16 Basic Features of the Kinetic Sub-model

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16.1 The Kinetic Sub-model Is Based on a Differential Growth Equation

Chapters 14 and 15 have shown how experiments should be done in order to select an appropriate empirical equation to describe the growth kinetics. This involves working with experimental growth curves and fitting the integrated form of the appropriate kinetic equation, which could be, for example, one of the equations from Table 14.1. However, the integrated form is not appropriate for direct incorporation into the bioreactor model. This can be understood by considering a simple model such as that shown in Fig. 12.4. In the logistic equation used to describe the growth kinetics in this model, the parameter μ is expressed as a function of temperature. If the integrated form of the equation were to be used (Eq. (14.6) in Table 14.1), then μ would have to be maintained constant, which is not consistent with the fact that the temperature and therefore μ vary during the fermentation. On the other hand, this does not present any problem for the numerical integration of the differential equation (Eq. (16.3) in Table 16.1), since μ can take on a new value for each step in the integration process.

The current chapter concentrates on how the differential form of the kinetic equation is incorporated into the bioreactor model. The kinetic sub-model expresses the various parameters in the growth equation as functions of the local conditions: This is the link that allows the bioreactor model to describe how growth is restricted by poor macroscale transport, since such transport limitation will lead to unfavorable local conditions for growth. The manner in which this is done is covered in the current chapter. The question of how to describe the manner in which growth in turn affects the local conditions is considered in Chap. 17.

Note that this chapter and the next consider growth in terms of the dry biomass itself. However, if the kinetic equation is determined in terms of a biomass component, the same considerations can be applied. Of course, the units must be changed appropriately. For example, biomass has the units of g-dry-biomass g-substrate^{-1}. If glucosamine were used, it would be necessary to write a term for it with units of mg-glucosamine g-substrate^{-1}, and this will affect the significance and units of other parameters, such as yield coefficients.

16.2 The Basic Kinetic Expression

The various types of growth profiles that have been found in SSF systems were presented in Table 14.1. Section 14.3 pointed out that biomass profiles in SSF can be plotted on two different bases, referred to as relative biomass concentrations (kg-biomass kg-dry-solids^{-1}) and absolute biomass concentrations (kg-dry-biomass kg-initial-dry-solids^{-1}). It also argued that the basic kinetic profile should be plotted in terms of "absolute concentration", since various of the effects of growth on the environment will depend on the absolute and not the relative concentration. Assuming that this has in fact been done, the integrated form of the equation selected from Table 14.1 by regression analysis will be expressed in terms of absolute biomass concentration. The corresponding differential form of the equation will then be selected from Table 16.1, for incorporation into the kinetic sub-model of the bioreactor model. Note that, in order to describe the whole profile, it may be necessary to use several equations. Further, an integrated equation other than the four presented in Table 14.1 may have been used, in which case it will be necessary to differentiate the equation. Each of these equations has one or more parameters. It may be interesting to express some of these parameters as functions of key environmental variables such as the temperature and the water activity of the substrate. Experimental approaches to doing this are described later (Sect. 16.4).

However, even though it is desirable to determine the kinetic profile based on absolute biomass concentrations, the bioreactor model should be able to predict the relative biomass concentration, in order to allow comparison between the model predictions and experimental results obtained in the bioreactor, which are typically obtained in terms of relative biomass concentrations. In order to convert

Table 16.1. Differential forms of the equations that have been used to describe growth profiles or parts of growth profiles in SSF systems

Name	Equation[a]	Equation number	Parameters[b]
Linear	$\frac{dC_{XA}}{dt} = k$	(16.1)	k
Exponential	$\frac{dC_{XA}}{dt} = \mu C_{XA}$	(16.2)	μ
Logistic	$\frac{dC_{XA}}{dt} = \mu C_{XA}\left(1 - \frac{C_{XA}}{C_{XAM}}\right)$	(16.3)	C_{XAM}, μ
Deceleration	$\frac{dC_{XA}}{dt} = kAC_{XA}e^{-kt}$	(16.4)	k, A

[a] The integrated form of these equations are given in Table 14.1. These equations are expressed in terms of absolute biomass concentration (e.g., g-dry-biomass g-IDS^{-1}).
[b] These parameters may later be expressed as functions of the environmental conditions.

a relative concentration to an absolute basis, it would be necessary to know to what initial dry weight of substrate the removed sample corresponded. To do this it would be necessary to weigh the whole bioreactor contents and determine the moisture content of the bed just before each sampling time. It is not a simple matter to weigh the whole bioreactor, especially at large scale. It is easier to use the kinetic sub-model to predict the relative biomass concentration.

Such a conversion can be done in the following manner. If the total dry weight of solids in the bioreactor (D, kg) is given as:

$$D = X + S, \tag{16.5}$$

where X is the total dry weight of biomass (kg) and S the total dry weight of residual substrate (kg), then for the absolute amount of biomass in the bioreactor (X, kg) we have:

$$\frac{dX}{dt} = \frac{d(C_{XA} D_o)}{dt} = D_o \frac{dC_{XA}}{dt}, \tag{16.6}$$

while for the "relative concentration" we have:

$$\frac{dX}{dt} = \frac{d(C_{XR} D)}{dt} = D \frac{dC_{XR}}{dt} + C_{XR} \frac{dD}{dt}. \tag{16.7}$$

Equation (16.6) can be substituted into Eq. (16.7) in order to eliminate the term dX/dt. The resulting equation can be rearranged to be explicit in dC_{XR}/dt:

$$\frac{dC_{XR}}{dt} = \frac{D_o}{D} \frac{dC_{XA}}{dt} - \frac{C_{XR}}{D} \frac{dD}{dt}. \tag{16.8}$$

Equation (16.8) says that the change in relative concentration (kg-dry-biomass kg-dry-solids^{-1}) during growth occurs due to growth itself in absolute terms, as described by the first term on the right-hand side, and due to the decrease in dry solids that occurs during growth, as described by the second term on the right-hand side. Growth leads to an overall loss of dry solids, and therefore dD/dt will be negative; given that this term is subtracted, its effect is to increase the relative concentration.

The rate of change in the total dry weight of solids is the sum of the rates of change in dry biomass and residual dry substrate:

$$\frac{dD}{dt} = \frac{dX}{dt} + \frac{dS}{dt}. \tag{16.9}$$

The rate of consumption of the residual dry substrate is related to the rate of growth by the following equation:

$$\frac{dS}{dt} = -\frac{1}{Y_{XS}} \frac{dX}{dt} - m_S X, \tag{16.10}$$

where Y_{XS} is the true growth yield (kg-dry-biomass kg-dry-substrate^{-1}) and m_S is the maintenance coefficient (kg-dry-substrate kg-dry-biomass^{-1} h^{-1}).

Substituting Eq. (16.10) into Eq. (16.9) and using the distributive law to separate out dX/dt on the right hand side gives:

$$\frac{dD}{dt} = \left(1 - \frac{1}{Y_{XS}}\right)\frac{dX}{dt} - m_S X \,. \tag{16.11}$$

Equation (16.11) can be rewritten in terms of the absolute biomass concentration by replacing X with $C_{XA}D_o$

$$\frac{dD}{dt} = D_o\left(\left(1 - \frac{1}{Y_{XS}}\right)\frac{dC_{XA}}{dt} - m_S C_{XA}\right). \tag{16.12}$$

Given a kinetic equation written in terms of the absolute biomass concentration, such as one of the equations from Table 16.1, it is possible to use Eqs. (16.8) and (16.12) to predict the growth profile that would be obtained for measurements made on a relative basis (C_{XR}). Figure 16.1 shows how this is done.

In order to undertake this conversion, it is necessary to have values for Y_{XS} and m_S. One method of estimating these parameters is to obtain experimental data in the initial kinetic studies in terms of both the absolute and the relative biomass concentrations. Figure 16.2 shows how this data can be used to obtain estimates for these two parameters.

This conversion is not limited to biomass. It is possible to use the model to convert measurements of biomass components between absolute and relative measurement bases. In this case X will represent the component, Y_{XS} will have the units of kg-component kg-dry-substrate^{-1}, and m_S will have the units of kg-dry-substrate kg-component^{-1} h^{-1}.

16.3 Incorporating the Effect of the Environment on Growth

The kinetic sub-model needs to describe how growth depends on the key environmental variables, since these variables typically cannot be simply controlled at their optimum values in an SSF bioreactor. The bioreactor model will be most useful if it can be used to explore how the operating variables affect the values of the key environmental variables, and how changes in the environmental variables in turn affect the overall performance of the bioreactor.

So which environmental variables are the "key environmental variables"? This question was raised in Sect. 13.2.1, where it was recommended that, at the very least, the effects of temperature and water activity on growth should be described. During a fermentation, these variables can change quite significantly. For example, the temperature might start at the optimum temperature for growth, but it can increase quite substantially during the mid parts of the fermentation, falling again

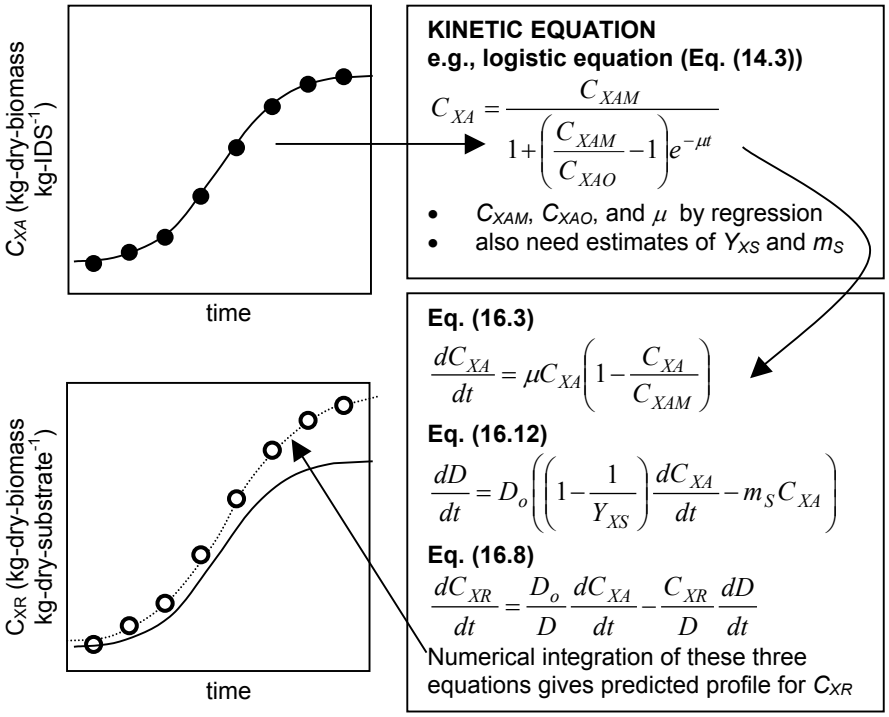

Fig. 16.1. How kinetics determined on an absolute basis can be converted to a relative basis, in order to allow comparison between the model predictions and experimental results. This is necessary since samples removed from a bioreactor are processed to give biomass contents on a relative basis. Note that, even though growth has finished by the end of the fermentation in absolute terms, the relative biomass concentration continues to rise through the conversion of substrate into CO_2 due to maintenance metabolism

as the growth decelerates at the end of the process. In addition, the water activity of the substrate bed may start at the optimum but may then decrease during the fermentation due to the evaporation of water from the bed. Further, these two variables can be influenced significantly by the manner in which the bioreactor is operated, and bioreactor models that describe the effects of these two variables on growth can be used to explore strategies of bioreactor operation that attempt to minimize the deviation of these variables from the optimum values for growth and product formation.

In kinetic models, the effect of these varying environmental variables on growth is taken into account by expressing the parameters in the kinetic equation as functions of the local conditions. Table 16.1 indicates, for each of the kinetic equations, which of the parameters might be expressed as functions of the environmental variables.

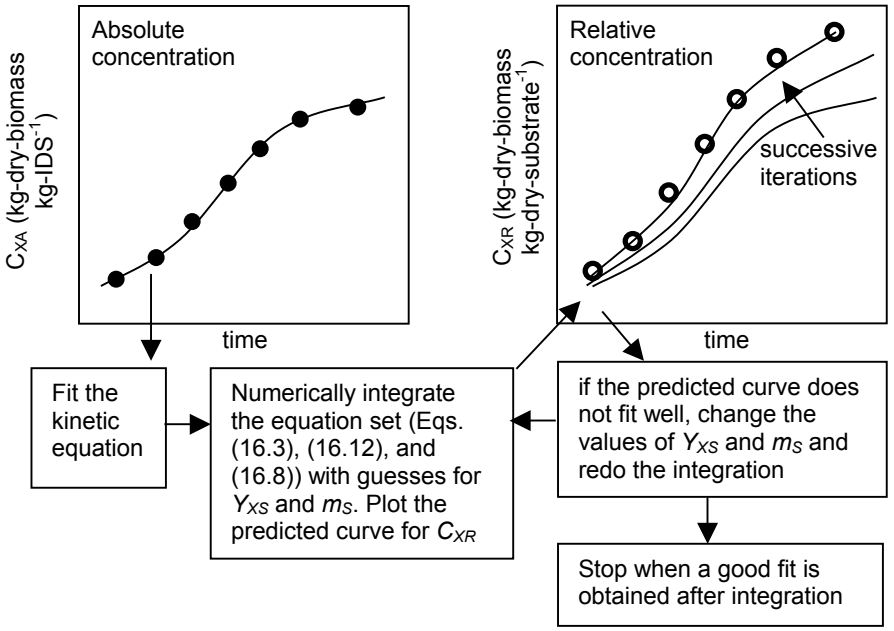

Fig. 16.2. How estimates of Y_{XS} and m_S can be obtained if, during the initial laboratory studies (See Chaps. 14 and 15), growth profile data is obtained in both the absolute and relative concentrations. Note that optimization programs can be used to undertake the iterative fitting of the relative biomass curve

The sections below present experimental approaches that can be used to gather experimental data, and approaches to developing appropriate equations, for the case of temperature and the case of water activity. Note that the recommendations are for "isothermal" and "isohydric" studies, in which conditions are maintained constant throughout the growth cycle, whereas in real SSF processes the temperature and the water activity change during the process. It is possible that expressions for the effects of temperature and water activity that are obtained on the basis of the isothermal and isohydric approaches will not describe the true effect on growth of the time-varying conditions that are encountered by the organism in SSF processes at large scale (Ikasari et al. 1999). The advantage of the isothermal and isohydric approaches is that they are easy to carry out. Possible approaches to determining the effects of temporal variations in the environmental variable are also discussed.

16.3.1 Incorporating the Effect of Temperature on Growth

16.3.1.1 The "Isothermal Approach"

This experimental approach is as follows (see Fig. 14.2):

1. A small-scale experimental system is used so that heat transfer will not be limiting (see Sect. 15.1) and therefore the substrate will be at the temperature of the incubator or waterbath used;
2. Cultures are incubated at various different temperatures, with the temperature experienced by each culture being held constant during the entire growth cycle;
3. The growth profile for each culture is then plotted and the appropriate kinetic equation is fitted to each profile, allowing determination of the values of the parameters of the kinetic equation for each temperature. For example, if the growth curve is logistic, the integrated form of the logistic equation is fitted by non-linear regression to the growth profile. This will yield a specific growth rate constant and a maximum biomass concentration for each temperature;
4. The parameters that are sensitive to temperature are then plotted against temperature and an empirical equation is used to describe this curve, being fitted to the curve by non-linear regression.

16.3.1.2 Equations that Have Been Developed Using this Approach

Equations that have been used to describe the effect of temperature on growth are presented below. All are simply empirical fits to the data.

Saucedo-Castaneda et al. (1990) used a "double Arrhenius" equation to describe the effect of temperature on the specific growth rate constant:

$$\mu_T = A \exp\left(\frac{-E_{a1}}{R(T+273)}\right) \Bigg/ \left(1 + B \exp\left(\frac{-E_{a2}}{R(T+273)}\right)\right), \tag{16.13}$$

where A (h^{-1}), B (dimensionless), and E_{a1} and E_{a2} (J mol^{-1}) are simply fitting parameters, R is the universal gas constant (J mol^{-1} $°C^{-1}$), μ_T is the specific growth rate parameter (h^{-1}), and T is the temperature (°C). The symbol μ_T is used to denote that the equation describes specifically the effect of temperature on the specific growth rate parameter. Note that this equation does not describe a maximum temperature for growth, since the value of μ_T is always positive and greater than zero. The shape of this curve is shown in Fig. 16.3(a).

The maximum biomass concentration (C_m, g-biomass 100-g-dry-$matter^{-1}$), which is a parameter in the logistic growth equation, was modeled with a polynomial equation:

$$C_m = a_o + a_1 T + a_2 T^2 + a_3 T^3 + a_4 T^4, \tag{16.14}$$

for temperature T in °C. The parameters a_o to a_4 are simply fitting parameters.

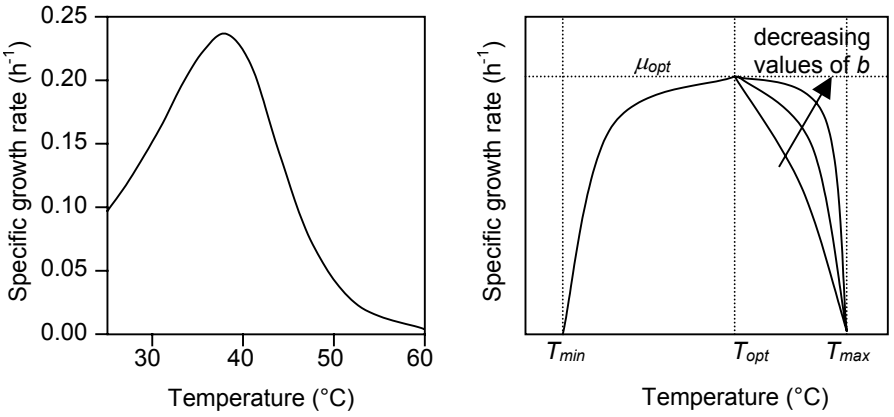

Fig. 16.3. The dependence of the specific growth rate parameter (μ_T) on temperature, as described by two different equations. **(a)** The "double-Arrhenius" equation of Saucedo-Castaneda et al. (1990). Their values for the parameters of the equation were used to plot the curve, being A = 2.694 x 10^{11} h^{-1}, B = 1.3x10^{47}, E_{a1} = 70225 J mol^{-1}, E_{a2} = 283356 J mol^{-1}. Adapted from Saucedo-Castaneda et al. (1990) with kind permission from John Wiley & Sons, Inc. **(b)** The general shape of the profile described by the equation set of Sangsurasak and Mitchell (1998). The parameter b allows the model to describe greater or lesser sensitivities of μ_T to increases in temperature above the optimum

The advantage of modeling the effect of temperature is not as obvious for C_m as it is for μ_T. In Eq. (16.14) the maximum biomass concentration depends only on the actual temperature. Therefore C_m varies throughout the fermentation and, if the temperature falls back to the value that gives the maximum value for C_m, then the biomass is predicted to reach this value, regardless of the previous high temperatures that the culture may have suffered. In this manner, the effect of Eq. (16.14) (in combination with the kinetic equation) is simply to modify the instantaneous growth rate, not the maximum biomass concentration obtained.

It is highly likely that the temperature history affects the value of C_m. However, there is simply not sufficient data available in the literature to enable an equation to be proposed to describe this effect. One possibility might be to use Eq. (16.14), but only to allow decreases in C_m as the temperature varies above the optimum temperature. That is, once the temperature begins to fall from the maximum temperature reached during the fermentation, the value of C_m then remains fixed at the value it had at the time when the maximum temperature was reached. Experimental validation will be necessary to confirm whether this approach is appropriate.

Sangsurasak and Mitchell (1998) developed a set of empirical equations, which, although being more cumbersome than the equation used by Saucedo-Castaneda et al. (1990), does describe minimum and maximum temperatures for growth. Below the minimum temperature for growth (T_{min}, °C) and above the maximum temperature for growth (T_{max}, °C) the specific growth rate parameter was set to zero. Between the minimum temperature and the optimum temperature (T_{opt}, °C) the following equation was used:

$$\mu_T = \mu_{opt} (F_1 + F_2.(T+273) + F_3.(T+273)^2), \quad (16.15)$$

where F_1, F_2, and F_3 are simply fitting constants, determined by non-linear regression of the appropriate part of the curve. Between the optimum and the maximum temperature the following equation was used:

$$\mu_T = \mu_{opt} \left(\frac{b + (T_{\max} - T_{opt})}{(T_{\max} - T_{opt})} \right) \left(\frac{T_{\max} - T}{b + (T_{\max} - T)} \right), \quad (16.16)$$

where μ_{opt}, T_{max}, and T_{opt} were determined by visual inspection of the plot of μ_T against temperature, and the fitting parameter b determines the degree of curvature (Fig. 16.3(b)).

16.3.1.3 Is the "Isothermal Approach" Valid?

The dependence of the growth rate on temperature that is predicted by an equation developed using data obtained by the isothermal approach might not actually be the behavior demonstrated during an actual SSF process (Ikasari et al. 1999). There is a significant difference between the "isothermal approach" and a large-scale SSF process: the temperature in the SSF process does not remain constant; rather, it varies as a function of time. It typically begins at the optimal temperature for growth, and during the early periods the temperature is near the optimal temperature. An organism experiencing a temperature rise from the optimum to say 5°C above the optimum would very likely be healthier than an organism reaching the same temperature during the later stages of the fermentation (Fig. 16.4(a)). In the latter case the organism has recently been exposed to temperatures of as much as 10°C above the optimum, which very likely have had deleterious effects on cell structure and metabolism. The isothermal approach does not predict this, rather it assumes that the specific growth rate constant at any given instant is simply a function of the temperature at that instant (Fig. 16.4(b)).

It is highly likely that the recent history of temperatures experienced by the microorganism influences its current growth rate. For example, intracellular enzymes may denature at high temperatures, and it may take some time to replace them, meaning that high growth rates cannot immediately be re-established, even if the organism is returned to the optimum temperature. Another possibility is that senescence or sporulation may be triggered and, once triggered, may be irreversible, even if in the meantime the organism is returned to the optimal temperature. On the other hand, microorganisms do have mechanisms of adaptation to higher temperatures. Various heat shock proteins are produced and processes are induced that lead to a change in the lipid composition of the membrane. These might take several hours after an elevation of temperature to come into effect, but then growth might accelerate. Unfortunately, there is very little information available in the literature about the effect on growth kinetics of what might be called "sub-lethal temperature excursions". In the absence of more information, the best current strategy is to use the isothermal approach.

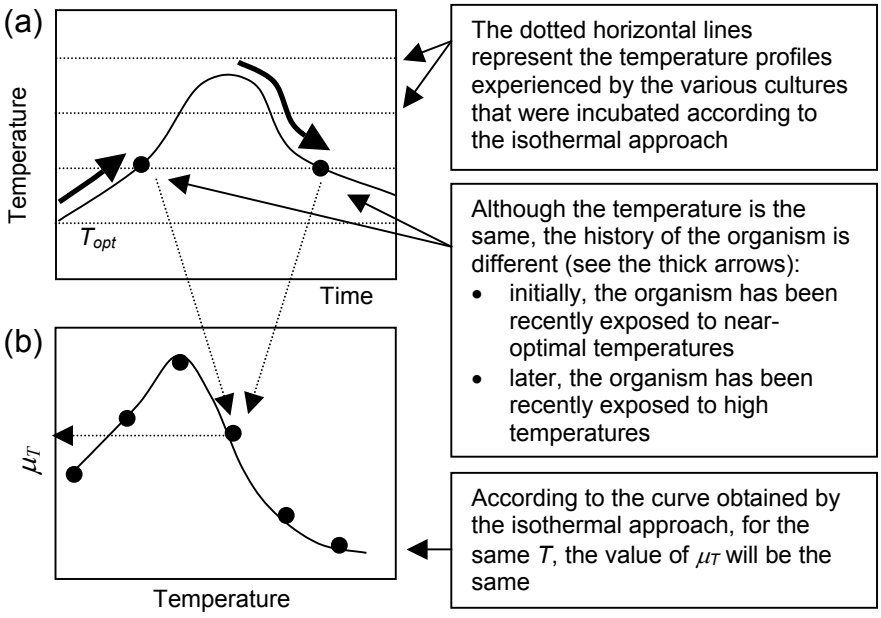

Fig. 16.4. Is the isothermal approach valid? **(a)** A typical temperature profile that might occur in a large-scale bioreactor, demonstrating how the same supra-optimal temperature will be reached twice, once before the temperature peak and once after the temperature peak; **(b)** The isothermal approach gives the same value for μ_T, regardless of the recent temperature history of the microorganism

Recently, a model has been proposed that is capable of describing delayed temperature effects (Dalsenter et al. 2005). The model describes the effect of temperature on the relative rates of synthesis and denaturation of a pool of key metabolic enzymes (Fig. 16.5). In turn, the growth rate of the microorganism depends on the state of this enzyme pool. At the moment this model has not been sufficiently validated to have confidence that it will accurately predict growth rates under a wide range of conditions, however, it does suggest a general strategy by which future models might be developed.

16.3.2 Incorporating the Effect of Water Activity on Growth

16.3.2.1 The Experimental Approach to Collecting Data

A similar concept to the isothermal approach for determining temperature effects has been used to determine the effect of water activity on growth. Various cultures are incubated in various atmospheres of controlled relative humidity (in which the substrate is pre-equilibrated, such that its water activity is equal to the percentage

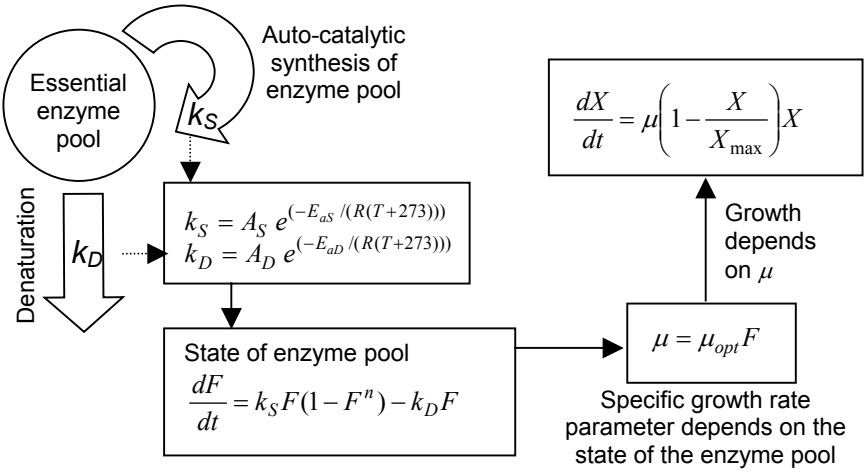

Fig. 16.5. Schematic representation of a model that can describe the effects of the recent temperature history on the growth rate (Dalsenter et al. 2005). F is a nondimensional variable representing the state of the intracellular "essential enzyme pool" and its value varies between 0 and 1. The coefficient of the autocatalytic synthesis reaction (k_S) depends on temperature (T, °C) according to the Arrhenius equation (with frequency factor A_S and activation energy E_{aS}). The coefficient of the denaturation reaction (k_D) depends on temperature according to the Arrhenius equation (with frequency factor A_D and activation energy E_{aD})

relative humidity divided by 100). The growth profile for each culture is analyzed to determine the parameters of the kinetic equation. These parameters are plotted against water activity (see Fig. 14.2) and an empirical equation is fitted to this plot. This approach is referred to here as the "isohydric approach".

In fact, the effect of water activity on growth rates in real SSF systems has been relatively little studied. Instead of this, many studies that involve fungi characterize the effect of water activity on the radial expansion rate of colonies. Furthermore, no effort has been made to look at the effect on growth of variations in the water activity during the growth cycle.

16.3.2.2 Equations that Have Been Developed Using this Approach

A simple empirical equation was used by von Meien and Mitchell (2002):

$$\mu_W = \mu_{opt} \exp\left(D_1 a_{ws}^3 + D_2 a_{ws}^2 + D_3 a_{ws} + D_4\right), \tag{16.17}$$

where D_1 to D_4 are fitting parameters and a_{ws} is the water activity of the solid substrate phase. The symbol μ_W is used to denote that the equation describes specifically the effect of water activity on the specific growth rate parameter. von Meien and Mitchell (2002) fitted this equation to data for two different fungi, presented by Glenn and Rogers (1998) (Fig. 16.6).

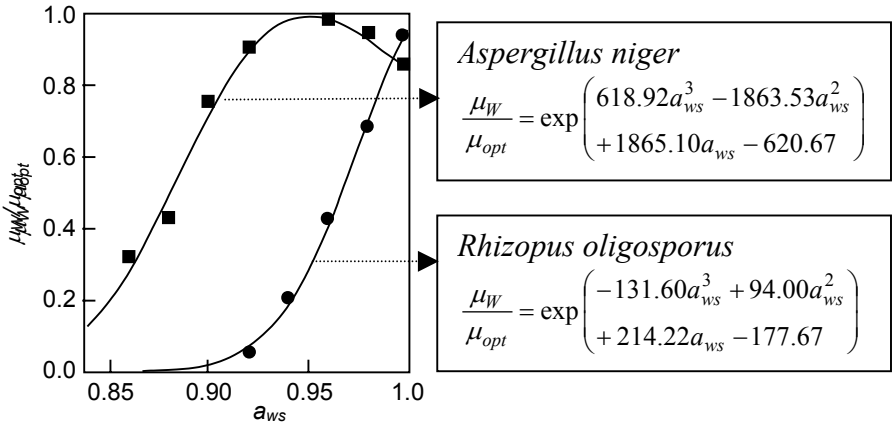

Fig. 16.6. The dependence of the specific growth rate parameter (μ_W) on water activity, as described by the equation of von Meien and Mitchell (2002) for two different organisms. The experimental data is from Glenn and Rogers (1988) and is reproduced with kind permission from the authors

16.3.3 Combining the Effects of Several Variables

If the kinetic model attempts to take into account the effect of both temperature and water activity on growth, the question arises as to how best to combine the effects of simultaneous variations in both variables. The best approach might be to determine the specific growth rate parameter at a large number of different combinations of water activity and temperature and simply use regression against two independent variables to determine an empirical equation (Fig. 16.7). However, to date most studies in which both water activity and temperature have been varied have not explored a sufficiently large number of combinations to allow such equations to be proposed. In the absence of this data, simple rules have been proposed for combining the effects determined in studies in which the variables are varied one-by-one, typically one variable being varied at the optimum value of the other. The maximum value of the specific growth rate constant, determined at the optimum values of water activity and temperature, is denoted μ_{opt}. During the experiments to determine the effect of each environmental variable on growth, the specific growth rate can be expressed as a fraction of this optimum:

$$f = \frac{\mu_{measured}}{\mu_{opt}}. \tag{16.18}$$

For example, in the case of temperature effects, using Eq. (16.13) gives:

$$f_T = \frac{\mu_T}{\mu_{opt}} = \frac{1}{\mu_{opt}} A \exp\left(\frac{-E_{a1}}{R(T+273)}\right) \Bigg/ \left(1 + B\exp\left(\frac{-E_{a2}}{R(T+273)}\right)\right), \tag{16.19}$$

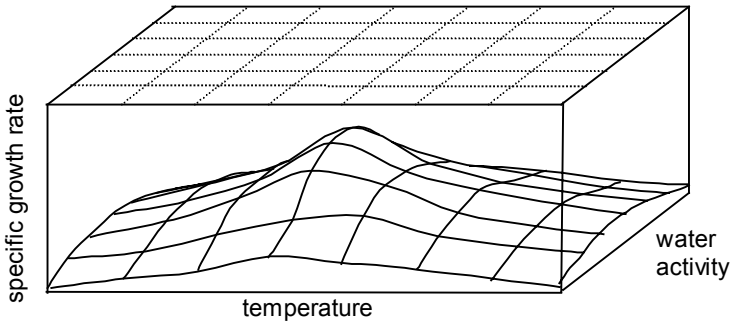

Fig. 16.7. One strategy for determining the combined effect of temperature and water activity on the specific growth rate parameter would be to determine the "response surface", that is, to determine the specific growth rate parameter at various different combinations of temperature and water activity. An equation, involving two independent variables, can then be fitted to this surface. Such a strategy was recently used by Hamidi-Esfahani et al. (2004). The disadvantage is the number of experiments required. This example involves all possible combinations of 8 temperatures and 7 water activities, that is, a total of 56 different experiments.

where the subscript "*T*" in f_T denotes that this is the fractional specific growth rate based on variations in temperature. Similarly, in the case of water activity effects, using Eq. (7.18) gives:

$$f_W = \frac{\mu_W}{\mu_{opt}} = \frac{1}{\mu_{opt}} \exp\left(D_1 a_{ws}^3 + D_2 a_{ws}^2 + D_3 a_{ws} + D_4\right), \tag{16.20}$$

If equations are written for all of the environmental variables that are taken into account in the model, then the overall fractional specific growth rate can be calculated on the basis of the geometric mean of the individual fractional specific growth rates (Sargantanis et al. 1993). In the case in which only temperature and water activity are taken into account, the equation for the combined effect on the specific growth rate would be:

$$\mu = \mu_{opt} \sqrt{f_T f_W} \ . \tag{16.21}$$

16.4 Modeling Death Kinetics

16.4.1 General Considerations in Modeling of Death Kinetics

Given the difficulty in controlling the fermentation conditions, especially the temperature, in large-scale SSF bioreactors, it is quite possible that conditions will occur that cause cells to die. Therefore it might be of interest to describe death kinetics within the kinetic sub-model of the bioreactor model. Note that this has often

not been done. In various bioreactor models the kinetics are written in terms of viable biomass only, with the growth rate reflecting the net increase in viable biomass, that is, the true growth rate minus the death rate. In other words, the equation only describes the overall outcome of growth and death, and does not segregate the biomass into live and dead biomass. Note that such an approach can lead to inaccuracies, since if there is significant death then the increase in viable biomass does not represent the overall growth activity. In this case growth-related activities such as metabolic heat generation would be underestimated.

In cases were death is taken into account explicitly, the growth equation is written in terms of the underlying true growth rate and a separate equation expresses the death rate. Note that many SSF processes involve fungi, and it is not necessarily a simple matter to measure fungal death experimentally. The difficulty can be seen by comparing the situation with that of studies of the death of unicellular organisms. In this case, the total cell number can be determined from total counts done in a Neubauer chamber, while the number of viable cells can be determined by viable counts, that is, agitating the culture well to separate the cells, then plating the culture out and counting the number of colonies that arise. In the case of fungi, it is not possible to separate out individual cells in this manner, since they are linked together in the mycelium. Death is often inferred by indirect means, such as a decrease in the specific O_2 uptake rate. As a result, only relatively few attempts have been made to model fungal death kinetics in SSF. Further, no attempts have been made to validate the model predictions about the relative populations of live and dead biomass, rather the growth equations have simply been empirically adjusted to agree with observed growth curves.

Another factor needs to be considered. If the model describes the dry weight of the biomass, death will only cause this dry weight to decrease if the model describes a process of autolysis. In a model in which biomass dies and is converted into dead biomass, which then remains stable, it is not possible for the model to describe decreases in the overall biomass.

16.4.2 Approaches to Modeling Death Kinetics that Have Been Used

The simplest assumption is that death is a first order process, giving the equation:

$$\frac{dC_{XAD}}{dt} = r_d = k_d C_{XAV}\,, \tag{16.22}$$

where C_{XAV} and C_{XAD} are the absolute concentrations of viable and dead biomass, respectively, and k_d is the specific death rate coefficient (h^{-1}).

This term might simply be subtracted from the equation for the production of viable biomass. In the case in which growth follows logistic kinetics then the equation for total biomass production might be:

$$\frac{dC_{XAT}}{dt} = \mu C_{XAV}\left(1 - \frac{C_{XAT}}{C_{XAM}}\right), \tag{16.23}$$

where C_{XAT} is the absolute concentration of total biomass (i.e., both viable and dead). C_{XAT} appears in the numerator of the term within the parentheses since it is assumed that the biomass-associated limitation of growth is due to the total biomass concentration and not simply the viable biomass concentration. This could be true for the case in which growth is limited by the availability of nutrients.

Subtracting the rate of death (Eq. (16.22)) from the overall rate of biomass production (Eq. (16.23)) gives the rate of increase of viable biomass:

$$\frac{dC_{XAV}}{dt} = \mu C_{XAV}\left(1 - \frac{C_{XAT}}{C_{XAM}}\right) - k_d C_{XAV} \,. \tag{16.24}$$

Arrhenius equations can be used to express the effect of environmental conditions such as temperature on growth:

$$\mu = A_g \exp\left(\frac{-E_{ag}}{R(T+273)}\right), \tag{16.25}$$

and on death:

$$k_d = A_d \exp\left(\frac{-E_{ad}}{R(T+273)}\right), \tag{16.26}$$

where T is the temperature (°C), A_g and A_d are the frequency factors for growth and death (h^{-1}) and E_{ag} and E_{ad} are the activation energies for growth and death (J mol^{-1}). Typical profiles that could be expected for these two rate constants against temperature are shown in Fig. 16.8.

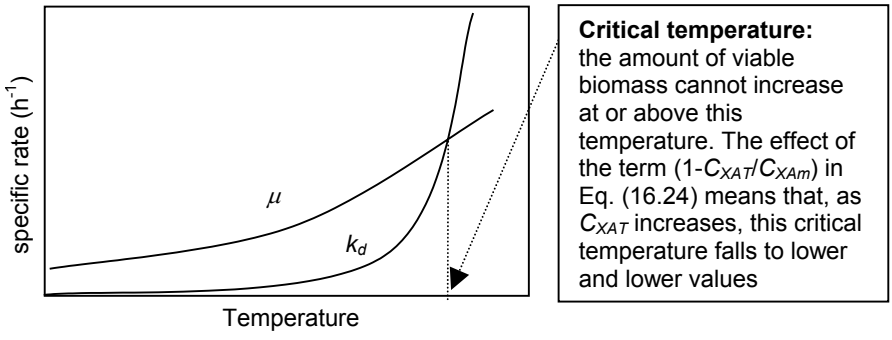

Fig. 16.8. Typical behavior that might be expected for the specific growth rate and specific death rate parameters as a function of temperature according to the Arrhenius equations (Eqs. (16.25) and (16.26))

16.5 Conclusion

This chapter has shown how the basic empirical kinetic equation is written, and how the parameters of the equation can be written as functions of the key environmental variables. The next chapter extends the discussion to how we can model the effects that growth has on the environment of the organism.

Further Reading

A detailed development of a system of equations for converting between biomass profiles expressed on relative and absolute bases

Viccini G, Mitchell DA, Krieger N (2003) A model for converting solid state fermentation growth profiles between absolute and relative measurement bases. Food Technol Biotechnol 41:191–201

Alternative approaches to modeling temperature effects

Dalsenter FDH, Viccini, G, Barga MC, Mitchell DA, Krieger N (2005) A mathematical model describing the effect of temperature variations on the kinetics of microbial growth in solid-state culture. Process Biochemistry 40:801–807

Combined temperature and moisture effects on growth kinetics

Hamidi-Esfahani Z, Shojaosadati SA, Rinzema A (2004) Modelling of simultaneous effect of moisture and temperature on *A. niger* growth in solid-state fermentation. Biochem Eng J 21:265–272