coefficients are consistent.

The growth yield, Y_S, and true growth yield, $Y_S^{\max}$, in eq. (1) are considered for the case where $z = 0$ (no extracellular products are formed). When $z = 0$, eqs. (3) and (4) reduce to

$$y_c + d = 1.0 \tag{17}$$

and

$$4b/\gamma_s + y_c(\gamma_b/\gamma_s) = 1.0 \tag{18}$$

When extracellular products can be neglected and when maintenance energy results from organic substrate oxidation to CO_2 and H_2O, relationships between growth yields can be found using eqs. (17) and (18). Equations (1) and (16) and the relationship between biomass energetic growth yield, η, and Y_S

$$\eta = (\sigma_b\gamma_b/\sigma_s\gamma_s)Y_S \tag{19}$$

gives

$$1/\eta = 1/\eta_{\max} + m_e/\mu \tag{20}$$

where

$$\eta_{\max} = (\sigma_b\gamma_b/\sigma_s\gamma_s)Y_S^{\max} \tag{21}$$

The biomass carbon yield, y_c, is also related to the biomass energetic yield, η, as eq. (7) indicates. Equations (7), (11), and (20) may be combined to give

$$1/y_c = 1/y_c^{\max} + m_c/\mu \tag{22}$$

where

$$y_c^{\max} = (\gamma_s/\gamma_b)\eta_{\max} \tag{23}$$

The biomass yield with respect to oxygen may be obtained by combining eqs. (7) and (18) to obtain

$$\eta = \frac{y_c(\gamma_b/\gamma_s)}{4b/\gamma_s + y_c(\gamma_b/\gamma_s)} = \frac{\gamma_b(y_c/b)}{4 + (y_c/b)\gamma_b} \tag{24}$$

Defining $y_o = y_c/b$ (g atoms biomass carbon/g mol O_2), this equation can be written in the form

$$1/\eta = 4/\gamma_b y_o + 1 \tag{25}$$

Combining eqs. (13), (20), and (25) gives

$$1/y_o = 1/y_o^{\max} + m_o/\mu \tag{26}$$

where

$$1/y_o^{\max} = (\gamma_b/4)(1/\eta_{\max} - 1) \tag{27}$$

which is analogous to eq. (25).

If the biomass energetic yield with respect to heat evolution is considered to be $y_\epsilon = \eta/\epsilon$ (kcal incorporated into biomass/kcal heat involved), equations analogous to those for biomass yield with respect to oxygen may be obtained. Since $\epsilon + \eta = 1.0$ is another form of eq. (18),

$$\eta = \eta/(\epsilon + \eta) = y_\epsilon/(1 + y_\epsilon) \tag{28}$$

Thus,

$$1/\eta = 1/y_\epsilon + 1 \tag{29}$$

Combining eqs. (20) and (29) gives

$$1/y_\epsilon = 1/y_\epsilon^{\max} + m_e/\mu \tag{30}$$

where

$$1/y_\epsilon^{\max} = 1/\eta_{\max} - 1 \tag{31}$$

The first term in eq. (30), $1/y_\epsilon$, is the total heat evolution per unit of energy incorporated into biomass; the second and third terms give the growth and maintenance portions, respectively, of this heat evolution. The relative size of these two contributions depends on specific growth rate. Equation (18) may also be written for the true biomass energetic growth yield, $\eta_{\max}$; i.e.,

$$\epsilon_{\min} + \eta_{\max} = 1.0 \tag{32}$$

where $\epsilon_{\min}$ is the fraction of the substrate energy evolved as heat when substrate energy utilized for maintenance is neglected; i.e.,

eq. (2) may be written in the form (assuming no extracellular products)

$$\gamma_s = 4b_g + 4b_m + y_c\gamma_b \tag{33}$$

where b_g and b_m are oxygen consumption per amount of substrate containing 1 g atom carbon for growth and maintenance, respectively. Since the maintenance energy is neglected in eq. (32),

$$\epsilon_{\min} = 4b_g/(4b_g + y_c\gamma_b) \tag{34}$$

$$\eta_{\max} = y_c\gamma_b/(4b_g + y_c\gamma_b) \tag{35}$$

Since $y_\epsilon^{\max} = \eta_{\max}/\epsilon_{\min}$,

$$y_\epsilon^{\max} = y_c\gamma_b/4b_g = (\gamma_b/4)y_o^{\max} \tag{36}$$

The biomass yield with respect to carbon dioxide evolution, $y_d = y_c/d$, may be written (using eqs. (7) and (17)):

$$y_d = \frac{y_c}{d} = \frac{y_c}{1 - y_c} = \frac{\eta(\gamma_s/\gamma_b)}{1 - \eta(\gamma_s/\gamma_b)} \tag{37}$$

or

$$1/y_d = \gamma_b/\gamma_s\eta - 1 \tag{38}$$

Combining eqs. (15), (20), and (38) gives

$$1/y_d = 1/y_d^{\max} + m_d/\mu \tag{39}$$

where

$$1/y_d^{\max} = \gamma_b/\gamma_s\eta_{\max} - 1 \tag{40}$$

Equations (1), (20), (22), (26), (30), and (39) are related to each other as shown above whenever the assumption of no extracellular products is valid. These relationships may be used to test the consistency of experimental data if a sufficient number of variables are followed experimentally. In testing the consistency of experimental data obtained at a series of dilution rates, there are several consistency tests that may be utilized:

1) At each dilution rate the consistency of the data may be evaluated using the carbon balance, eq. (3), and the available electron balance, eq. (2), together with average values of γ_b, σ_b, and Q_o. This should be done while data are being collected. If measurement errors appear to be present, efforts can be made to correct them. If extracellular products appear to be present, analytical work to identify them can be carried out.

2) The consistency of estimates of yield, true growth yield, and

maintenance parameters may be evaluated using eqs. (11), (13), (15), and (16) which relate various maintenance parameters, and eqs. (7), (19), (21), (23), (25), (27), (29), (31), (38), and (40) which relate various yield parameters. This can be done by using eqs. (1), (20), (26), (30), and (39) to estimate true growth yield and maintenance parameters from the appropriate experimental data, and then examining the consistency of the estimated parameters. An alternative method is to estimate η at each specific growth rate from various sets of the available data, and then use eq. (20) to estimate η_{max} and m_e by plotting $1/\eta$ vs. $1/\mu$.

Equation (33) may be written in the form

$$4b_g/\gamma_s + 4b_m/\gamma_s + y_c(\gamma_b/\gamma_s) = 1 \tag{41}$$

where

$$\eta = y_c(\gamma_b/\gamma_s) \tag{42}$$

and

$$\epsilon = 4b_g/\gamma_s + 4b_m/\gamma_s = \epsilon_g + \epsilon_m \tag{43}$$

where ϵ_g and ϵ_m are the fractions of substrate energy evolved as heat because of growth and maintenance, respectively. Note that

$$m_e/\mu = \epsilon_m/\eta \tag{44}$$

Thus, at each specific growth rate, the fraction of organic substrate energy utilized for maintenance can be estimated after the parameters η_{max} and m_e have been estimated in eq. (20).

Equation (20) may be written in the form

$$\mu/\eta = \mu/\eta_{max} + m_e \tag{45}$$

Combining eqs. (44) and (45) gives

$$1/\epsilon_m = \mu/m_e\eta_{max} + 1 \tag{46}$$

This equation may be used to test the consistency of the experimental data and to estimate the fraction of energy in the organic substrate utilized for maintenance.

Equations (20) and (44) and eq. (41) in the form

$$\epsilon_g + \epsilon_m + \eta = 1.0 \tag{47}$$

may be combined to obtain

$$\epsilon_g/\eta = 1/\eta_{max} - 1 \tag{48}$$

Comparison with eq. (31) shows that

$$\epsilon_g/\eta = 1/y_\epsilon^{\max} \tag{49}$$

The fraction of the growth associated energy that is incorporated into biomass, $\eta_{\max}$, is assumed to be constant and not a function of specific growth rate. Equation (48) shows that this implies that the ratio ϵ_g/η, the ratio of growth associated heat evolution to energy incorporated into biomass, is also independent of specific growth rate.

RESULTS AND DISCUSSION

In order to illustrate the application of the theory, some of the results of Herbert[28] will be used. *Aerobacter aerogenes* was grown on glycerol, ammonia, and mineral salts under glycerol limitation in a chemostat at dilution rates ranging from 0.05 to 1.0 hr^{-1} at pH = 7.4 and a temperature of 37°C. Measured values were cell dry weight, feed and effluent glycerol concentrations, dilution rate, oxygen uptake rate, carbon dioxide evolution rate, and dilution rate. Cell number, % RNA, % DNA, and % protein in the biomass were also measured. Figures 1 and 2 show some of the results of Herbert[28] as he reported them.

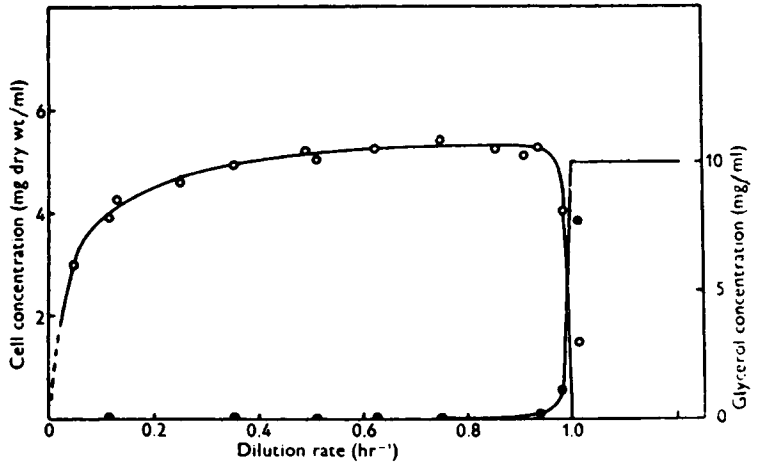

Fig. 1. Data of Herbert[28] on growth of *A. aerogenes* in continuous culture with glycerol as limiting substrate. (○) Cell concentration; (●) glycerol concentration.

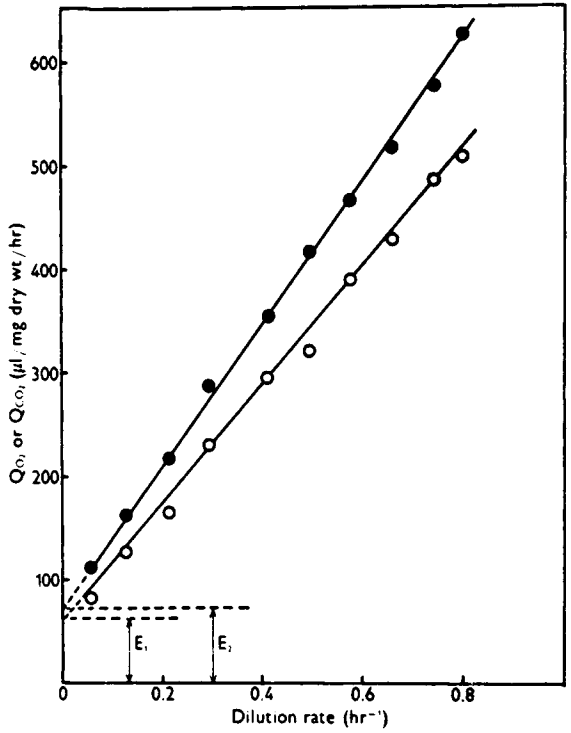

Fig. 2. Data of Herbert[28] on respiration of *A. aerogenes* growing in continuous culture; (●) oxygen uptake, Q_{O_2}, and (○) carbon dioxide evolution, Q_{CO_2}, of steady-state cultures as a function of dilution rate. E_1 and E_2 are O_2 uptake and CO_2 evolution requirements for maintenance.

In the present work, the average values,[17] $\sigma_b = 0.462$ (for the weight fraction carbon in dry biomass) and $\gamma_b = 4.291$ (for the equiv available electrons/amount biomass containing 1 g atom carbon) were used. For glycerol, $\sigma_s = 0.391$ and $\gamma_s = 4.67$. A pressure of 1 atm and temperature of 37°C were assumed in converting gas volumes to molar quantities.

Graphical methods of data analysis, which are similar to those used in Figure 2, are described in detail by Pirt.[29] If every term in eq. (1) is multiplied by the specific growth rate, μ,

$$\mu/Y_S = \mu/Y_S{}^{\max} + m_S$$

The left-hand side of this equation is the rate of substrate consumption/g dry biomass/hr. A graph of μ/Y_S vs. μ is analogous to the curves shown in Figure 2.

The data of Herbert[28] may be examined for consistency by using a carbon balance, eq. (17), and an available electron balance, eq. (18). At each dilution rate, the organic substrate, cell dry weight, and CO_2 evolution data may be used to check the carbon balance. For example, at $\mu = D = 0.05\ hr^{-1}$.

$$y_c + d = 0.35 + 0.64 = 0.99$$

where y_c and d are the fractions of substrate carbon converted to biomass and CO_2, respectively. At $\mu = D = 0.58\ hr^{-1}$, for example,

$$y_c + d = 0.61 + 0.42 = 1.03$$

The carbon balance results show that extracellular products are not present and that the data are reasonably consistent.

The oxygen uptake rate, cell dry weight, and organic substrate data may be used to check the available electron balance at each dilution rate. For example, at $\mu = D = 0.05\ hr^{-1}$,

$$\epsilon + \eta = 0.68 + 0.33 = 1.01$$

where ϵ is the fraction of available electrons in the consumed substrate that are transferred to oxygen and η is the fraction of available electrons in the consumed substrate that are incorporated into the biomass. At $\mu = D = 0.58\ hr^{-1}$, for example,

$$\epsilon + \eta = 0.44 + 0.56 = 1.0$$

The available electron balance results also indicate that extracellular products are not present and that the data are reasonably consistent.

The cell dry weight and glycerol data of Herbert[28] may be used to directly estimate the parameters Y_S^{max} and m_S in eq. (1). This gives $Y_S^{max} = 0.56$ g cell dry wt/g glycerol, and $m_S = 0.076$ g glycerol/g cell dry wt/hr, when a plot of $1/Y_S$ vs. $1/\mu$ is used. The data in Figure 2 may be used to obtain the parameters y_o^{max} and m_o in eq. (26) by noting that Figure 2 is a plot of μ/y_o vs. μ with different units for oxygen and biomass. From the intercept in Figure 2, the maintenance coefficient is 0.074 ml O_2/mg dry wt/hr or 0.078 g mol O_2/g atom biomass carbon/hr. From the slope in Figure 2, the value of y_o^{max} is found to be 1.47 mg dry wt/ml O_2 or 1.40 g atom biomass carbon/g mol O_2. The CO_2 data may similarly be used to obtain the parameters y_d^{max} and m_d in eq. (39). From the intercept in Figure 2, the maintenance coefficient is found to be 0.064 ml/mg dry wt/hr or $m_d = 0.0675$ g mol CO_2/g atom biomass carbon/hr. The reciprocal of the slope in Figure 2 is 1.79 mg dry wt/ml CO_2 or $y_d^{max} = 1.70$ g atom biomass carbon/g mol CO_2.

The consistency of the estimated values of the maintenance coefficients m_S, m_o, and m_d can be examined by using eqs. (16), (13), and (15), respectively, to obtain values of m_e of 0.070, 0.073, and 0.073 g equiv available electrons/g equiv available electrons in biomass/hr, respectively. Similarly, eqs. (21), (27), and (40) may be used with the estimated values of Y_S^{max}, y_o^{max}, and y_d^{max}, respectively, to obtain values of η_{max} of 0.60, 0.60, and 0.58, respectively. These results show that eqs. (1), (20), (26), and (39) are consistent with the data of Herbert.[28] Note that this consistency test examines the consistency of the biomass, glycerol, oxygen, and CO_2 data at several dilution rates.

The biomass energetic yield can also be estimated from each of the three sets of data (biomass and glycerol, biomass and oxygen, and biomass and carbon dioxide). Equation (19) may be used to calculate the biomass energetic yield, η, from values of Y_S. Values of η may also be obtained from oxygen and biomass data using eq. (25) after the data in Figure 2 are converted to the units of y_o. Equation (38) may similarly be used to calculate values of η from carbon dioxide and biomass data after the data in Figure 2 are converted to the units of y_d.

Figure 3 is a plot of $1/\eta$ vs. $1/\mu$ for these three sets of data. The

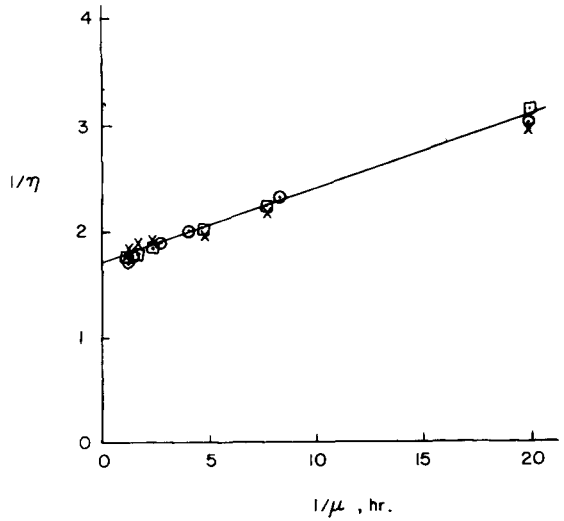

Fig. 3. Test of eq. (20) using data of Herbert[28] for glycerol limited growth of *A. aerogenes*; values of biomass energetic yield, η, from (⊙) biomass and glycerol measurements; (⊡) oxygen and biomass measurements, (×) carbon dioxide and biomass measurements.

estimated values of η_{max} and m_e in eq. (20) are $\eta_{max} = 0.59$ and $m_e = 0.07$ g equiv available electrons/g equiv available electrons in biomass/hr. Figure 3 shows that the data of Herbert[28] are reasonably consistent.

Equation (44) may be used to estimate the fraction of organic substrate energy utilized for maintenance, ϵ_m, from dilution rate, glycerol utilization, and biomass production measurements, and the estimated value of $m_e = 0.07$ g equiv available electrons/g equiv available electrons in biomass/hr. In Figure 4, $1/\epsilon_m$ is plotted versus the specific growth rate, μ, as suggested by eq. (46). Comparison of the slope of this graph with $1/m_e\eta_{max}$ where $m_e = 0.07$ and $\eta_{max} = 0.59$ gives a graphical value of 23 compared to 24 from $1/m_e\eta_{max}$. This graph shows that $\epsilon_m = 1.0$ at $\mu = 0$ (pure maintenance), that $\epsilon_m = 0.46$ at $\mu = 0.05$ hr^{-1} and that $\epsilon_m = 0.1$ at $\mu = 0.4$ hr^{-1}, for example.

In this work, extracellular products are not present in significant quantities. This is important in identifying the portion of energy evolved that is associated with growth, ϵ_g, the energy utilized for maintenance, ϵ_m, and energy incorporated into biomass, η, where $\epsilon_g + \epsilon_m + \eta = 1.0$ [eq. (47)] as indicated in eq. (41). Using eq. (47) and values for ϵ_m and η, values of ϵ_g may be estimated by differ-

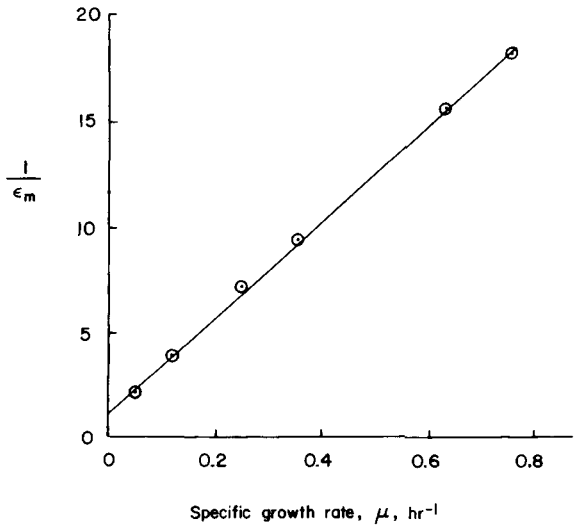

Fig. 4. Test of eq. (46) using data of Herbert[28] for glycerol-limited growth of *A. aerogenes*; values of maintenance energy calculated from biomass and organic substrate measurements.

ence. For example, $\epsilon_g = 0.21$ at $\mu = 0.05$ hr^{-1} and $\epsilon_g = 0.37$ at $\mu = 0.4$ hr^{-1}.

When extracellular products are present, it is much more difficult to identify how the energy is utilized because the energy evolved as heat may be divided into three parts. Energy evolved as heat is associated with or utilized for maintenance, product formation, and growth.

CONCLUSIONS

Material and energy balances may be used to check the consistency of sets of data at each dilution rate. The consistency of equations that identify the fractions of energy utilized for maintenance and growth may also be tested. When extracellular products are not present, the fraction of organic substrate energy utilized for maintenance can be determined and expressed as a function of specific growth rate. The remaining energy is growth associated and may be clearly divided into that incorporated into biomass and that evolved as heat.

Nomenclature

a	mol NH_3/quantity organic substrate containing 1 g atom carbon (g mol/g atom carbon)
b	mol O_2/quantity organic substrate containing 1 g atom carbon (g mol/g atom carbon)
b_g	moles O_2 associated with growth/quantity organic substrate containing 1 g atom carbon (g mol/g atom carbon)
b_m	mol O_2 associated with maintenance/quantity organic substrate containing 1 g atom carbon (g mol/g atom carbon)
c	moles H_2O/quantity organic substrate containing 1 g atom carbon (g mol/g atom carbon)
D	dilution rate (hr^{-1})
d	mol CO_2/quantity organic substrate containing 1 g atom carbon (g mol/g atom carbon)
g	atomic ratio of nitrogen to carbon in biomass (dimensionless)
k	atomic ratio of nitrogen to carbon in organic substrate (dimensionless)
l	atomic ratio of oxygen to carbon in organic substrate (dimensionless)
m	atomic ratio of hydrogen to carbon in organic substrate (dimensionless)
m_c	rate of organic substrate consumption for maintenance (g atom carbon/g atom biomass carbon/hr)
m_d	rate of CO_2 evolution for maintenance (g mol/g atom biomass carbon/hr)
m_e	rate of organic substrate consumption for maintenance (g equiv available electrons/g equiv available electrons in biomass/hr or kcal/kcal biomass/hr)

m_o rate of O_2 uptake for maintenance (g mol/g atom biomass carbon/hr)

m_S rate of organic substrate consumption for maintenance (g/g dry biomass/hr)

n atomic ratio of oxygen to carbon in biomass (dimensionless)

p atomic ratio of hydrogen to carbon in biomass (dimensionless)

Q_o heat evolution in fermentation/equivalent of oxygen uptake (kcal/g equiv)

Q_{CO_2} rate of evolution of CO_2 (ml/g dry wt/hr)

Q_{O_2} rate of consumption of O_2 (ml/g dry wt/hr)

r atomic ratio of hydrogen to carbon in products (dimensionless)

s atomic ratio of oxygen to carbon in products (dimensionless)

t atomic ratio of nitrogen to carbon in products (dimensionless)

Y_S biomass yield on organic substrate (g dry weight/g substrate)

Y_S^{max} maximum biomass yield based on organic substrate (g dry weight/g substrate)

y_c biomass carbon yield (fraction of organic substrate carbon in biomass) (dimensionless)

y_c^{max} maximum biomass carbon yield (dimensionless)

y_d biomass yield based on CO_2 evolution (g atoms biomass carbon/g mol CO_2 evolved)

y_d^{max} maximum biomass yield based on CO_2 evolution (g atoms biomass carbon/g mol CO_2 evolved)

y_o biomass yield based on oxygen (g atoms biomass carbon/g mol O_2)

y_o^{max} maximum biomass yield based on O_2 (g atoms biomass carbon/g mol O_2)

y_ϵ biomass yield based on heat evolved (kcal incorporated into biomass/kcal evolved or equiv available electrons incorporated into biomass/equiv available electrons transferred to O_2)

y_ϵ^{max} maximum biomass yield based on heat evolution (kcal incorporated into biomass/kcal evolved)

z fraction of organic substrate carbon in products (dimensionless)

γ_b reductance degree of biomass as defined by eq. (2) (equiv available electrons/g atom carbon)

γ_p reductance degree of products (equiv available electrons/g atom carbon)

γ_s reductance degree of organic substrate (equiv available electrons/g atom carbon)

ϵ fraction of energy in organic substrate that is evolved as heat (dimensionless)

ϵ_g growth-associated fraction of energy in organic substrate that is evolved as heat (dimensionless)

ϵ_m fraction of energy in organic substrate that is evolved as heat because of cell maintenance (dimensionless)

ϵ_{min} $= 1 - \eta_{max}$, fraction of growth-associated energy that is evolved as heat, $\epsilon_{min} = \epsilon_g/(\epsilon_g + \eta)$ (dimensionless)

η fraction of energy in organic substrate that is converted to biomass or biomass energetic yield (dimensionless)

η_{max} maximum biomass energetic yield (dimensionless)

μ specific growth rate (hr^{-1})

ξ_p fraction of energy in organic substrate that is converted to products (dimensionless)

σ_b weight fraction carbon in biomass (dimensionless)
σ_s weight fraction carbon in organic substrate (dimensionless)

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