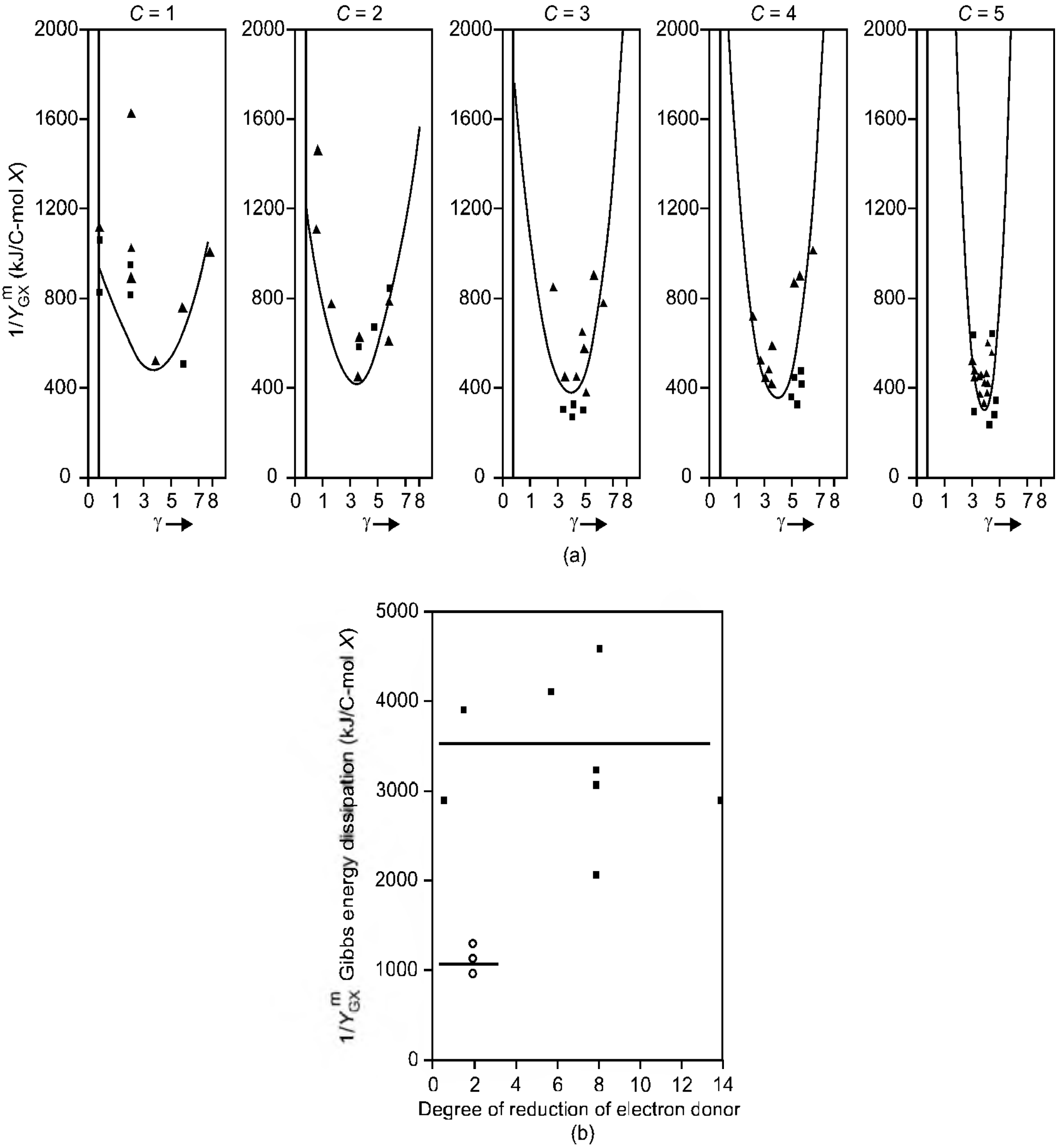

Fig. 2.5. Reciprocal maximal yield of biomass on Gibbs energy, $1/Y_{GX}^{m}$, (kJ/C-mol X); (a) Heterotrophic growth (triangles, aerobic; squares, fermentation, X's denitrifying systems); C is the number of carbon atoms in the carbon source; γ is the degree of reduction of the carbon source. (b) Autotrophic growth (squares, electron donors where reversed electron transport [RET] is needed; circles, donors without RET). The lines represent Eqs 2.3a and 2.3b.

Equation 2.3a further shows that for heterotrophic growth $1/Y_{GX}^{m}$ ranges between about 200 and 1000 kJ/C-mol biomass, for the *C* sources explored, for which:

1. The number of carbon atoms in the carbon source ranges between $C = 1$ (e.g. CO_2, formate, methane) and $C = 6$ (e.g. glucose, citrate).
2. The degree of reduction of the C source γ ranges between 0 (for CO_2) and 8 (for CH_4).

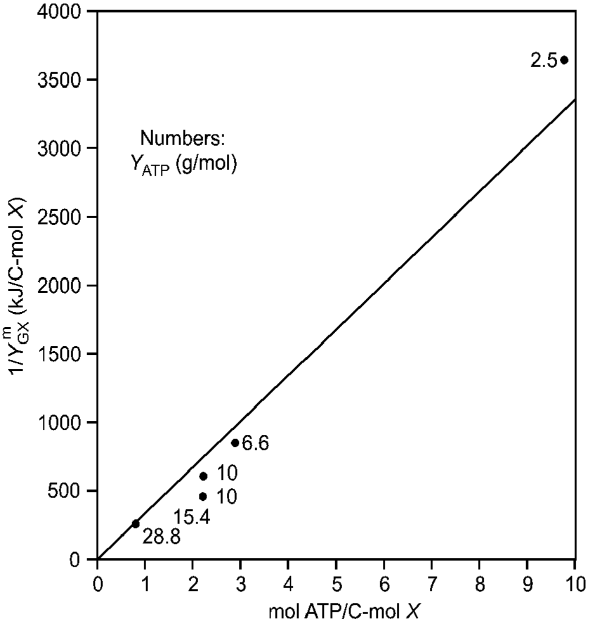

Fig. 2.6. Comparison of energy needed for biomass synthesis on different carbon sources in mol ATP/C-mol biomass and in kJ/C-mol biomass ($1/Y^m_{GX}$). The numbers refer to the conventional biomass yield on ATP in gram biomass/mol ATP for different carbon sources.

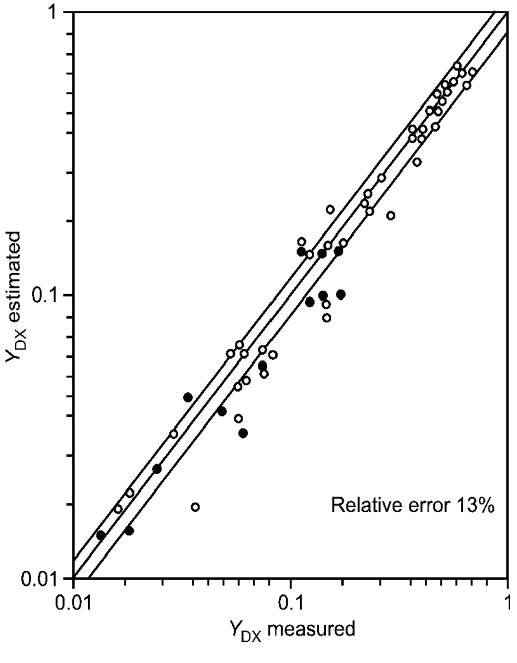

Fig. 2.7. Comparison of measured and predicted biomass yield Y_{DX} (solid circles, fermentative; open circles, aerobic growth systems).

USEFUL REFERENCE SYSTEM TO SIMPLIFY GROWTH STOICHIOMETRIC AND ENERGETIC CALCULATIONS AND TO GAIN INSIGHT

Growth Reference System

In the preceding sections, the stoichiometric coefficients for the macrochemical reaction equation of biomass formation have been solved by setting up the proper conservation equations (C, H, O, N, charge, enthalpy) and the Gibbs energy balance. Although this is a sufficient and straightforward method, solving these linear equations remains unattractive and does not provide insight. To simplify these calculations and to gain insight, a special reference system has been designed—the growth reference system. This reference system is based on the observation that, in all chemotrophic growth systems, H_2O, HCO_3^-, H^+, and N source (mostly NH_4^+) occur as chemical compounds (see earlier section on growth system definition). In this special reference system each chemical compound is assigned three new numbers.

γ	The degree of reduction, which represents the electron content per C-mol (for organic compounds) or per mol (for inorganic compounds).
ΔG_e	The Gibbs energy per electron present in the compound.
ΔH_e	The enthalpy per electron present in the compound.

Clearly γ is a stoichiometric quantity and ΔG_e and ΔH_e are energetic parameters.

The reference system is designed such that for H_2O, HCO_3^-, H^+ (pH = 7), N source for growth, HPO_4^{2-}, NO_3^-, SO_4^{2-}, and Fe^{3+}, the values of γ, ΔG_e, and ΔH_e are zero. For ΔG_e, the biochemical standard conditions (1 mol/l, 1 bar, pH = 7298 K) are assumed, ΔH_e is calculated for CO_2 (gas) because of the large heat effect of HCO_3^- (liq) ⇔ CO_2 (gas) transfer. The calculation of γ, ΔG_e, and ΔH_e follows from the reference redox half reaction where 1 C-mol of organic or 1 mol of inorganic compound is converted into the reference chemicals and a number of electrons. The number of electrons is by definition equal to γ (Example 2.5). From the Gibbs energy and enthalpy of this reference reaction, called ΔG_{ref} and ΔH_{ref} (calculated with the usual thermodynamic ΔG_f^{01}, and ΔH_f^{01} values, see Table 2.2), the values of ΔG_e and ΔH_e follow from equations 2.4a and 2.4b.

$$\Delta G_e = \frac{-\Delta G_{ref}}{\gamma} \qquad \text{... (2.4a)}$$

$$\Delta H_e = \frac{-\Delta H_{ref}}{\gamma} \qquad \text{... (2.4b)}$$

Example 2.5. The reference redox half reaction and calculation of γ and ΔG_e for chemical compounds.

For methanol the following reference redox half reaction can be set up according to the preceding definition by converting methanol to the reference compounds HCO_3^-, H_2O, and H^+

$$-1CH_4O - 2H_2O + HCO_3^- + 7H^+ + 6e^-$$

In this reference redox half reaction, 1 C-mol methanol is converted and six electrons are produced, hence $\gamma = +6$ for methanol. Using the ΔG_f^{01} values from Table 2.2, the ΔG_{ref} for the methanol-reference redox half reaction follows as (standard conditions)

$$\Delta G_{ref}^{01} = (7)(-39.87) + 1(-586.85) - (2)(-237.18) - (1)(-181.75) = -216.192 \text{ kJ}$$

This gives for the ΔG_e^{01} value of methanol by Eq. 2.4a

$$\Delta G_e^{01} = -\left(\frac{-216.192}{6}\right) = +36.032 \text{ kJ/e-mol}$$

Obviously ΔH_e can be calculated in a similar way by calculation of ΔH_{ref}.

For biomass the following redox half reaction can be set up, assuming that NH_4^+ is the N source:

$$-1CH_{1.8}O_{0.8}N_{0.2} - 2.5H_2O + HCO_3^- + 0.2NH_4^+ + 5H^+ + 4.2e^-$$

Obviously, the degree of reduction for biomass is 4.2. The ΔG_{ref}^{01} value is obtained similarly as earlier for methanol. ΔG_{ref}^{01} can be calculated to be –142.128 kJ, giving

$$\Delta G_e = -(-142.128)/(4.2) = +33.840 \text{ kJ/e-mol}$$

In a similar way as shown in Example 2.5 for each chemical compound, the values of γ, ΔG_e, and ΔH_e can be calculated for a large number of relevant compounds. Table 2.3 contains all relevant stoichiometric and energetic information for growth systems, clearly shown in the following. A point of attention is the finding (Table 2.3) that for biomass the degree of reduction depends on the N source used in the growth system. For example $\gamma = 4.2$ for NH_4^+ and 5.8 for NO_3^- as N source. This is a consequence of the reference definition. The advantage is that the N source disappears from the stoichiometric calculations using γ, ΔG_e, and ΔH_e. The defined reference system is closely related to the generalised degree of reduction as defined by Roels and Erickson. It can be seen that for reduced organic compounds γ is between 0 and 8 (per C-mol). For inorganic compounds, such an upper limit does not exist (because there is not a normalisation per atom). For O_2, γ is negative (–4), which is logical for an acceptor. ΔG_e is related to the conventional redox potential of redox half reactions ($\Delta G_e^{01} = -FE_0^1$). ΔG_e is calculated using HCO_3^- (the most abundant form of carbon dioxide at pH = 7); ΔH_e has been calculated using CO_2 (gas) as reference, to take the large heat effect of $HCO_3^- \rightarrow CO_2$ (gas) into account.

Table 2.3. Calculated γ, ΔG_e^{01}, and ΔH_e^0 values for chemical compounds under standard conditions.

Compound	γ *Degree of reduction per C-mole for organic and per mole for inorganic compounds in electrons/(C)-mole*	ΔG_e^{01} *(kJ/e-mol)*	ΔH_e^0 *(kJ/e-mol)*
Biomass/NH_4^+ – N source	+4.2	+33.480	–26.1
Biomass/NO_3 – N source	+5.8	+14.820	–44.2
Biomass/N_2 – N source	+4.8	+32.948	–26.3
N source for growth	0	0	0
HCO_3^-	0	0	0
Oxalate	+1	+52.522	–20
Formate	+2	+39.186	–15.50
Glyoxylate	+2	+48.229	–
Tartrate	+2.5	+39.577	–
Malonate	+2.67	+28.976	–
Fumarate	+3	+33.662	–31.60
Malate	+3	+33.354	–32.20
Citrate	+3	+32.282	–33.90
Pyruvate	+3.33	+34.129	–23.60
Succinate	+3.50	+28.405	–36.30

(Contd ...)

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