

# A theoretical reassessment of microbial maintenance and implications for microbial ecology modeling

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## Introduction

Maintenance requirements of microbial biomass represent the additional consumption of energy and carbon for purposes other than the production of biomass (Marr et al., 1963; Anderson & Domsch, 1985a). The early terminology 'endogenous metabolism' postulated by Herbert is thought to be equivalent to the maintenance energy requirements (Dawes & Ribbons, 1962, 1964, 1965; Pirt, 1965; Mason et al., 1986). Although the concept of maintenance energy is largely studied in starving cells, growing cells should also be included (Dawes & Ribbons, 1962, 1964). Some studies presume that growth is a secondary feature of energy utilization after maintenance purposes (Dawes & Ribbons, 1964). van Bodegom (2007) summarized eight nongrowth components for microbial maintenance: (1) cell motility, (2) osmoregulation, (3) proofreading, synthesis and turnover of macromolecular compounds, (4) defense against O<sub>2</sub> stress, (5) shifts in metabolic pathways, (6) energy spilling reactions, (7) changes in stored polymeric carbon, and (8) extracellular

### Abstract

We attempted to reconcile three microbial maintenance models (Herbert, Pirt, and Compromise) through a theoretical reassessment. We provided a rigorous proof that the true growth yield coefficient ( $Y_G$ ) is the ratio of the specific maintenance rate (*a* in Herbert) to the maintenance coefficient (*m* in Pirt). Other findings from this study include: (1) the Compromise model is identical to the Herbert for computing microbial growth and substrate consumption, but it expresses the dependence of maintenance on both microbial biomass and substrate; (2) the maximum specific growth rate in the Herbert ( $\mu_{max,H}$ ) is higher than those in the other two models ( $\mu_{max,P}$  and  $\mu_{max,C}$ ), and the difference is the physiological maintenance factor ( $m_q = a$ ); and (3) the overall maintenance coefficient ( $m_T$ ) is more sensitive to  $m_q$  than to the specific growth rate ( $\mu_G$ ) and  $Y_G$ . Our critical reassessment of microbial maintenance provides a new approach for quantifying some important components in soil microbial ecology models.

losses of compounds not involved in osmoregulation. The first four components were classified as the physiological maintenance (van Bodegom, 2007).

Mathematical modeling of the growth of microbial biomass and consumption of substrate usually follows (Tempest & Neijssel, 1984):

$$\mu(s) = \frac{1}{x} \frac{\mathrm{d}x}{\mathrm{d}t} \tag{1}$$

$$q(s) = -\frac{1}{x}\frac{ds}{dt} \tag{2}$$

$$-Y\frac{\mathrm{d}s}{\mathrm{d}t} = \frac{\mathrm{d}x}{\mathrm{d}t} \text{ or } Y \cdot q(s) = \mu(s)$$
(3)

where x and s are the concentrations (contents) of microbial biomass and substrate, respectively;  $\mu(s)$  is the observed specific growth rate of microbial biomass (h<sup>-1</sup>); q (s) is the observed specific consumption rate of substrate (h<sup>-1</sup>); and Y denotes the apparent growth yield coefficient.

It is noted that Eqn (3) is a general formula relating the growth of microbial biomass to the consumption of substrate (van Bodegom, 2007). However, the expressions for Eqns (1) and (2) are specific and can be different based on different assumptions (Beeftink *et al.*, 1990). Two models have been widely used and their major difference is associated with the maintenance component. One is the Herbert model specified by the specific maintenance rate (*a*) in Eqn (1), which may be regarded as an endogenous metabolism rate resulting in consumption of maintenance energy and decrease in the biomass (Beeftink *et al.*, 1990). The other is the Pirt model characterized by the maintenance coefficient (*m*) in Eqn (2) representing the consumption of substrate for nongrowth functions (Pirt, 1965).

The two models have caused the debates on the relationship between the two rate constants, that is, a and m. Most of the studies postulated or derived that the true growth yield  $(Y_G)$  was the key connecting the two parameters (Schulze & Lipe, 1964; Pirt, 1965; Nagai et al., 1969; Van de Werf & Verstraete, 1987; Beeftink et al., 1990). Another interpretation was that the apparent yield coefficient (Y) rather than  $Y_G$  served as the link, and the overall maintenance coefficient was insensitive to the variation in physiological maintenance (van Bodegom, 2007). In addition, Beeftink et al. (1990) put forward a model called the 'Compromise', based on mechanistic considerations that combined the features of previous models. However, the maximum specific growth rates were regarded as the same for all models, and the solutions for  $\mu$  and q from the Compromise model were thought to be between the solutions from the Herbert and Pirt models.

A complete analysis of all the maintenance components is beyond the scope of this study. The present contribution attempts to reconcile the models describing microbial maintenance through clarifying the relationships between the three models and deriving a new equation for the overall maintenance coefficient  $(m_T)$ . We also aim to elucidate implications for the modeling of soil organic carbon (SOC) decomposition based on our reassessment of microbial maintenance.

# Models for microbial maintenance

## Herbert model

In the Herbert model (Dawes & Ribbons, 1964; Pirt, 1965), the specific maintenance rate (endogenous metabolism) is regarded as a negative growth rate:

$$\mu(s) = \mu_{\max,H} \cdot g(s) - a \tag{4}$$

$$q(s) = \mu_{\max,H} \cdot g(s) / Y_G \tag{5}$$

where *a* is termed the specific maintenance rate  $(h^{-1})$ ;  $\mu_{\max,H}$  is the maximum specific growth rate for the Herbert

model (h<sup>-1</sup>); and  $Y_G$  is the 'true' growth yield (Pirt, 1965; Neijssel & Tempest, 1976) or potential (maximum) growth yield coefficient (Kuhn *et al.*, 1980; Tempest & Neijssel, 1984) of microbial biomass. The function  $g(s) = s/(K_s + s)$ satisfies the requirements that g(s) = 0 at s = 0 and  $g(s) \rightarrow 1$ when  $s \gg K_s$ , where  $K_s$  is the half-saturation constant with the same units of substrate.

The Herbert model allows the decrease in microbial biomass resulting from microbial turnover rather than maintenance respiration per se at low substrate concentration where  $\mu_{\max,H} \cdot g(s) < a$ . The maintenance energy results in a decrease in the growth of microbial biomass. It is worth noting that Eqn (4) and (5) should be presented together to express the basic idea of the Herbert model. In some studies (e.g., Schulze & Lipe, 1964; van Bodegom, 2007), only Eqn (4) was used for analysis, which resulted in misunderstanding or incorrect derivation of the relationship between the specific maintenance rate (*a*) and the maintenance coefficient (*m*) of the Pirt model.

## Pirt model

The Pirt model postulates that the consumption of substrate also supplies energy for maintenance in addition to microbial growth (Pirt, 1965):

$$\mu(s) = \mu_{\max,P} \cdot g(s) \tag{6}$$

$$q(s) = \mu_{\max,P} \cdot g(s) / Y_G + m \tag{7}$$

where  $\mu_{\max,P}$  is the maximum specific growth rate for the Pirt model, and *m* is the maintenance coefficient (h<sup>-1</sup>). The same substrate function *g*(*s*) is used here as in the Herbert model. In the Pirt model the observed specific growth rate is always nonnegative.

#### **Compromise model**

Both the Herbert and Pirt models presume that maintenance energy depends only on time and microbial biomass. However, many experiments observed that maintenance energy varies with growth stage and specific growth rate (Pirt, 1965, 1982; van Bodegom, 2007). The assumption of constant specific maintenance rates was thought to be invalid for Escherichia coli and Bacillus polymyxa cultures (van Verseveld et al., 1984). As a result, the maintenance coefficient or the specific maintenance rate can vary with the substrate concentrations. Experiments have indicated that maintenance energy is supplied by substrate under sufficient substrate conditions (Dawes & Ribbons, 1964). Thus, the equation including a maintenance component like Eqn (7) is more explicit than Eqn (5). In addition, the biomass yield might decrease at slower growth rates (Dawes & Ribbons, 1964), which

means that microorganisms might cover their maintenance requirements from biomass when substrate becomes depleted and the formula like Eqn (4) is somewhat more advantageous than Eqn (6). Therefore, the models of Herbert and Pirt have their own attractive features. It is feasible to combine these features to develop a compromise model.

Based on the above analysis, assuming that maintenance energy is supplied by both substrate and biomass:

$$q(s) = \mu_{\max,C} \cdot h(s) / Y_G + m_q \cdot h(s) / Y_G \tag{8}$$

$$\mu(s) = \mu_{\max,C} \cdot h(s) - b(s) \tag{9}$$

where  $\mu_{\max,C}$  is the maximum specific growth rate for the Compromise model,  $m_q$  denotes the specific physiological maintenance factor  $(h^{-1})$ , h(s) is a function of *s* fulfilling the requirements of h(0) = 0 and  $h(s) \rightarrow 1$  when  $s \gg K_s$ , and b(s) is a function of *s*.

Assuming that Eqns (8) and (9) satisfy the relationship as indicated in Eqn (1) of Pirt (1982):

$$q(s) = \mu(s)/Y_G + m_q/Y_G \tag{10}$$

Substituting Eqn (8) and (9) into (10), one obtains that  $b(s) = m_{a} [1 - h(s)]$  and

$$\mu(s) = \mu_{\max,C} \cdot h(s) - m_q \cdot [1 - h(s)] \tag{11}$$

Equations (8) and (11) constitute a model presented in Beeftink *et al.* (1990), where the model was derived by mechanistic considerations. It is a compromise between the Herbert and the Pirt model. The Compromise model follows four assumptions (Beeftink *et al.*, 1990): (1) negative net growth at  $s \rightarrow 0$ , (2) no substrate consumption at s = 0, (3) no microbial biomass degradation at  $s \gg K_s$ , and (4)  $\mu(s) \rightarrow \mu_{\max,C}$  at  $s \gg K_s$ . Therefore,  $h(s) = s/(K_s + s)$ , the same as g(s) in the Pirt model, is a suitable selection. It is noted that we modified the condition for sufficient substrate from  $s \rightarrow \infty$  stated by Beeftink *et al.* (1990) to  $s \gg K_s$  since  $h(s) \rightarrow 1$  can be easily achieved under the latter condition.

## **Relationship between three models**

Two forms of relationship have been proposed to relate m to a: one is the commonly used  $a = Y_G \cdot m$  (Pirt, 1965), the other is  $a = Y \cdot m$  (van Bodegom, 2007). Although the first one has been widely used, no rigorous and clear derivations are available. We agree that the first form  $(a = Y_G \cdot m)$  is correct and the proof is shown as follows.

Two assumptions are made for the derivations: (1)  $Y_G$  is a constant and identical for the three models; and (2) the observed maximum specific growth rate [i.e.,

maximum  $\mu(s)$  in Eqns (4), (6), or (11), denoted by  $\mu_m$ ] at  $s \gg K_s$  for the three models should be equal, as well as the observed maximum specific consumption rate [i.e., maximum q(s) in Eqns (5), (7), or (8), denoted by  $q_m$ ].

When  $s \gg K_s$ ,  $g(s) \rightarrow 1$ , from Eqns (4) and (6), one can derive that

$$\mu_{\max,H} - a = \mu_{\max,P} \Rightarrow a = \mu_{\max,H} - \mu_{\max,P}$$
(12)

Similarly, from Eqns (5) and (7), it follows that

$$\mu_{\max,H}/Y_G = \mu_{\max,P}/Y_G + m \Rightarrow m$$
  
=  $(1/Y_G) \cdot (\mu_{\max,H} - \mu_{\max,P})$  (13)

Combination of Eqns (12) and (13) shows that

$$a = Y_G \cdot m \tag{14}$$

Equations (13) and (14) also imply that  $\mu_{\max,H} > \mu_{\max,P}$  since both *a* and *m* are greater than 0.

Substitution of Eqns (6) and (7) into (3) shows that

$$1/Y = 1/Y_G + m/\mu_P$$
(15)

where  $\mu_P = \mu_{\max,P} \cdot g(s)$ .

Substituting Eqn (14) into (15) gives

$$\frac{Y_G}{Y} = \frac{\mu_P + a}{\mu_P} \tag{16}$$

Similarly, from Eqns (3), (4), and (5), we can derive

$$\frac{Y_G}{Y} = \frac{\mu_H}{\mu_H - a} \tag{17}$$

where  $\mu_H = \mu_{\max,H} \cdot g(s)$ .

Equations (16) and (17) imply that Y depends on substrate concentration (s) since  $Y_G$  has been assumed constant and both  $\mu_H$  and  $\mu_P$  are s dependent.

Previous studies did not correctly or convincingly show the validity of Eqn (14). It seemed that Schulze & Lipe (1964) derived Eqn (14), but they mixed Y with  $Y_G$  and presumed that  $Y = Y_G$ . Regardless of this equality, there were sign errors in Eqns (31a) and (32) of Schulze & Lipe (1964). The same sign error occurred in Eqn (2) of Marr et al. (1963). Pirt (1965) directly defined the relation between m and a using the same expression as Eqn (14) and then worked out the same formula as Eqn (16) (Pirt, 1982). van Bodegom (2007) thought that  $a = Y_G \cdot m$  was wrong, but his derivation process was incorrect. Eqn (8b) in van Bodegom (2007) was correct (i.e., the same as Eqn (17) of this study); however, he misrepresented ' $\mu$ ' in his Eqn (8b), as equivalent to the ' $\mu_H$ ' in our study, but the ' $\mu$ ' in his Eqn (8a) should be the ' $\mu_P$ ' in our study. Because of the confusion between  $\mu_H$  and  $\mu_P$ , his Eqn (9) relating  $a = Y \cdot m$  was incorrect.

We show [Eqn (12)] that the maximum specific growth rates in the Herbert and Pirt models are not equal (i.e.,  $\mu_{\max,H} > \mu_{\max,P}$ ). This was not realized by Beeftink et al. (1990). In his Eqns (6-9) and Figs 1 and 2, he indicated that the maximum specific growth rates ( $\mu_{max,H}$ and  $\mu_{\max,P}$ ) for the two models were the same, which could result in different observed maximum specific growth rate  $(\mu_m)$  or consumption rate  $(q_m)$  using different models. This is inconsistent with our knowledge that the maximum observations (i.e.,  $\mu_m$  or  $q_m$ ) in a given experiment should be the same.

Similarly, with the assumption of  $h(s) = g(s) \rightarrow 1$  at  $s \gg K_s$  in combination with Eqns (6), (7), (8), and (11), it follows that

$$m_q = Y_G \cdot m = a \tag{18}$$

$$\mu_{\max,C} = \mu_{\max,P} = \mu_{\max,H} - a \tag{19}$$

Comparing the Compromise model with the models of Herbert and Pirt, we found that the Compromise model is identical to the Herbert model for  $\mu$  and q from the mathematical perspective. However, the Compromise model explicitly expresses that the microbial maintenance is associated with both microbial biomass and substrate and decomposes the overall maintenance into two components in Eqns (8) and (11), respectively. As illustrated in Fig. 1, the solutions of  $\mu$  and q from the Herbert and the Compromise model are identical given the additional

constraints that  $Y_G$  is the same in all model formulations. The values of  $\mu$  and q by the Pirt model are higher than the  $\mu$  and q by the Herbert and Compromise models at low substrate concentration. However, with the increasing of substrate concentration, the  $\mu$  and q by the three models approach the same  $\mu_m$  and  $q_m$ , respectively. Our analysis indicates that the illustrations of Figs 1 and 2 in Beeftink et al. (1990) were incorrect.

# Overall maintenance coefficient and sensitivity analysis

The overall maintenance coefficient  $(m_T)$  derived by van Bodegom (2007) was based on the relation of  $a = Y \cdot m$ . This incorrect relation resulted in an incorrect expression for  $m_T$  [see Eqn (18) of his article]. In this study, we did not consider the partitioning of microbial biomass into inactive/reactive fractions. According to the Compromise model described by Eqns (8) and (11), we can add the two maintenance items  $(m_a \cdot h(s)/Y_G \text{ and } m_a \cdot [1 - h(s)])$  to give

$$m_T = m_q \cdot \left[ 1 + \left( \frac{1}{Y_G} - 1 \right) \cdot h(s) \right]$$
$$= m_q \cdot \left[ 1 + \left( \frac{1}{Y_G} - 1 \right) \cdot \frac{\mu_G}{\mu_{\max,C}} \right]$$
(20)

where  $\mu_G = \mu_{\max,C} \cdot h(s)$  denotes the specific growth rate.

Fig. 1. Comparison of three models: Pirt, Herbert, and Compromise.  $\mu_{\max,\mu}$  and  $\mu_{\max,\mu}$  (h<sup>-1</sup>) are maximum specific growth rates for the Herbert and Pert model, respectively;  $K_s$  is the half-saturation constant with the same units of substrate, and  $Y_G$  is the true growth yield coefficient.





**Fig. 2.** Multi-parameter sensitivity analysis of the overall maintenance coefficient  $(m_7)$  to three variables: the physiological maintenance factor  $(m_q)$ , the specific growth rate  $(\mu_G)$ , and the true growth yield  $(Y_G)$ . Greater discrepancy between the two (Acceptable and Unacceptable) cumulative probability distribution curves means higher parameter sensitivity.

Equation (20) shows that  $m_T$  depends on the physiological maintenance factor  $(m_q)$ , the specific growth rate  $(\mu_G)$ , and the true growth yield  $(Y_G)$  with the assumption of  $\mu_{\max,C}$  being a constant. It is evident that  $m_T$  is not a constant with a range of  $a = m_q \le m_T \le m_q/Y_G = m$ when  $0 \le YG \le 1$ . Therefore, the overall maintenance coefficient from the Compromise model is between the values from the Herbert model (i.e., a) and the Pirt model (i.e., m).

To determine the relative importance of the three variables in Eqn (20), we carried out a sensitivity analysis (Wang & Xia, 2010; Wang *et al.*, 2012a). The sensitivities of  $m_T$  to the changes in the three variables are

$$\frac{\partial m_T}{\partial m_q} = 1 + \left(\frac{1}{Y_G} - 1\right) \cdot \frac{\mu_G}{\mu_{\max,C}} \tag{21}$$

$$\frac{\partial m_T}{\partial u_G} = \left(\frac{1}{Y_G} - 1\right) \cdot \frac{m_q}{\mu_{\max,C}} \tag{22}$$

$$\frac{\partial m_T}{\partial Y_G} = -m_q \cdot \frac{\mu_G}{\mu_{\max,C}} \cdot Y_G^{-2} \tag{23}$$

Defining the sensitivity index (Lenhart et al., 2002):

$$I = \left| \left( \frac{\partial m_T}{\partial X} / \frac{m_T}{X} \right) \right|_{X = X_0}$$
(24)

where X represents  $m_q$ ,  $\mu_G$ , or  $Y_G$ , I denotes the sensitivity of  $m_T$  to X at  $X = X_0$ .

We used the variable ranges  $m_q \in (0.01, 0.3)$  h<sup>-1</sup> and  $\mu_G \in (0.01, 0.85)$  h<sup>-1</sup> from Pirt (1982), and  $Y_G \in (0.2, 0.7)$  from Devevre & Horwath (2000). Assuming that  $m_p$  and  $\mu_G$  follow log-uniform distributions and  $Y_G$  follows a uniform distribution, we computed the median values as 0.06, 0.09, and 0.45 for  $m_q$ ,  $\mu_G$ , and  $Y_G$ , respectively. Using these medians as  $X_0$ , we finally calculated that the values of I were 1.0, 0.1, and 0.2 for  $m_q$ ,  $\mu_G$ , and  $Y_G$ , respectively. According to Lenhart *et al.* (2002), the sensitivities of  $m_T$  to  $m_q$ ,  $\mu_G$ , and  $Y_G$  were classified as very high, medium, and high.

We also conducted a sensitivity analysis using the multi-parameter sensitivity analysis (MPSA) method. Different from the above single-point (i.e., medians) analysis, MPSA assesses the parameter sensitivity in the entire parameter space based on the Monte Carlo simulations (Wang et al., 2009). The procedure of MPSA is summarized as follows (Wang & Chen, 2012): (1) Select the parameters and determine their value ranges/distributions. (2) Randomly generate a series of parameter values from certain probability distributions within their ranges. (3) Run the model using these parameter sets and compute the objective function values (OBFs). The OBFs are defined as the sum of squared errors between observed and simulated values. In particular, observed values achieve the OBF using the median of the characteristic range for each parameter. (4) Identify which parameter sets are acceptable or unacceptable by comparing the OBFs to a given criterion, for example, the 50th

percentile of the sorted OBFs. A parameter set with its OBF less than the criterion is classified as an acceptable one, otherwise it is classified as unacceptable. (5) Evaluate the sensitivity of each parameter by comparing the degree of difference between two cumulative distribution curves for acceptable and unacceptable parameter values. A greater discrepancy between the two curves means higher parameter sensitivity. From the results of MPSA shown in Fig. 2, the sensitivity of  $m_q$  was much higher than that of  $\mu_G$  and  $Y_G$ .

Based on the sensitivity analysis from the two methods, we can conclude that the physiological maintenance factor  $(m_q)$  is the most sensitive parameter. In contrast, van Bodegom (2007) found that the overall maintenance coefficient was insensitive to the physiological maintenance, however, this results from an incorrect analysis of  $m_T$ .

# Implications for microbial ecology modeling

In the microbial-enzyme modeling of SOC decomposition, dissolved organic carbon (DOC) serves as a substrate for microbial biomass (MBC) (Chapman & Gray, 1986; Conant *et al.*, 2011). Regarding the DOC-MBC system, we need to take into account specific growth respiration rate ( $R_g$ ), specific maintenance respiration rate ( $R_m$ ), specific enzyme synthesis/production rate ( $P_E$ ), and specific microbial mortality rate ( $r_M$ ) (Ryan, 1990; Blagodatsky *et al.*, 2000; Jin & Bethke, 2003; Blagodatskaya *et al.*, 2011; Franklin *et al.*, 2011). Our critical reassessment of microbial maintenance provides a clear diagram (Fig. 3) for quantifying these components:

$$R_g = (1/Y_G - 1) \cdot \mu_{\max,C} \cdot h(s) \tag{25}$$

$$R_m = (1/Y_G - 1) \cdot m_q \cdot h(s) \tag{26}$$

$$P_E + r_M = m_q \tag{27}$$

Equations (25–27) were derived from a re-analysis of the Compromise model with 0 < YG < 1. The overall maintenance coefficient  $(m_T)$  is resolved into two components: the first component accounts for the synthesis and turnover of macromolecular compounds majorly including enzyme synthesis and microbial mortality and the second is the maintenance respiration. It is evident that the notation for the specific maintenance respiration rate  $(R_m)$  in Eqn (26) is similar to  $R_g$  with  $m_q$  instead of  $\mu_{\max,C}$  in Eqn (25). Different from the existing models where the maintenance respiration rate is a constant (e.g., Schimel & Weintraub, 2003; Lawrence *et al.*, 2009),  $R_m$  derived herein also depends on the concentration of substrate that is included in the function of h(s). The allowance of



**Fig. 3.** A diagram for the DOC-MBC system. DOC: dissolved organic carbon; MBC: microbial biomass carbon. Components include: specific growth respiration rate ( $R_g$ ), specific maintenance respiration rate ( $R_m$ ), specific enzyme synthesis rate ( $P_E$ ), and specific microbial mortality rate ( $r_M$ );  $\mu_{max,C}$  ( $h^{-1}$ ) is the maximum specific growth rate in the Compromise model; and  $h(s) = s/(K_s + s)$ ; see Figs 1 and 2 for other symbols.

specific maintenance respiration rate varying with substrate is consistent with the experimental observations of maintenance energy depending on the specific growth rate (van Verseveld *et al.*, 1984), since the specific growth rate is controlled by the substrate concentration for a given maximum specific growth rate.

Equations (26–27) and Fig. 3 indicate that (1) the parameter  $m_q$  represents a combined specific maintenance rate for both enzyme synthesis and microbial mortality, which are dominant microbial maintenance components (Mandelstam, 1958; van Bodegom, 2007); and (2) a combination of  $m_q$  and  $Y_G$ , that is,  $(1/Y_G - 1) \cdot m_q$ , denotes the specific maintenance respiration rate under sufficient substrate conditions. The synthesis of enzymes and the mortality of microbial biomass are presumed to be independent of substrate, whereas the maintenance respiration depends upon both microbial biomass and substrate.

It is noted that the values of  $m_q$  and  $\mu_G$  used in the above sensitivity analysis come from the continuous-flow cultures (Kuhn *et al.*, 1980). In soil conditions, these reaction rates could be one to several orders of magnitude lower than the values shown above (Anderson & Domsch, 1985b). The discrepancy of  $m_q$  and  $\mu_G$  in the soil from those in pure-culture conditions might be explained by the facts that the substrate discontinuity or occlusion within soil aggregates and the existence of inactive biomass fractions could slow the reaction rates between microorganisms and substrates (Anderson & Domsch, 1985b; Conant *et al.*, 2011; Wang *et al.*, 2012b).

## Conclusions

Our theoretical reassessment of microbial maintenance provided a rigorous proof that  $a = Y_G m$ . Comparison of the three models indicates that the Compromise model is identical to the Herbert model for computing microbial growth and substrate consumption from the mathematical perspective, but the Compromise model is capable of decomposing microbial maintenance into two components [see Eqns (8) and (11)] depending on both biomass and substrate. In contrast to the illustration of Beeftink et al. (1990), we proposed a new one (Fig. 1) to show that the maximum specific growth rate  $(\mu_{\max,H})$  in the Herbert model is higher than those ( $\mu_{max,P}$  and  $\mu_{max,C}$ ) in the other two models, with the difference attributed to the specific maintenance factor  $(m_a \text{ or } a)$ . From the Compromise model, we derived a new expression for the overall maintenance coefficient  $(m_T)$  and found that  $m_T$  was more sensitive to  $m_a$  than to  $\mu_G$  and  $Y_G$ . Finally, we proposed an approach to quantify the specific growth respiration rate  $(R_{q})$ , specific maintenance respiration rate  $(R_m)$ , enzyme synthesis rate  $(P_E)$  plus microbial mortality rate  $(r_M)$  in the microbial ecology model. Although the Compromise model was derived on a mechanistic basis and is a compromise between the Herbert and the Pirt model (Beeftink et al., 1990), the inability to describe the competition between the growth and maintenance energy requirements is a limitation of this model. Further modifications of the maintenance concepts and models are needed to solve this issue.

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# References

- Anderson TH & Domsch K (1985a) Determination of ecophysiological maintenance carbon requirements of soil microorganisms in a dormant state. *Biol Fertil Soils* 1: 81–89.
- Anderson TH & Domsch K (1985b) Maintenance carbon requirements of actively-metabolizing microbial populations under in situ conditions. *Soil Biol Biochem* **17**: 197–203.

 Beeftink H, Van der Heijden R & Heijnen J (1990)
 Maintenance requirements: energy supply from simultaneous endogenous respiration and substrate consumption. *FEMS Microbiol Lett* **73**: 203–209.

Blagodatskaya E, Yuyukina T, Blagodatsky S & Kuzyakov Y (2011) Turnover of soil organic matter and of microbial biomass under  $C_3$ - $C_4$  vegetation change: consideration of <sup>13</sup>C fractionation and preferential substrate utilization. *Soil Biol Biochem* **43**: 159–166.

- Blagodatsky SA, Heinemeyer O & Richter J (2000) Estimating the active and total soil microbial biomass by kinetic respiration analysis. *Biol Fertil Soils* **32**: 73–81.
- Chapman SJ & Gray TRG (1986) Importance of cryptic growth, yield factors and maintenance energy in models of microbial growth in soil. *Soil Biol Biochem* **18**: 1–4.
- Conant RT, Ryan MG, Ågren GI *et al.* (2011) Temperature and soil organic matter decomposition rates – synthesis of current knowledge and a way forward. *Glob Change Biol* **17**: 3392–3404.
- Dawes EA & Ribbons DW (1962) The endogenous metabolism of microorganisms. *Annu Rev Microbiol* 16: 241–264.
- Dawes EA & Ribbons DW (1964) Some aspects of the endogenous metabolism of bacteria. *Microbiol Mol Biol Rev* 28: 126–149.
- Dawes EA & Ribbons DW (1965) Studies on the endogenous metabolism of *Escherichia coli*. *Biochem J* **95**: 332–343.
- Devevre OC & Horwath WR (2000) Decomposition of rice straw and microbial carbon use efficiency under different soil temperatures and moistures. *Soil Biol Biochem* **32**: 1773– 1785.
- Franklin O, Hall EK, Kaiser C, Battin TJ & Richter A (2011) Optimization of biomass composition explains microbial growth-stoichiometry relationships. *Am Nat* 177: E29–E42.
- Jin QS & Bethke CM (2003) A new rate law describing microbial respiration. Appl Environ Microbiol 69: 2340–2348.
- Kuhn H, Cometta S & Fiechter A (1980) Effects of growth temperature on maximal specific growth rate, yield, maintenance, and death rate in glucose-limited continuous culture of the thermophilic *Bacillus caldotenax*. *Appl Microbiol Biotechnol* **10**: 303–315.
- Lawrence CR, Neff JC & Schimel JP (2009) Does adding microbial mechanisms of decomposition improve soil organic matter models? A comparison of four models using data from a pulsed rewetting experiment. *Soil Biol Biochem* **41**: 1923–1934.
- Lenhart T, Eckhardt K, Fohrer N & Frede HG (2002) Comparison of two different approaches of sensitivity analysis. *Phys Chem Earth* **27**: 645–654.
- Mandelstam J (1958) Turnover of protein in growing and non-growing populations of *Escherichia coli*. *Biochem J* 69: 110–119.
- Marr AG, Nilson EH & Clark DJ (1963) The maintenance requirement of *Escherichia coli*. Ann N Y Acad Sci **102**: 536–548.
- Mason C, Hamer G & Bryers J (1986) The death and lysis of microorganisms in environmental processes. *FEMS Microbiol Lett* **39**: 373–401.
- Nagai S, Nishizawa Y & Aiba S (1969) Energetics of growth of *Azotobacter vinelandii* in a glucose-limited chemostat culture. J Gen Microbiol 59: 163–169.
- Neijssel O & Tempest D (1976) Bioenergetic aspects of aerobic growth of *Klebsiella aerogenes* NCTC 418 in carbon-limited and carbon-sufficient chemostat culture. *Arch Microbiol* 107: 215–221.
- Pirt SJ (1965) Maintenance energy of bacteria in growing cultures. *Proc R Soc Lond B Biol Sci* 163: 224–231.

Pirt SJ (1982) Maintenance energy: a general model for energy-limited and energy-sufficient growth. Arch Microbiol 133: 300–302.

Ryan MG (1990) Growth and maintenance respiration in stems of *Pinus contorta* and *Picea engelmannii. Can J For Res* **20**: 48–57.

- Schimel JP & Weintraub MN (2003) The implications of exoenzyme activity on microbial carbon and nitrogen limitation in soil: a theoretical model. *Soil Biol Biochem* 35: 549–563.
- Schulze KL & Lipe RS (1964) Relationship between substrate concentration, growth rate, and respiration rate of *Escherichia coli* in continuous culture. *Arch Microbiol* **48**: 1–20.

Tempest DW & Neijssel OM (1984) The status of  $Y_{ATP}$  and maintenance energy as biologically interpretable phenomena. *Annu Rev Microbiol* **38**: 459–513.

van Bodegom P (2007) Microbial maintenance: a critical review on its quantification. *Microb Ecol* **53**: 513–523.

Van de Werf H & Verstraete W (1987) Estimation of active soil microbial biomass by mathematical analysis of respiration curves: development and verification of the model. *Soil Biol Biochem* **19**: 253–260. van Verseveld H, Chesbro W, Braster M & Stouthamer A (1984) Eubacteria have 3 growth modes keyed to nutrient flow. Consequences for the concept of maintenance and maximal growth yield. *Arch Microbiol* **137**: 176–184.

Wang G & Chen S (2012) A review on parameterization and uncertainty in modeling greenhouse gas emissions from soil. *Geoderma* **170**: 206–216.

Wang G & Xia J (2010) Improvement of SWAT2000 modelling to assess the impact of dams and sluices on streamflow in the Huai River basin of China. *Hydrol Process* 24: 1455–1471.

Wang G, Xia J & Chen J (2009) Quantification of effects of climate variations and human activities on runoff by a monthly water balance model: a case study of the Chaobai River basin in northern China. *Water Resour Res* **45**: W00A11.

Wang G, Chen S & Frear C (2012a) Estimating greenhouse gas emissions from soil following liquid manure applications using a unit response curve method. *Geoderma* **170**: 295–304.

Wang G, Post WM, Mayes MA, Frerichs JT & Jagadamma S (2012b) Parameter estimation for models of ligninolytic and cellulolytic enzyme kinetics. *Soil Biol Biochem* **48**: 28–38.