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Analysis of Growth Kinetic Profiles in Solid-State Fermentation

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Summary

Currently, mathematical models that propose to describe the performance of solid state fermentation bioreactors use simple empirical equations to describe the growth kinetics. However, a systematic analysis of the growth profiles in solid state fermentation systems has not previously been undertaken. In the present work various empirical equations, including the linear, exponential and logistic equations, were fitted to profiles obtained from the literature. The logistic equation gave an adequate description of the whole growth profile in the majority of cases, although in many cases the description is not perfect, with systematic deviations from the best fitting logistic curve, especially decreases in biomass concentration in the later stages of the fermentation and over- or underestimation of the initial biomass concentration by the fitted curve. Clearly, although the logistic equation is commonly used in mathematical models of bioreactor performance, it cannot be treated as though it is a universally applicable equation in solid state fermentation systems. Various improvements that will be necessary before empirical growth equations become truly useful are identified and discussed.

Key words: growth kinetics, solid-state fermentation, regression analysis, empirical model

Introduction

This paper provides a systematic analysis of the microbial growth profiles that have been reported for solid--state fermentation (SSF) systems over the last 20 years, concentrating on identifying empirical kinetic equations appropriate for use in current models of SSF bioreactors.

Solid-state fermentation involves the growth of microorganisms in beds of moist solid substrate particles in the absence or near-absence of free liquid water in the spaces between the particles. This fermentation technique has the potential to produce a number of biotechnological products more efficiently than the more traditional submerged liquid fermentation (SLF). For example, in the production of fungal spores for use as biopesticides, not only are spore yields typically higher in SSF than in SLF *(1)* but also the spores produced in SSF are more robust and more virulent than spores produced in

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SLF *(2)*. Another example is the production of fungal enzymes, where higher yields are often obtained in SSF systems *(3)*. Commodity chemicals for which SSF could be a competitive technology include citric acid, food colorants based on microbial pigments, gibberellic acid, aromas, flavors and polysaccharides, amongst others *(3)*. However, despite this potential, relatively few SSF processes manage to be successfully commercialized.

The major problem that hinders the commercialization of new SSF processes is that in large scale bioreactors it is difficult to control the conditions within the substrate bed at the optimum values for growth and product formation. This problem arises from the poor heat and mass transfer properties of solid beds (4). Until recently the understanding of how to overcome these challenges was very poor, due to the physical and dynamic complexity of the system. Several factors contribute to this complexity. Within the substrate bed there is a complex 3-dimensional arrangement of substrate particles, microbial biomass and air. Temperature gradients occur across the substrate bed when the bed is static or only infrequently mixed. Concentration gradients of oxygen and nutrients arise within substrate particles since mass transfer within the particle is limited to diffusion. Within this complex system, either physical or microbial phenomena may limit growth at different stages of the fermentation. Further, the way in which these phenomena interact is different in different microbe-substrate-bioreactor systems. This complexity is not encountered in SLF systems, and, as a result, bioengineering principles for SLF are well-established, but similar principles are only now beginning to be established for SSF. Due to this poor understanding, the design and operation of bioreactors for SSF processes has typically been done on a trial and error basis, which results in processes of low efficiency and therefore prejudices the economic performance of the processes. As a result, very few of the large number of processes being researched at laboratory scale manage to become commercialized. There is an urgent need to develop rational strategies for optimizing the design and operation of SSF bioreactors in order to increase the efficiency of the processes and therefore their economic viability.

Mathematical models will be essential tools in the development of rational strategies for the design and optimization of operation of large-scale bioreactors, as has recently been shown for various bioreactor types: traditional packed-bed bioreactors (*5,6*), the Zymotis bioreactor, which is a variant of the packed bed design with internal heat transfer plates *(7)*, rotating drum bioreactors (*8*), scraped drum bioreactors *(9,10)* and stirred bioreactors *(10)*.

Mathematical models of SSF bioreactors can be thought of as consisting of macroscale and microscale submodels *(11)*: The macroscale submodel describes the transfer of heat and mass across the substrate bed as a whole and between the bed and the headspace and the bioreactor wall (Fig. 1, right hand side). The microscale submodel describes the growth kinetics of the microorganism and how these kinetics depend on various of the processes that occur at the scale of individual particles (Fig. 1, left hand side). The microscale phenomena that could po-

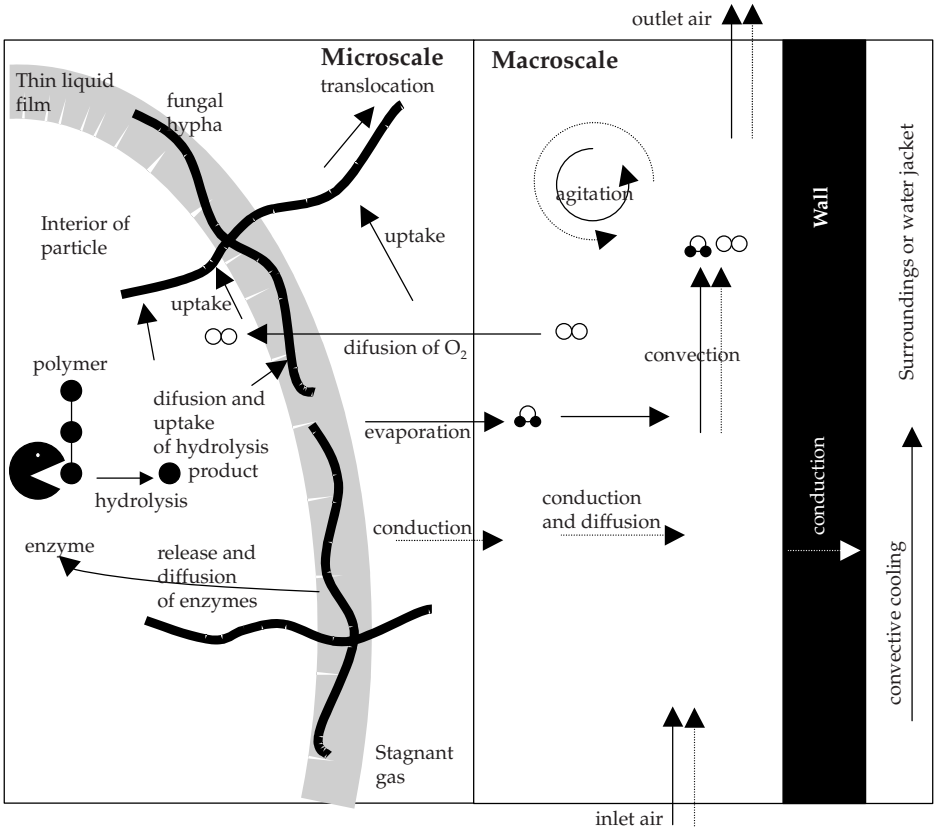

Fig. 1. The macroscale and microscale processes that occur within an SSF bioreactor

tentially be included in the growth kinetic submodel include: how the growth rate of the microorganism depends on the local environmental conditions such as temperature, water activity, pH, and oxygen and nutrient concentrations; intraparticle processes such as diffusion of enzymes, hydrolysis of polymers by these enzymes and the diffusion of the hydrolysis products; and (3) morphological characteristics such as the division of cells and, in the case of processes involving fungi, the extension and branching of hyphae.

It is possible to model these microscale phenomena in some detail. A model relating growth to the intraparticle diffusion of enzymes and hydrolysis products was proposed by Mitchell *et al. (12)*, and used to show that the rate of diffusion of the hydrolysis products to the surface could potentially limit growth. This model was extended to describe oxygen diffusion *(13)*, the reduction of particle size *(14)*, and the transport of nutrients within the microbial biomass layer *(15)*. Viniegra-Gonzalez *et al. (16,17)* proposed a model for growth that was based on an assumption of symmetrical branching within the mycelium, with this model being later extended to describe the effect of temperature on growth *(18)*.

However, in combining the microscale submodel with the macroscale submodel to produce a bioreactor model, a decision must be made about the level of detail with which the microscale phenomena will be described, this decision being made on the basis of the trade-off between the predictive power and flexibility of the model and its simplicity. Given the fact that in the majority of bioreactors there are significant gradients at the macroscale, which leads to the appearance of partial differential equations in the macroscale submodel, the approach to modeling the microscale phenomena that has been employed to date in bioreactor models is to use relatively simple equations to describe the growth kinetics, and not to try to describe the microscale mass transfer and growth mechanisms involved *(11)*. An important consequence of this decision is that such bioreactor models do not describe the dependence of growth on the substrate concentration, because to do so would require modeling of the intraparticle diffusion processes *(12)*. Note that the one exception to this is the case of air-solid fluidized beds, in which, due to the macroscale homogeneity, models have concentrated on describing the intraparticle processes (*19,20*).

The desire to avoid the situation in which growth is modeled as depending on the substrate concentration limits the growth kinetic submodels of SSF bioreactor models to simple empirical equations. Given the importance of these empirical growth equations, it is essential that they be well-founded in experimental data. However, a systematic analysis of growth profiles in SSF systems has not been previously made. The current work undertakes such an analysis and raises and discusses a number of issues related to the characterization of growth kinetics in SSF systems.

Survey of Empirical Kinetic Equations that Have Been Proposed and Issues Related to their Use

The linear, exponential and logistic equations have typically been used to characterize growth profiles in SSF *(21)*. Table 1 shows the differentiated and integrated forms of these equations and a more recent empirical growth model that was developed in order to describe those profiles in which there is a rapid early acceleration of growth followed by a sudden deceleration and a drawn out period during which the growth rate decelerates further *(22)*. This model is referred to as the two-phase model because it uses different equations for the two growth phases.

Note that none of the equations describes the lag phase of the growth cycle, although with very low initial biomass concentrations both the exponential equation and the logistic equation can give a very slow initial increase in biomass concentration, which can appear to be a lag phase. Only the logistic equation describes a final limitation on the amount of biomass. Since none of the equations actually proposes to describe the whole growth phase, for the fitting of the equation it is often necessary to select only that interval of the data that follows the particular growth kinetics being fitted.

Various different units can be and have been used by researchers for the measurement of biomass (X) in the construction of growth profiles. In some cases the profiles are plotted as the grams of dry biomass per gram of initial dry substrate, whereas in other cases they are plotted as the grams of dry biomass per gram of dry matter in the sample. These two systems of units are not the same, due to the fact that the growth process results in the loss of mass from the system in the form of the carbon within the carbon dioxide liberated by the microorganism. In the case of the biomass concentration expressed as grams of dry biomass per gram of initial dry substrate, the value of this variable can only increase as a result of the production of new biomass. In the case of the biomass concentration expressed as grams of dry biomass per gram of dry matter in the sample, the variable changes as a result of two processes, the production of new biomass and the loss of dry matter from the substrate in the form of carbon dioxide. For example, in the extreme case of a culture that is not growing but is respiring for maintenance purposes, the grams of dry biomass per gram of dry matter in the sample will continue to increase. It is not possible to convert from one system of units to the other by use of a simple conversion factor. Conversion requires the use of a growth and substrate consumption model, and knowledge of the yield and maintenance coefficients. More will not be said on this topic in the current work, however, the difference of the two systems must be kept in mind when analyzing the graphs. A kinetic profile obtained using one measurement system would not necessarily have had the same shape if it had been obtained using the other measurement system. Note that, in themselves, the empirical growth kinetic equations simply describe the shape of the growth profile, and make no assumption about the units used to measure the biomass.

The units of grams of dry biomass per gram of initial dry substrate are commonly used in those studies that employ an experimental strategy in which a large number of identical flasks, or small packed-bed columns, are prepared, with one or more individual flasks being removed at each sampling time. The contents of each flask or column are homogenized and then sub-

Table 1. Differentiated and integrated forms of the various empirical growth equations that have been applied to SSF systems

	Differentiated form			Integrated form		
Linear	$\frac{dX}{dt} = K$		/1/	$X = Kt + X_0$		/5/
Exponential	$\frac{dX}{dt} = \mu X$		/2/	$X = X_0 e^{\mu \cdot t}$		/6/
Logistic	$\frac{dX}{dt} = \mu X\left(1 - \frac{X}{X_m}\right)$		/3/	$X = \frac{X_m}{1 + \left(\frac{X_m}{X_0} - 1\right)e^{-\mu \cdot t}}$		/7/
Two phase	$\frac{dX}{dt} = \mu X$	$t < t_a$	/4a/	$X = X_0 e^{\mu \cdot t}$	$t < t_a$	/8a/
	$\frac{dX}{dt} = \mu L e^{-k(t-t_a)} X$	$t \geq t_a$	/4b/	$X = X_A \exp\left[\frac{\mu L}{k}\left(1 - e^{-k(t-t_a)}\right)\right]$	$t \geq t_a$	/8b/

jected to analysis. With this experimental strategy, it is simple to know to how much initial dry matter the material in the flask at the time of sampling corresponds. In effect, this strategy involves the separation of the samples before the fermentation. It is common in SSF studies due to the problems encountered when removing samples from a static bed: Firstly, due to the heterogeneity in a static bed, no one sample is representative of the whole bed, and secondly, in the removal of samples from one large bed, it is virtually impossible to prevent the disruption of the material that remains in the bed. The strategy of separating the samples before the fermentation allows samples to be removed without disruption of the other samples and theoretically at any sampling time all the flasks or columns are identical.

The units of grams of dry biomass per gram of dry matter in the sample are commonly used when samples are removed from a larger mass within a bioreactor. This is a reasonable experimental strategy for a continuously or intermittently mixed bed, in which any sample should be reasonably representative of the whole bed. It is not a simple matter in this case to know to how much initial dry matter the sample corresponds, although this could be calculated if the whole bioreactor contents were weighed before and after each sampling event and the dry weight of the samples were determined.

A further complication of kinetic studies is that typically in SSF systems it is not possible to measure the dry weight of biomass directly, especially in processes involving fungi, since the fungal biomass penetrates into the substrate and it is usually not possible to separate and recover the biomass quantitatively. In this case, indirect measurements of growth will typically be used, such as the measurement of biomass components such as glucosamine, ergosterol and protein, and therefore the variable X will represent a component of the biomass and not the dry biomass itself. Analysis of the kinetics of growth profiles obtained with indirect methods is complicated by the fact that the biomass composition typically varies during the growth cycle. This has been noted for protein content *(23)* and glucosamine content *(10)*. The implications of this variation are discussed later. As a result of these difficulties in biomass measurements, several studies of growth in SSF have been undertaken in artificial systems designed to mimic the environment of SSF while allowing the direct measurement of the biomass, such as membrane culture *(24)* and amberlite resin *(25)*. Several of the growth profiles analyzed in the present work were obtained in such systems.

It is also possible to follow the growth process by measuring the consumption of oxygen or the liberation of carbon dioxide by cultures. However, conversion of measured cumulative gas consumption or evolution profiles into biomass is not simple due the fact that gas metabolism is related to both growth metabolism and maintenance metabolism. In fact, to interpret such profiles, it is typically necessary to be able to undertake calibration experiments in which the growth kinetics are determined on the basis of direct measurement of the biomass, such as in the artificial systems mentioned in the previous paragraph. These issues are beyond the scope of the current work, and therefore analysis of kinetics based on gas metabolism is not done here.

The above considerations show that the variable X within the kinetic equations presented in Table 1 can have different units, depending on how the experiment was undertaken. The units of X affect the units of the parameters of the equations, which must have the necessary units to maintain the dimensional consistency of the equations.

Application of the Empirical Equations to Kinetic Profiles from the Literature

The various growth profiles in SSF systems that are available in the literature were analyzed by fitting the integrated forms of the equations to the data by non-linear regression. A wide range of papers were consulted, although relatively few show growth profiles for which kinetic analysis can be done. The papers that contained such growth profiles are summarized in Table 2 *(12,18, 25–75)*. The results of the analyses are shown in Tables 3 to 6.

One of the most striking points is that only relatively few of the growth profiles presented in the literature are of sufficient quality, in terms of the number of data points collected, to allow the type of kinetics to be determined with confidence. Many of the growth profiles have relatively few points. In some cases this lack

Table 2. Literature studies that permit the analysis of the kinetics of growth in solid-state fermentation

Microorganism	Substrate	Ref.	Location in the original article
Rhizopus oligosporus	Rice bran in a membrane culture system	*18*	Fig. 4(A), 37 °C
Rhizopus oligosporus	Cassava starch in a membrane culture system	*12*	Fig. 2
Bacillus licheniformis	Wheat bran	*26(a)*	Fig. 3, standardized WB medium
	Wheat bran	*26(b)*	Fig. 3, basal WB medium
Aspergillus niger	Sugar cane bagasse	*27(a)*	Fig. 2, sugar cane bagasse
	Impregnated Amberlite	*27(b)*	Fig. 2, Amberlite IRA-900
Penicillium commune	Yeast extract sucrose agar in a membrane culture system	*28(a)*	Table 1, dry weight/mg
		28(b)	Table 1, protein
Aspergillus flavus	Yeast extract sucrose agar in a membrane culture system	*28(c)*	Table 2, dry weight/mg
		28(d)	Table 2, protein
Trichoderma reesei	Wheat bran	*29(a)*	Fig. 2, 305 K
		29(b)	Fig. 2, 299 K
		29(c)	Fig. 2, 311 K
		29(d)	Fig. 2, 293 K
Beauveria bassina	Impregnated clay granules	*30(a)*	Fig. 2a
Gibberella fujikurol	Sponge	*30(b)*	Fig. 2b
Fusarium oxysporum	Sugar beet pulp	*30(c)*	Fig. 2c
Aspergillus niger	Impregnated Amberlite	*25*	Fig. 1
Aspergillus parasiticus	Cassava meal	*31*	Fig. 2
Aspergillus carbonarius	Canola meal	*32(a)*	Fig. 2, 12 g glucose
		32(b)	Fig. 2, 24 g glucose
		32(c)	Fig. 2, 4 g glucose
		32(d)	Fig. 2, 6 g glucose
		32(e)	Fig. 2, 0 g glucose
		32(f)	Fig. 2, 2 g glucose
Aspergillus oryzae	Long-grain milled rice	*33*	Fig. 3
Rhizopus oryzae	Cassava	*34(a)*	Fig. 1, 4,5 g/100 g cassava
		34(b)	Fig. 1, 6,8 g/100 g cassava
Rhizopus oligosporus	Sago	*35(a)*	Fig. 2, 4 mm
		35(b)	Fig. 2, mixed
		35(c)	Fig. 2, 2 mm
		35(d)	Fig. 2, 3 mm
Rhizopus sp.	Sago	*35(e)*	Fig. 3, 2 mm
		35(f)	Fig. 3, 2 mm
		35(g)	Fig. 3, 4 mm
		35(h)	Fig. 3, mixed
Phanerochaete chrysosporum	Waste cellulose	*36*	Fig. 3, protein
Gibberella fujikuroi	Commercial wheat bran	*37*	Fig. 1, dry biomass
Sporotrichum cellulophilum	Wheat bran seed culture	*38(a)*	Fig. 5, 65 % water content
		38(b)	Fig. 5, 54 % water content
		38(c)	Fig. 5, 43 % water content
		38(d)	Fig. 5, 36 % water content
Aspergillus oryzae var. *brunneus*	Steamed rice	*39(a)*	Fig. 2, 40 % water content
		39(b)	Fig. 2, 35 % water content
		39(c)	Fig. 2, 30 % water content
		39(d)	Fig. 2, 25 % water content
Rhizopus oligosporus	Cassava starch	*40(a)*	Fig. 1, MAX
		40(b)	Fig. 1, mashed MZ-2N
		40(c)	Fig. 2, mashed cassava
		40(d)	Fig. 2, chipped cassava
Rhizopus oligosporus	Cassava starch	*41(a)*	Fig. 1, conical flasks
		41(b)	Fig. 1, packed bed
		41(c)	Fig. 1, tray
		41(d)	Fig. 1, roller bottle
Agaricus bisporus	Autoclaved rye grain	*42(a)*	Fig. 1, mycelial dry wt
		42(b)	Fig. 4, mycelial extension
Aspergillus niger	Cassava starch	*43*	Fig. 2

Table 2. Cont.

Microorganism	Substrate	Ref.	Location in the original article
Aspergillus niger	Cassava meal	*44(a)*	Fig. 3, moisture content 55 %
		44(b)	Fig. 3, moisture content 60 %
		44(c)	Fig. 3, moisture content 50 %
		44(d)	Fig. 3, moisture content 45 %
		44(e)	Fig. 3, moisture content 40 %
		44(f)	Fig. 3, moisture content 35 %
		44(g)	Fig. 4, temperature 45 °C
		44(h)	Fig. 4, temperature 30 °C
		44(i)	Fig. 4, temperature 35 °C
		44(j)	Fig. 4, temperature 40 °C
		44(k)	Fig. 5, protein, urea 0 %, NH_4 100 %
		44(l)	Fig. 5, protein, urea 10 %, NH_4 90 %
		44(m)	Fig. 5, protein, urea 20 %, NH_4 80 %
		44(n)	Fig. 5, protein, urea 40 %, NH_4 60 %
		44(o)	Fig. 5, protein, urea 60 %, NH_4 40 %
		44(q)	Fig. 7, protein synthesis
Rhizopus oligosporus	Flour-free yellow corn grit	*45*	Fig. 3, biomass content
Aspergillus niger	Kumara	*46(a)*	Fig. 5, 1st layer
		46(b)	Fig. 5, 2nd layer
		46(c)	Fig. 5, 3rd layer
		46(d)	Fig. 5, 4th layer
Aspergillus niger	Impregnated Amberlite	*47(a)*	Fig. 3, z = 0.9 cm
		47(b)	Fig. 3, z = 2.5 cm
		47(c)	Fig. 3, z = 3.9 cm
		47(d)	Fig. 3, z = 5.4 cm
		47(e)	Fig. 3, z = 6.9 cm
Saccharomyces cerevisiae	Wheat bran powder	*48(a)*	Fig. 2, fluidized bed culture (solid circles)
		48(b)	Fig. 6, fluidized bed culture (solid circles)
Aspergillus niger	Impregnated Amberlite	*49(a)*	Fig. 4, Q = 1.7 min^{-1}
		49(b)	Fig. 4, Q = 6.8 min^{-1}
		49(c)	Fig. 4, Q = 14.9 min^{-1}
Trichoderma reesei	Sweet sorghum silage	*50(a)*	Fig. 2, mixed culture
Aspergillus niger			
		50(b)	Fig. 2, *T. reesei* alone
		50(c)	Fig. 2, *A. niger* alone
Trichoderma reesei	Wheat bran	*51*	Fig. 2
Trichoderma reesei	Sugar cane bagasse	*52(a)*	Fig. 1A, *T. reesei* alone
Trichoderma reesei		*52(b)*	Fig. 1A, *T. reesei* alone
Aspergillus phoenicis		*52(c)*	Fig. 1A, *T. reesei* and *A. phoenicis*
		52(d)	Fig. 1A, *T. reesei* and *A. phoenicis*
Aspergillus oryzae	Wheat bran	*53(a)*	Fig. 2, glucosamine
		53(b)	Fig. 3, glucosamine a
		53(c)	Fig. 3, glucosamine b
		53(d)	Fig. 3, glucosamine c
		53(e)	Fig. 3, glucosamine d
Aspergillus kawachii	Rice	*54(a)*	Fig. 4
		54(b)	Fig. 8, sterile water as a control
		54(c)	Fig. 8, 2 g glucose
		54(d)	Fig. 8, 1 g tryptone
		54(e)	Fig. 8, 2 g glucose + 1 g tryptone
Trichoderma viride	Sugar beet pulp	*55(a)*	Fig. 10, averages (squares)
		55(b)	Fig. 10, raw data (crosses)
Aspergillus oryzae	Artificial gel substrate	*56(a)*	Fig. 2, 3.0 kg gel substrate at 0 rpm
		56(b)	Fig. 2, 1.5 kg gel substrate at 0 rpm
		56(c)	Fig. 2, 3.0 kg gel substrate at 30 rpm
		56(d)	Fig. 2, 1.5 kg gel substrate at 30 rpm
		56(e)	Fig. 2, 3.0 kg gel substrate at 50 rpm
		56(f)	Fig. 2, 1.5 kg gel substrate at 50 rpm
Trichoderma viride	Potato dextrose agar (PDA)	*57(a)*	Fig. 3
		57(b)	Fig. 5

Table 2. Cont.

Microorganism	Substrate	Ref.	Location in the original article
Coniothyrium minitans	Potato dextrose agar (PDA),	*58(a)*	Fig. 2a
	Nutrient agar glucose (NAG),	*58(b)*	Fig. 2b
	Nutrient agar starch (NAS)	*58(c)*	Fig. 2c
Penicillium citrinum	Wheat bran	*59*	Fig. 1
Rhyzopus oligosporus	Chickpea	*60*	Fig. 1
Penicillium roqueforti	Buckwheat seeds	*61(a)*	Fig. 3, protein content
		61(b)	Fig. 5, protein content
		61(c)	Fig. 7, protein content
		61(d)	Fig. 11, total biomass
		61(e)	Fig. 14, total protein
		61(f)	Fig. 14, biomass protein
Candida utilis	Impregnated Amberlite	*62(a)*	Fig. 2, Amberlite
	Wheat bran	*62(b)*	Fig. 2, Wheat Bran
	Impregnated bagasse	*62(c)*	Fig. 2, Bagasse
	Impregnated Amberlite	*62(d)*	Fig. 6a, 44 mg dextrose/g IDM
		62(e)	Fig. 6a, 135 mg dextrose /g IDM
		62(f)	Fig. 6a, 200 mg dextrose /g IDM
Candida utilis	Impregnated Amberlite	*63(a)*	Fig. 2, 1.4×10^7 cells/g IDM
		63(b)	Fig. 2, 2.2×10^7 cells/g IDM
		63(c)	Fig. 2, 3.6×10^7 cells/g IDM
		63(d)	Fig. 3, 40 mg glucose /g IDM
		63(e)	Fig. 3, 135 mg glucose/g IDM
		63(f)	Fig. 3, 240 mg glucose/g IDM
		63(g)	Fig. 7, mineral limitation
		63(h)	Fig. 7, no mineral limitation
		63(i)	Fig. 8, biomass
Aspergillus terreus	Sugar cane	*64(a)*	Fig. 3, 25 °C
		64(b)	Fig. 3, 30 °C
		64(c)	Fig. 3, 35 °C
		64(d)	Fig. 3, 40 °C
Beauveria bassiana	Impregnated clay granules	*65(a)*	Fig. 1, R1
		65(b)	Fig. 1, R2
		65(c)	Fig. 1, R3
Aspergillus carbonarius	Canola meal	*66(a)*	Fig. 1, Triton X-100
		66(b)	Fig. 1, Distilled water
		66(c)	Fig. 1, Tween – 80
		66(d)	Fig. 1, Sodium oleate
		66(e)	Fig. 2, 2 % Na-oleate
		66(f)	Fig. 2, 0 % Na-oleate
		66(g)	Fig. 2, 0,1 % Na-oleate
		66(h)	Fig. 2, 0,3 % Na-oleate
		66(i)	Fig. 2, 0,5 % Na-oleate
		66(j)	Fig. 2, 1 % Na-oleate
Brevibacterium sp.	Sugar cane bagasse	*67*	Fig. 1, protein
Chaetomium cellulolyticum	Sugar cane bagasse	*68(a)*	Fig. 2, NT bagasse
		68(b)	Fig. 2, WT2 bagasse
		68(c)	Fig. 2, AT1 bagasse
Aspergillus niger	Impregnated Amberlite	*69(a)*	Fig. 2a, 300 g glucose/L
		69(b)	Fig. 2a, 400 g glucose/L
Aspergillus awamori	Wheat bran	*70(a)*	Fig. 1, glucosamine content, SAC
		70(b)	Fig. 1, glucosamine content, MAC
		70(c)	Fig. 1, glucosamine content, WAC
Aspergillus oryzae	Steamed rice	*71(a)*	Fig. 1A, steamed rice
	Rice extrudate	*71(b)*	Fig. 1A, rice extrudate
Aspergillus kawachii	Rice	*72(a)*	Fig. 1B, moisture content 0,5
		72(b)	Fig. 1B, moisture content 0,9
		72(c)	Fig. 1B, moisture content 0,7
Gibberella fujikoroi	Impregnated inert support	*73(a)*	Fig. 1A, initial sugar 2.5 g/g dm
		73(b)	Fig. 2A, initial sugar 0.5 g/g dm
Monascus purpureus	Rice	*74*	Fig.2, biomass (mg/g IDS)
Gibberella fujikoroi	Impregnated inert support	*75*	Fig. 6, biomass (g/g.i.s)

Table 3. Kinetic analysis of literature growth profiles using the logistic equation

Ref.	Interval of data used / h	X_o	X_m	Units for X_o and X_m	μ / h	Sum of squares of residuals (SSR)	Comments
27(a)	0–31	0.0001	59.0	mg biomass/g dry matter	1.70	304	8 data points, however, there are very few points during the rapid growth phase. Reasonable fit.
27(b)	0–54	0.0001	51.0	mg biomass/g dry matter	0.481	1.53	8 data points, however, there are very few points during the rapid growth phase. Good fit.
28(a)	72–168	1.14	299	mg dry biomass	0.049	837	5 data points, well-distributed. Reasonable fit, but it is difficult to be confident that the kinetics are indeed logistic since there is only one point within the rapid growth phase.
28(b)	72–168	0.004	837	ng protein/agar disk	0.094	1098	5 data points, only 1 during the rapid growth phase. Very good fit.
28(d)	72–168	0.413	6165	ng protein/agar disk	0.066	10086	5 data points. Very good fit, however, there is no flattening out of the data at the end.
29(a)	2–98	0.023	8.58	mg glucosamine/ g initial dry matter	0.155	0.475	13 data points, well-distributed. Overall fit is good although the early biomass points are slightly overestimated.
29(b)	2–125	0.018	8.04	mg glucosamine/ g initial dry matter	0.123	9.66	29 data points, well-distributed. Overall fit is good. The scatter of the data points in the final stationary phase is relatively large.
29(c)	2–98	0.036	6.43	mg glucosamine/ g initial dry matter	0.112	0.797	13 data points, reasonably well distributed, although a large gap between the first two points in the early acceleration phase. Reasonably good fit.
29(d)	0–116	0.004	4.79	mg glucosamine/ g initial dry matter	0.086	4.70	9 data points, but appears to be a large experimental error, such that no equation will fit well.
30(a)	0–120	3.87	53.0	mg dry biomass/ g dry support	0.060	55.8	6 data points, with only 1 during the rapid growth phase. Reasonable fit but the first data point is underestimated.
30(b)	0–120	20.4	144	mg dry biomass/ g dry support	0.041	124	Good fit, but only 5 data points with only 2 in the rapid growth phase. The linear equation would fit reasonably to the first 4 points.
30(c)	0–120	46.1	456	mg dry biomass/ g dry support	0.034	4651	Only 6 data points, with only 2 during the rapid growth phase. The curve appears sigmoidal but the logistic equation does not adjust well, the deviations being systematic and not random.
25	0–30	0.545	7.89	mg protein/g initial dry matter	0.181	3.20	14 data points, well-distributed. The first two data points are significantly underestimated.
31	0–72	0.491	12.1	protein % (w/w)	0.206	10.3	8 data points but only two during the period of rapid growth, many during the stationary phase. The logistic equation underestimates the initial biomass significantly and does not describe the late decrease in biomass.
32(a)	0–168	1.64	8.70	(g biomass/ g wet solid) $\times 10^{-2}$	0.032	0.599	8 data points, well-distributed. Good fit.
32(c)	0–120	1.34	8.57	(g biomass/ g wet solid) $\times 10^{-2}$	0.062	0.399	6 data points but only 2 during the rapid growth phase. Good fit.
32(d)	0–120	1.31	8.83	(g biomass/g wet solid) $\times 10^{-2}$	0.065	0.346	6 data points with only 2 during the rapid growth phase. Good fit.
32(e)	0–120	1.33	7.70	(g biomass/g wet solid) $\times 10^{-2}$	0.060	0.165	6 data points with only 2 during the rapid growth phase. Good fit.
32(f)	0–120	1.31	8.23	(g biomass/g wet solid) $\times 10^{-2}$	0.060	0.615	6 data points with only 2 during the rapid growth phase. Good fit.
33	0–90	0.147	7.94	g dry biomass	0.081	0.123	7 data points, reasonably well distributed. Good fit.
35(e)	0–48	0.136	19.6	mg protein/g IDS	0.173	0.062	5 points, well-distributed. The logistic fit was done by subtracting 17 from each of the biomass data points and ignoring the last two points, for which the biomass concentration was falling (death phase?). Without this modification none of the curves fitted.
36	0–84	0.008	0.353	mg protein	0.142	0.003	8 points, 5 of which seem to be in a final stationary phase, with only 1 during the rapid growth period. The logistic equation underestimates significantly the initial point, but fits well to all the remaining points.
38(a)	0–65	0.010	8.13	mg glucosamine/ g solid	0.198	0.495	9 data points, well-distributed. Good fit.

Table 3. Cont.

Ref.	Interval of data used / h	X_o	X_m	Units for X_o and X_m	μ / h	Sum of squares of residuals (SSR)	Comments
38(b)	0–65	0.131	5.72	mg glucosamine/g solid	0.144	1.27	9 data points, well-distributed. Good fit, although there is some scatter in the last three points.
38(d)	0–69	0.00002	1.98	mg glucosamine/g solid	0.288	0.153	7 data points, only 1 during the rapid growth phase. Reasonable fit, although there is scatter in the final points.
39(a)	0–71	0.118	38.0	g dry biomass/kg dry matter	0.220	13.0	7 data points, well-distributed. Good fit, although the initial biomass concentration is underestimated.
39(c)	0–71	0.290	24.0	g dry biomass/kg dry matter	0.150	4.55	8 data points, well-distributed. Good fit, although the initial biomass concentration is underestimated.
41(a)	0–40	1.13	13.8	mg protein/g initial wet substrate	0.208	0.202	4 data points, poorly-distributed. Good fit, although the lack of data points during the rapid growth phase means that it is impossible to determine the kinetic type with confidence.
41(b)	0–40	0.005	13.6	mg protein/g initial wet substrate	0.503	1.01	4 data points, poorly-distributed. Reasonable fit, although the initial biomass concentration is significantly underestimated. In addition, the lack of data points during the rapid growth phase means that it is impossible to determine the kinetic type with confidence.
41(c)	0–40	0.036	12.0	mg protein/g initial wet substrate	0.320	0.935	4 data points, poorly-distributed. Reasonable fit, although the initial biomass concentration is significantly underestimated. In addition, the lack of data points during the rapid growth phase means that it is impossible to determine the kinetic type with confidence.
42(a)	0–1344	4.00	157	mg dry biomass	0.006	146	9 data points, well-distributed. Good fit.
43	0–31	0.001	0.237	dry biomass/g initial dry matter	0.365	0.003	10 data points, well-distributed. Good fit.
44(a)	0–38	0.092	11.4	g protein/100 g substrate	0.345	3.80	5 data points, only 1 during rapid growth phase. The initial biomass concentration is underestimated.
44(b)	0–38	0.035	11.2	g protein/100 g substrate	0.381	1.72	5 data points, only 1 during rapid growth phase. The initial biomass concentration is underestimated.
44(c)	0–38	0.015	11.6	g protein/100 g substrate	0.404	1.86	5 data points, only 1 during rapid growth phase. The initial biomass concentration is underestimated.
44(d)	0–38	0.018	11.5	g protein/100 g substrate	0.338	2.06	5 data points, only 1 during rapid growth phase. The initial biomass concentration is underestimated.
44(e)	0–38	0.562	13.4	g protein/100 g substrate	0.118	1.08	5 data points, well-distributed. Good fit, although the data does not show a final leveling off.
44(h)	8–34	0.335	10.8	g protein/100 g substrate	0.244	1.53	6 data points, only 1 during the rapid growth phase. Reasonable fit.
44(i)	8–34	0.580	12.3	g protein/100 g substrate	0.233	0.623	6 data points, only 1 during the rapid growth phase. Reasonable fit.
44(j)	6–30	0.773	11.2	g protein/100 g substrate	0.295	0.194	6 data points, only 1 during the rapid growth phase. Reasonable fit.
44(k)	0–62	1.13	9.05	g protein/100 g substrate	0.097	4.15	6 data points, only 1 during the rapid growth phase. Poor fit.
44(l)	0–62	0.246	9.71	g protein/100 g substrate	0.170	7.87	6 data points, only 1 during the rapid growth phase. Poor fit, especially since the initial biomass is significantly underestimated.
44(m)	0–62	1.03	12.5	g protein/100 g substrate	0.114	3.79	6 data points, only 1 during the rapid growth phase. Poor fit, especially since the initial biomass is significantly underestimated.
44(n)	0–62	0.165	12.3	g protein/100 g substrate	0.220	9.25	6 data points, only 1 during the rapid growth phase. Poor fit, especially since the initial biomass is significantly underestimated.
44(o)	0–62	0.134	13.4	g protein/100 g substrate	0.245	9.66	6 data points, only 1 during the rapid growth phase. Poor fit, especially since the initial biomass is significantly underestimated.
44(p)	0–30	0.004	9.38	g protein/100 g substrate	0.456	3.04	14 data points. Good fit, except for the last two points where the biomass is decreasing.
45	5–48	2.73	125	g biomass/100 g solids	0.209	143	10 data points, well-distributed. Good fit.

Table 3. Cont.

Ref.	Interval of data used / h	X_o	X_m	Units for X_o and X_m	μ / h	Sum of squares of residuals (SSR)	Comments
46(a)	0–144	0.973	28.0	g protein/100 g dry matter	0.066	8.49	9 data points, well-distributed. Good fit.
46(b)	0–144	0.902	25.4	g protein/100 g dry matter	0.069	7.59	9 data points, well-distributed. Good fit.
46(c)	0–144	0.673	22.9	g protein/100 g dry matter	0.076	14.1	9 data points, well-distributed. Good fit.
46(d)	0–144	0.256	23.3	g protein/100 g dry matter	0.105	2.72	9 data points, well-distributed. Good fit.
47(a)	8–15	2.34	49.1	mg biomass/g	0.144	6.48	4 data points. With few data points and large scatter impossible to identify the kinetics.
47(d)	8–17	0.1	60.2	mg biomass/g	0.445	55.0	5 data points. Reasonable fit.
47(e)	8–17	0.119	75.5	mg biomass/g	0.400	71.7	5 data points. Poor fit.
48(b)	0–115	1.17 x10^9	1.81 x10^{11}	cells/g	0.051	5.42 x10^{20}	9 data points, well-distributed. Fit is adequate, but the first 5 data points are overestimated, and the data does not show a final leveling off.
49(b)	0–27	3.52	26.0	g dry biomass/g dry substrate	0.157	27.5	16 points, well-distributed. The logistic equation fits the later part of the curve well but poorly in the initial part.
49(c)	0–27	0.681	24.5	g dry biomass/g dry substrate	0.290	49.3	16 data points, well-distributed. Good fit, but the initial data point is greatly underestimated.
50(a)	0–120	5.0	17.9	% (w/w) dry basis	0.061	3.62	6 data points, poorly-distributed, with only 1 during the rapid growth phase. The logistic equation fits well, but shows only a deceleration phase.
50(b)	0–120	3.21	14.6	% (w/w) dry basis	0.130	2.77	6 data points, poorly-distributed, with only 1 during the rapid growth phase. The logistic equation fits well, but shows only a deceleration phase.
50(c)	0–120	4.91	17.3	% (w/w) dry basis	0.055	1.06	6 data points, poorly-distributed, with only 2 during the rapid growth phase. The logistic equation fits well, but shows only a deceleration phase.
51	3–206	0.024	8.48	mg glucosamine/g	0.072	11.8	26 data points, well-distributed. Good fit, although the data shows significant scatter during the stationary phase.
52(a)	0–120	1.32	8.11	protein % (w/w) dry basis	0.046	0.248	6 data points, 3 during the rapid growth phase. The logistic equation fits well, but shows only a deceleration phase.
52(c)	0–120	0.758	13.4	protein % (w/w) dry basis	0.055	2.32	6 data points, 3 during the rapid growth phase. Reasonable fit, but the first data point is underestimated.
52(d)	0–120	0.700	14.7	protein % (w/w) dry basis	0.062	1.62	6 data points, 3 during the rapid growth phase. Reasonable fit, but the first data point is underestimated.
53(a)	0–128	0.032	1.63	g/L bulk volume	0.050	0.023	7 data points, well-distributed. Good fit.
53(b)	0–118	0.072	0.891	g/L bulk volume	0.189	0.0483	Original curve was shown without the original data points. The logistic equation fits reasonably, but does not describe the slow decrease in biomass near the end.
53(c)	0–118	0.0789	1.45	g/L bulk volume	0.160	0.0222	Original curve was shown without the original data points. The logistic equation fits reasonably, but does not describe the slow decrease in biomass near the end.
53(d)	0–118	0.0786	1.89	g/L bulk volume	0.154	0.0596	Original curve was shown without the original data points. The logistic equation fits reasonably, but does not describe the slow decrease in biomass near the end.
53(e)	0–118	0.122	2.16	g/L bulk volume	0.121	0.0325	Original curve was shown without the original data points. Good fit, but the first data point is overestimated.
54(a)	10–50	0.004	2.69	g dry biomass/ 150 g koji	0.167	0.0192	10 points, reasonably well-distributed. Good fit, although the data does not show a final leveling off.
54(b)	10–51	0.001	13.8	g dry biomass/ 150 g koji	0.205	5.62	14 points, poorly-distributed with most in an early slow-growth phase, only 3 in the rapid growth phase. Reasonable fit, but the data does not show a final leveling off.

Table 3. Cont.

Ref.	Interval of data used / h	X_o	X_m	Units for X_o and X_m	μ / h	Sum of squares of residuals (SSR)	Comments
54(c)	10–51	0.01	3.43	g dry biomass/ 150 g koji	0.158	0.595	14 points, reasonably well-distributed. The logistic equation fits reasonably although it overestimates 7 points in mid growth cycle. The data does not show a final leveling off.
54(d)	10–51	0.0167	11.2	g dry biomass/ 150 g koji	0.182	2.11	14 points, well-distributed. Good fit.
54(e)	10–51	0.00615	9.23	g dry biomass/ 150 g koji	0.215	1.88	14 data points, well-distributed. Good fit.
55(a)	0–48	0.696	14.5	protein % (w/w) dry basis	0.089	4.61	20 data points, well-distributed. This graph was made by subtracting 10 from each data point of the original graph (See Fig. 6). Good fit, although the data does not show a final leveling off.
55(b)	0–48	9.85	130	protein % (w/w) dry basis	0.018	44.3	50 data points, well-distributed. The logistic equation fits reasonably, but has relatively little curvature in the fitted region. The data does not show a final leveling-off.
55(b)	0–48	1.06	19.5	protein % (w/w) dry basis	0.068	40.0	50 data points. This graph was made by subtracting 10 from each data point of the original graph (See Fig. 6). Good fit, although the data does not show a final leveling off.
56(a)	0–69	5.40	12.0	mg protein/g initial fresh substrate	0.703	44.3	14 data points, very poorly-distributed, with all the points being in either the lag or stationary phase. Poor fit, with the initial data points underestimated.
56(b)	0–69	0.026	13.0	mg protein/g initial fresh substrate	0.349	9.00	14 data points, poorly-distributed, with only 3 during the rapid growth phase. Good fit, although there is significant scatter in the data during the stationary phase.
56(c)	0–69	0.648	8.89	mg protein/g initial fresh substrate)	0.277	51.3	16 data points, relatively poorly distributed, with most being in the initial lag phase or final stationary phase. The first few data points are underestimated. Large amount of scatter in the data during the stationary phase.
56(d)	0–69	0.0003	10.4	protein/g initial fresh substrate	0.535	21.5	16 data points, relatively poorly distributed, with most being in the initial lag phase or final stationary phase. The first few data points are underestimated. Large amount of scatter in the data during the stationary phase.
56(e)	0–69	0.158	5.92	protein/g initial fresh substrate	0.195	15.3	19 data points, 5 during the rapid growth phase. The logistic equation fits reasonably, although it underestimates the first few data points and does not describe the dropping off of protein concentration near the end.
56(f)	0–69	0.002	6.20	protein/g (initial fresh substrate)	0.477	26.4	19 data points, poorly-distributed with only 2 during the rapid growth phase. The logistic equation fits poorly, underestimating significantly the initial data points and failing to describe the decrease in protein concentration near the end.
57(a)	0–168	0.037	15.8	dry biomass % (w/w) dry basis	0.176	9.15	12 data points, poorly-distributed with only 1 during the rapid growth phase. The logistic equation slightly underestimates the initial data points and does not describe the slow decrease in biomass late in the fermentation.
57(b)	0–168	0.472	18.5	dry biomass % (w/w) dry basis	0.109	1.79	12 data points, poorly-distributed with only 2 points in the rapid growth phase. Good fit.
58(a)	0–480	1.14	88.4	dry weight (mg/dish)	0.022	95.5	12 data points, well-distributed. Good fit, although the biomass during the early acceleration phase is slightly overestimated.
58(b)	0–480	0.634	87.0	dry weight (mg/dish)	0.027	455	12 data points. Reasonably-distributed, with 6 during the rapid growth phase. Reasonable fit, but there is a slight fall off in biomass late in the growth phase.
58(c)	0–480	0.089	93.0	dry weight (mg/dish)	0.039	405	12 data points. Poorly-distributed, with a large gap during the rapid growth phase. Reasonable fit, but there is a slight fall off in biomass late in the growth phase.

Table 3. Cont.

Ref.	Interval of data used / h	X_o	X_m	Units for X_o and X_m	μ / h	Sum of squares of residuals (SSR)	Comments
59	0–120	3.28	207	mg dry biomass/g dry substrate	0.121	45.2	6 data points. Poorly-distributed. Good fit.
61(a)	38–338	65.3	127	mg protein/g dry matter	0.008	238	7 data points, poorly-distributed. The logistic equation fits poorly, as would the other equations.
62(a)	0–146	0.001	112	cells × 10^7/g initial dry matter	0.614	1609	10 data points. Poorly-distributed. Poor fit, the initial biomass points being underestimated.
62(c)	0–140	10.3	108	cells × 10^7/g initial dry matter	0.11	274	8 data points, only 3 in the rapid growth phase. Good fit, although the first point is overestimated.
62(e)	0–132	5.50	272	cells × 10^7/g initial dry matter	0.112	1673	8 data points, poorly-distributed, with a large gap during the rapid growth phase. Good fit.
62(f)	0–110	3.79	508	cells × 10^7/g initial dry matter	0.101	826	8 data points, well-distributed. Good fit.
63(a)	0–80	0.253	360	cells × 10^7/g initial dry matter	0.164	194	9 data points, but only 1 during the rapid growth period. Good fit.
63(b)	0–64	0.006	377	cells × 10^7/g initial dry matter	0.396	7380	9 data points, poorly-distributed, with none during the rapid growth phase. Good fit, but there seems to be a large experimental error during the stationary phase.
63(c)	0–64	0.021	364	cells × 10^7/g initial dry matter	0.364	5231	8 data points, large gap during the rapid growth phase. Good fit.
63(e)	0–68	0.003	338	cells × 10^7/g initial dry matter	0.416	4090	9 data points, poorly-distributed, with none during the rapid growth phase. Good fit, although there seems to be a large experimental error during the stationary phase.
63(g)	0–149	0.718	148	cells × 10^7/g initial dry matter	0.268	1222	9 data points, poorly-distributed, with only 1 during the rapid growth phase. Good fit, but there seems to be a large experimental error during the stationary phase.
63(h)	0–168	2.81	319	cells × 10^7/g initial dry matter	0.146	806	9 data points, poorly-distributed, with 2 during the rapid growth phase. Good fit.
63(i)	0–168	1.06	314	cells × 10^7/g initial dry matter	0.178	646	9 data points, poorly-distributed, with 2 during the rapid growth phase. Good fit.
64(a)	23–47	0.213	10.7	g protein/100 g dry matter	0.134	0.258	6 data points, well-distributed. The logistic equation fits well but shows only a deceleration phase.
64(b)	20–35	0.003	9.14	g protein/100 g dry matter	0.388	0.265	5 data points. The logistic equation fits well but shows only a deceleration phase.
64(c)	0–33	3.14	13.3	g protein/100 g dry matter	0.008	2.90	6 data points, poorly distributed, with 1 data point during the rapid growth period. The logistic equation fits poorly, as would the other equations.
64(d)	0–25	2.99	15.0	g protein/100 g dry matter	0.067	2.43	6 data points, poorly distributed, with 1 data point during the rapid growth period. The logistic equation fits poorly, as would the other equations.
65(e)	0–98	28.9	2300	μg glucosamine/dry matter	0.1	32285	11 data points, well-distributed. The logistic equation fits well to the later data, but underestimates the first 3 data points.
67	0–120	0.032	282	mg protein/g dry solids	0.354	11356	6 data points, not well-distributed with only 1 point in the rapid growth phase. The logistic equation underestimates significantly the initial biomass concentration and does not describe the fall off of biomass in the later stages of the fermentation
71(a)	24 –120	1.79	17.8	mg glucosamine/ g dry-matter	0.047	1.07	5 data points. Good fit.
71(b)	24–120	0.494	22.0	mg glucosamine/ g dry-matter	0.494	0.075	5 data points. Good fit.
73(a)	0–160	0.127	0.162	g biomass/ g dry matter	0.003	0.0004	14 data points, well-distributed. Good fit.
73(b)	0–160	0.0001	0.122	g biomass/ g dry matter	0.399	0.0001	11 data points, poorly-distributed with only 1 during the rapid growth phase. Reasonable fit.
74	0–240	5.47	200	mg biomass/ g initial dry substrate	0.052	1159	16 data points, well-distributed. Good fit.

Table 4. Kinetic analysis of literature growth profiles using the linear equation

Ref.	Interval of data used h	K biomass units per hour	Sum of squares	Comments
35(b)	0–72	0.543 (mg protein /g initial dry solids) h^{-1}	98.8	7 data points, well distributed. Early data appears linear but much scatter in the last 4 points.
60	12–72	0.028 (colony forming units/g sample) h^{-1}	0.0734	6 data points, well-distributed. Good fit.
61(e)	0–147	0.005 mg total protein/g pozzolano h^{-1}	0.0179	7 data points. Reasonable fit, although there appears to be scatter in the data.
61(f)	25–147	0.004 mg biomass protein/g pozzolano h^{-1}	0.0126	6 data points. Reasonable fit, although there appears to be scatter in the data.

Table 5. Kinetic analysis of literature growth profiles using the exponential equation

Ref.	Interval of data used h	X_o (units)	μ h	Sum of squares	Comments
26(a)	4 – 28	1.36×10^9 cells	0.318	6.48×10^{24}	7 data points, well-distributed. Good fit.
26(b)	4 – 36	2.29×10^8 cells	0.189	3.82×10^{21}	9 data points, well-distributed. Reasonable fit, although not as good as with 26(a).
34(a)	0 – 72	0.778 g protein/g dry matter	0.034	4.25	5 data points, poorly-distributed. Reasonable fit but the initial point is underestimated.
34(b)	0 – 72	1.182 g protein/g dry matter	0.021	0.834	4 data points, poorly-distributed. Reasonable fit but the initial point is underestimated.
35(g)	0 – 36	8.339 protein mg/g initial dry substrate	0.047	155	4 data points. Poor fit, but the linear or logistic equations will not fit either.
40(b)	0 – 24	0.773 mg protein/g initial wet substrate	0.122	1.52	4 data points. Good fit.
41(d)	0 – 40	1.41 mg protein/g initial wet substrate	0.049	0.352	4 data points. Good fit.
44(f)	0 – 38.5	0.681 g protein/100 g substrate	0.064	0.332	5 data points, well-distributed. Good fit, but the initial biomass concentration is underestimated.
44(g)	5 – 29	1.38 g protein/100 g substrate	0.066	1.70	6 data points, well-distributed. Good fit, but the initial biomass concentration is underestimated.
47(a)	8 – 17	1.05 mg biomass g/g	0.201	0.236	5 data points. Very good fit.
47(b)	8 – 17	1.61 mg biomass g/g	0.187	6.88	5 data points. Good fit.
48(a)	0 – 120	2.51×10^8 cells/g	0.033	4.90×10^{18}	11 points, well-distributed. Reasonable fit, although the first 6 data points are overestimated.
61(d)	66 – 159	11.1 mg total biomass/g pozzolato	0.011	11.8	4 data points. Good fit.
62(b)	0 – 68	28.7 cells $\times 10^7$/g initial dry matter	0.0347	995	6 points, well-distributed. Good fit, but the initial biomass concentration is overestimated.
65(a)	0 – 78	211 μg glucosamine/g dry matter	0.0211	49771	19 data points, well-distributed. Systematic deviations from the exponential curve, although clearly the logistic and linear equations will not fit.
65(c)	0 – 50	167 μg glucosamine/g dry matter	0.0235	22326	13 data points, well-distributed. Systematic deviations from the exponential curve, although clearly the logistic and linear equations will not fit.
70(a)	0 – 48	0.004 mg glucosamine/g dry solids	0.141	0.025	5 data points. Reasonable fit.

of data means that more than one of the models seems to give an adequate description, as shown in Fig. 2. More points would be needed in order to see whether the deviations from the curves corresponding to the equations were experimental error, or the actual tendencies of the growth profiles. Note that some of the works that have a reasonable number of points have only few points taken during the rapid growth phase. Ideally, for adequate kinetic analysis, the growth profile should have around 10 data points, with the majority of these located in the regions where the most rapid growth and the acceleration and deceleration phases occur. The reason for the current poor characterization of growth profiles is clear: in the majority of these works the growth

Table 6. Kinetic analysis of literature growth profiles using several equations

Ref.	Parameters determined by regression					
	Linear	**Exponential**	**Logistic**	**Two phase**	Units used for X_o, X_m and X_A	Comments
	K /X-units h^{-1}	X_o	X_o	X_A		
			X_m,	$\mu L/h^{-1}$		
		μ/h^{-1}	μ/h^{-1}	k/h^{-1}		
	SSR	SSR	SSR	SSR		
	Interval/h	Interval/h	Interval/h	Interval/h		
12	K = 0.287		X_o = 1.42	X_A = 5.43	mg dry biomass/cm^2	22 h taken as time zero due to long lag phase. 13 data points, well-distributed. The logistic equation fits well except that it overestimates the first point. The linear equation fits reasonably to all points except the first and last. Best overall fit with the two-phase model.
			X_m = 7.99	μL = 0.053		
			μ = 0.194	k = 0.103		
	SSR = 3.56		SSR = 2.25	SSR = 1.32		
	Int. = 22 – 46		Int. = 22 – 46	Int. = 24 – 46		
28(c)	K = 4.82		X_o = 3.68		mg dry biomass	5 data points. Both the linear and logistic equations fit reasonably, the fact that there are few data points making it impossible to decide between them.
			X_m = 587			
			μ = 0.043			
	SSR = 8576		SSR = 6064			
	Int. = 48 – 168		Int. = 48 – 168			
32(b)	K = 0.046		X_o = 2.01		(g biomass/g wet solid) $\times 10^{-2}$	8 data points, well-distributed. Both the linear and logistic equations fit well, the logistic curve showing little curvature.
			X_m = 11.4			
			μ = 0.018			
	SSR = 1.00		SSR = 1.57			
	Int. = 0 – 168		Int. = 0 – 168			
35(a)	K = 1.37		X_o = 8.46		mg protein/g IDS	7 data points, reasonably-distributed. The linear equation fits reasonably the first and last points are removed (lag and stationary phases). The logistic equation fits reasonably, however the first point is underestimated and the last point overestimated.
			X_m = 89.0			
			μ = 0.064			
	SSR = 65.3		SSR = 153			
	Int. = 12 – 60		Int. = 0 – 72			
35(c)	K = 0.784		X_o = 13.8		mg protein/mg initial dry solids	7 data points, well distributed. The linear equation fits well without the initial point and the last 2 points, which seem to represent a stationary phase. The logistic equation fits reasonably over the whole growth curve.
			X_m = 59.3			
			μ = 0.053			
	SSR = 29.1		SSR = 51.3			
	Int. = 12 – 48		Int. = 0 – 72			
35(d)	K = 0.734		X_o = 12.4		mg protein/mg initial dry solids	7 data points, well distributed. The linear equation fits well without the initial point (lag phase). The logistic equation fits reasonably over the whole growth curve.
			X_m = 70.2			
			μ = 0.046			
	SSR = 28.7		SSR = 26.3			
	Int. = 12 – 72		Int. = 0 – 72			
35(f)	K = 0.421	X_o = 15.2			mg protein/mg initial dry solids	Only 4 data points, since the last 3 were removed because the biomass concentration was falling. The linear equation does not fit well. The exponential equation fits better but underestimates the initial and final points.
		μ = 0.020				
	SSR = 17.0	SSR = 8.53				
	Int. = 0 – 36	Int. = 0 – 36				
35(h)	K = 0.382	X_o = 16.5			mg protein/mg initial dry solids	5 data points. Little difference in the goodness of fit with either the linear or exponential equations. In the case of the exponential equation the fitted curve has little curvature.
		μ = 0.017				
	SSR = 7.05	SSR = 4.78				
	Int. = 0 – 48	Int. = 0 – 48				
37	K = 0.145		X_o = 0.490		mg dry biomass/g wheat bran	10 data points, well-distributed, although the last 5 appear to represent a stationary phase. The linear equation fits well to the first 6 points. The logistic equation fits well to the whole curve.
			X_m = 10.5			
			μ = 0.642			
	SSR = 0.1		SSR = 0.880			
	Int. = 16 – 72		Int. = 16 – 172			
38(c)	K = 0.053		X_o = 0.134		mg glucosamine/g-solid	9 data points, reasonably well-distributed. The linear equation fits reasonably, although the deviations from the line do not appear random. The logistic equation fits well, although it overestimates the initial biomass concentration.
			X_m = 3.52			
			μ = 0.091			
	SSR = 0.421		SSR = 0.132			
	Int. = 0 – 69		Int. = 0 – 69			

Table 6. Cont.

Ref.	Parameters determined by regression					
	Linear	**Exponential**	**Logistic**	**Two phase**	Units used for X_o, X_m and X_A	Comments
	K /X-units h^{-1}	X_o	X_o	X_A		
			X_m,	$\mu L/h^{-1}$		
		μ/h^{-1}	μ/h^{-1}	k/h^{-1}		
	SSR	SSR	SSR	SSR		
	Interval/h	Interval/h	Interval/h	Interval/h		
39(b)	K = 0.535		X_o = 0.102		g dry biomass / kg dry matter	8 data points, well distributed. The logistic equation fits well. The linear equation fits reasonably, but the deviations from the line are not random.
			X_m = 1.21			
			μ = 0.102			
	SSR = 85.0		SSR = 38.7			
	Int. = 0 – 73		Int. = 0 – 73			
39(c)	K = 0.462		X_o = 1.12		g dry biomass / kg dry matter	7 data points, well-distributed. The linear equation fits well if the first point is removed (lag phase). The logistic equation fits reasonably to the whole curve.
			X_m = 29.2			
			μ = 0.074			
	SSR = 7.51		SSR = 12.4			
	Int. = 22– 71		Int. = 0 – 71			
40(a)		X_o = 0.160	X_o = 0.023		mg protein/ g initial wet substrate	6 data points, only 1 during the rapid growth phase. The exponential equation fits well until 24 h. The logistic. equation fits reasonably to the whole growth phase, but underestimates the first two data points.
			X_m = 23.6			
		μ = 0.420	μ = 0.350			
		SSR = 1.30	SSR = 4.44			
		Int. = 0 – 24	Int. = 0 – 48			
40(c)	K = 0.358		X_o = 3.31		mg protein/ g initial wet substrate	5 data points, well-distributed. Neither equation fits particularly well, although the logistic equation fits better.
			X_m = 18.0			
			μ = 0.111			
	SSR = 10.8		SSR = 6.66			
	Int. = 0 – 36		Int. = 0 – 36			
40(d)	K = 0.483		X_o = 3.72		mg protein/ g initial wet substrate	5 data points, well-distributed. Both the linear and logistic equations fit well. In the case of the logistic equation the fitted curve has little curvature.
			X_m = 24.7			
			μ = 0.097			
	SSR = 6.30		SSR = 3.81			
	Int. = 0 – 36		Int. = 0 – 36			
42(b)	K = 0.132	X_o = 12.3	X_o = 4.05		linear extension (mm)	7 data points, well-distributed. All three equations fit reasonably to a number of the points. The logistic equation fits reasonably over the whole growth phase.
			X_m = 109			
		μ = 0.003	μ = 0.007			
	SSR = 194	SSR = 403	SSR = 59.7			
	Int. = 0 – 720	Int. = 0 – 720	Int. = 0 – 720			
49(a)	K =1.16		X_o =1.22		g dry biomass / g dry substrate	16 data points, well-distributed. The logistic equation fits the later part of the curve well, but greatly underestimates the first data point. Removing the initial and final points (lag and stationary phases), the linear equation fits well.
			X_m = 25.2			
			μ = 0.208			
	SSR = 18.3		SSR = 33.6			
	Int. = 8 – 24		Int. = 0 – 31			
52(b)	K = 0.084	X_o = 2.17	X_o = 1.29		protein % (w/w) dry basis	6 data points, well-distributed. The logistic equation fits well, although it underestimates the initial point and the data does not show a leveling off. The exponential and linear equations fit reasonably, but not as well as the logistic.
			X_m = 14.0			
		μ = 0.014	μ = 0.031			
	SSR = 2.50	SSR = 3.14	SSR = 0.733			
	Int. = 0 – 120	Int. = 0 – 120	Int. = 0 – 120			
55(a)	K = 0.239		X_o = 9.85		protein % (w/w) dry basis	Analysis of Fig. 6, done without subtraction. 20 data points. The linear equation fits well although there appears to be an initial lag phase. The logistic equation fits reasonably, but there is relatively little curvature in the fitted region. The data does not show a final leveling off.
			X_m = 98.4			
			μ = 0.019			
	SSR = 14.0		SSR = 8.46			
	Int. = 0 – 48		Int. = 0 – 48			
61(b)	K= 0.307		X_o = 70.6		mg protein/ g dry matter	9 data points, poorly-distributed, with only 2 during the rapid growth phase. The logistic equation does not fit well. Removing the initial lag phase and final stationary phase, the linear equation fits well to four of the points.
			X_m = 129			
			μ = 0.008			
	SSR = 3.03		SSR = 366			
	Int. = 58 – 200		Int. = 0 – 575			

Table 6. Cont.

Ref.	Parameters determined by regression					
	Linear	**Exponential**	**Logistic**	**Two phase**	Units used for X_o, X_m and X_A	Comments
	K /X-units h^{-1}	X_o	X_o	X_A		
			X_m,	$\mu L/h^{-1}$		
		μ/h^{-1}	μ/h^{-1}	k/h^{-1}		
	SSR	SSR	SSR	SSR		
	Interval/h	Interval/h	Interval/h	Interval/h		
61(c)	K = 0.609	X_o = 41.09			mg protein/ g initial dry matter	4 data points. Neither the linear nor the exponential equation fits particularly well. The lack of data points would make it difficult to distinguish the type of kinetics.
		μ = 0.01				
	SSR = 135	SSR = 712.				
	Int. = 47 – 127	Int. = 47 – 127				
62(d)		X_o = 3.23	X_o = 0.1		cells × 10^7/g initial dry matter	11 data points, but only 3 during the rapid growth phase. The logistic equation does not fit well, although the exponential equation approximates the first 5 points well.
			X_m = 106			
		μ = 0.127	μ = 0.33			
		SSR = 295	SSR = 2687			
		Int. = 0 – 29	Int. = 0 – 137			
63(d)		X_o = 4.98	X_o = 0.00228		cells × 10^7/g initial dry matter	4 data points. The exponential equation fits reasonably to the early data, but more data points would be needed to discern the kinetics with confidence. The logistic equation fits reasonably but does not describe the fall off in biomass later in the growth cycle.
			X_m = 112			
		μ = 0.111	μ = 0.515			
		SSR = 496	SSR = 887			
		Int. = 0 – 29	Int. = 0 – 79			
63(f)		X_o = 4.26	X_o = 0.0193		cells × 10^7/g initial dry matter	8 data points. Poorly-distributed, with a large gap during the rapid growth phase. The logistic equation fits well. The exponential equation fits well to the first 7 points.
			X_m = 539			
		μ = 0.062	μ = 0.062			
		SSR = 3466	SSR = 3441			
		Int. = 0 – 78	Int. = 0 – 95			
66(a)	K = 0.021	X_o = 0.674	X_o = 0.564		mg glucosamine/g wet solids	5 data points, well-distributed. The logistic equation fits reasonably well, although the data does not show a final leveling out. The linear equation also fits reasonably well. The exponential equation fits well to the first 4 points. Difficult to determine the kinetics with so few data points.
			X_m = 2.82			
		μ = 0.017	μ = 0.037			
	SSR = 0.055	SSR = 0.013	SSR = 0.019			
	Int. = 0 – 96	Int. = 0 – 72	Int. = 0 – 96			
66(b)	K = 0.022	X_o = 0.883	X_o = 0.619		mg glucosamine/g wet solids	5 data points, well-distributed. The logistic equation fits reasonably well, although the data does not show a final leveling out. The linear equation also fits reasonably well. The exponential equation does not fit well. Difficult to determine the kinetics with so few data points.
			X_m = 2.94			
		μ = 0.012	μ = 0.037			
	SSR = 0.111	SSR = 0.268	SSR = 0.109			
	Int. = 0 – 96	Int. = 0 – 96	Int. = 0 – 96			
66(c)	K = 0.025	X_o = 1.08	X_o = 0.607		mg glucosamine/g wet solids	5 data points, well-distributed. The logistic equation fits better than either the linear or the exponential. However, it is difficult to determine the kinetics with so few data points.
			X_m = 3.01			
		μ = 0.011	μ = 0.051			
	SSR = 0.179	SSR = 0.526	SSR = 0.002			
	Int. = 0 – 96	Int. = 0 – 96	Int. = 0 – 96			
66(d)	K = 0.031	X_o = 1.15	X_o = 0.606		mg glucosamine/g wet solids	5 data points. The logistic and linear equations fit reasonably, the exponential fits poorly. Difficult to determine the kinetics with so few data points.
			X_m = 3.53			
		μ = 0.012	μ = 0.053			
	SSR = 0.234	SSR = 0.739	SSR = 0.056			
	Int. = 0 – 96	Int. = 0 – 96	Int. = 0 – 96			
66(e)	K = 0.018	X_o = 0.589			mg glucosamine/g wet solids	5 data points. The exponential equation fits well, the linear fits poorly. Difficult to determine the kinetics with so few data points.
		μ = 0.014				
	SSR = 0.079	SSR = 0.020				
	Int. = 0 – 96	Int. = 0 – 96				
66(f)	K = 0.020	X_o = 0.612			mg glucosamine/g wet solids	5 data points. The exponential equation fits well, the linear fits poorly.
		μ = 0.015				
	SSR = 0.089	SSR = 0.019				
	Int. = 0 – 96	Int. = 0 – 96				

Table 6. Cont.

Ref.	Parameters determined by regression					
	Linear	**Exponential**	**Logistic**	**Two phase**	Units used for X_o, X_m and X_A	Comments
	K /X-units h^{-1} SSR Interval/h	X_o μ/h^{-1} SSR Interval/h	X_o X_m, μ/h^{-1} SSR Interval/h	X_A $\mu L/h^{-1}$ k/h^{-1} SSR Interval/h		
66(g)	K = 0.022 SSR = 0.124 Int. = 0 – 96	X_o = 0.601 μ = 0.016 SSR = 0.009 Int. = 0 – 96			mg glucosamine/g wet solids	5 data points. The exponential equation fits well, the linear fits poorly.
66(h)	K = 0.023 SSR = 0.123 Int. = 0 – 96	X_o = 0.619 μ = 0.016 SSR = 0.006 Int. = 0 – 96			mg glucosamine/g wet solids	5 data points. The exponential equation fits well, the linear fits poorly.
66(i)	K = 0.024 SSR = 0.069 Int. = 0 – 96	X_o = 0.689 μ = 0.015 SSR = 0.050 Int. = 0 – 96			mg glucosamine/g wet solids	5 data points. The exponential equation fits well, the linear fits poorly.
66(j)	K = 0.027 SSR = 0.091 Int. = 0 – 96	X_o = 0.733 μ = 0.015 SSR = 0.084 Int. = 0 – 96	X_o = 0.586 X_m = 4.87 μ = 0.027 SSR = 0.023 Int. = 0 – 96		mg glucosamine/g wet solids	5 data points. All three equations fit reasonably well. Difficult to determine the kinetics with so few data points.
70(b)		X_o = 0.361 μ = 0.071 SSR = 6.63 Int. = 0 – 48	X_o = 0.0002 X_m = 10.6 μ = 0.314 SSR = 0.017 Int. = 0 – 48		mg glucosamine /g dry solids	5 data points. The logistic equation fits well, the exponential not.
70(c)		X_o = 0.400 μ = 0.075 SSR = 8.03 Int. = 0 – 48	X_o = 0.002 X_m = 15.1 μ = 0.256 SSR = 0.001 Int. = 0 – 48		mg glucosamine /g dry solids	5 data points. The logistic equation fits well, the exponential not.
72(a)	K = 0.101 SSR = 0.516 Int. = 20 – 48	X_o = 0.053 μ = 0.084 SSR = 0.206 Int. = 20 – 48	X_o = 0.007 X_m = 4.12 μ = 0.152 SSR = 0.078 Int. = 20 – 48		mg biomass/ g-*koj*	7 data points, well-distributed. The logistic equation fits best. The exponential fits reasonably and the linear fits poorly.
72(b)	K = 0.216 SSR = 1.53 Int. = 20 – 48	X_o = 0.119 μ = 0.082 SSR = 2.25 Int. = 20 – 48	X_o = 0.001 X_m = 5.84 μ = 0.249 SSR = 0.039 Int. = 20 – 48		mg biomass/g-*koj*	7 data points, well-distributed. The logistic equation fits best. The exponential and linear fit poorly.
72(c)	K = 0.310 SSR = 3.69 Int. = 20 – 48	X_o = 0.109 μ = 0.092 SSR = 2.63 Int. = 20 – 48	X_o = 0.002 X_m = 9.30 μ = 0.217 SSR = 0.039 Int. = 20 – 48		mg biomass/g-*koj*	7 data points, well-distributed. The logistic equation fits best. The exponential and linear fit poorly.
18			X_o = 0.387 X_m = 5.06 μ = 0.099 SSR = 1.46 Int. = 0 – 60	X_A =1.305 μL = 0.069 k = 0.044 SSR = 0.626 Int. = 12 – 60	mg dry biomass/cm^2	13 data points, well-distributed. The logistic equation overestimates the early biomass concentrations. The two-phase model fits well after 12 h.
68(a)	K = 0.007 SSR = 0.569 Int. = 0 – 168			X_A = 2.77 μL = 0.014 k = 0.034 SSR = 0.180 Int. = 0 – 168	protein content % (w/w) dry basis	8 data points but poorly-distributed with none in the period of most rapid growth. The linear equation does not fit well. The two phase equation adjusts well, although there is a lot of scatter in the data.
68(b)	K = 0.013 SSR = 0.069 Int. = 24 – 168			X_A = 2.87 μL = 0.030 k = 0.036 SSR = 0.575 Int. = 0 – 168	protein content % (w/w) dry basis	8 data points but poorly-distributed. The two phase equation fits reasonably, although there are systematic deviations from the curve. The linear equation fits well to the last 7 data points.

Table 6. Cont.

Ref.	Parameters determined by regression					
	Linear	**Exponential**	**Logistic**	**Two phase**	Units used for X_o, X_m and X_A	Comments
	K /X-units h^{-1}	X_o	X_o	X_A		
			X_m,	$\mu L/h^{-1}$		
		μ/h^{-1}	μ/h^{-1}	k/h^{-1}		
	SSR	SSR	SSR	SSR		
	Interval/h	Interval/h	Interval/h	Interval/h		
68(c)	K = 0.026			X_A = 3.19	protein content % (w/w) dry basis	8 data points, reasonably well distributed. The two phase equation fits well. The linear equation fits well to the last 7 data points.
				μL = 0.015		
				k = 0.014		
	SSR = 0.076			SSR = 0.934		
	Int. = 0 – 168			Int. = 0 – 168		
69(a)	K = 2.73		X_o = 0.001		mg biomass /g dry solids	26 data points, well-distributed, but a very significant death phase occupies half the fermentation. The logistic equation fits poorly. The linear equation fits well the rapid growth phase, which has 14 points.
			X_m = 34.2			
			μ = 0.387			
	SSR = 72.8		SSR = 2619			
	Int. = 23 – 41		Int. = 0 – 100			
69(b)	K = 3.91		$X_o = 1.77 \times 10^{-7}$		mg biomass /g dry solids	27 data points, well distributed, but a very significant death phase occupies half the fermentation. The logistic equation fits poorly. The linear equation fits well the rapid growth phase, which has 6 points.
			X_m = 30.0			
			μ = 0.798			
	SSR = 9.11		SSR = 1051			
	Int. = 23 – 31		Int. = 0 – 100			
75	K = 0.0003		X_o = 0.0008		g biomass / g initial substrate	13 points. The logistic equation fits reasonably, although it does not describe the decrease in biomass later in the growth phase. The linear equation fits well to the 6 data points in the rapid growth phase.
			X_m = 0.008			
			μ = 0.166			
	SSR = 1.8×10^{-6}		SSR = 2.4×10^{-5}			
	Int. = 8 – 33		Int. = 8 – 136			

profile is presented without any kinetic analysis, and therefore it is obvious that a good kinetic analysis was not part of the initial motivation for the work.

Typical fits with the logistic, linear and exponential equations, obtained from analyses of those graphs that contain a reasonable number of points that are well-distributed in time, are shown in Fig. 3. Table 3 shows that in the majority of cases the logistic equation gives an adequate, although not perfect, fit. Some problems with the fit of the logistic equation can be identified. Firstly, in some cases the logistic equation fits well to the data collected in the middle and latter stages of the fermentation, but clearly overestimates the initial biomass concentration (Fig. 4). This problem arises because the logistic equation is symmetrical around the inflection point at $X = 0.5X_m$: if the part of the curve before the inflection point is rotated 180 degrees it will lie directly on top of the part of the curve after this point. The equation will therefore not adjust well to growth profiles in which the initial acceleration phase and later deceleration phase are not symmetrical by rotation, which occurs when there is a short initial acceleration period followed by a long period during which the growth slowly decelerates. Fig. 4 shows that the two phase model of Ikasari and Mitchell *(22)* can fit well to such profiles, however, in practice it is problematic to fit the both phases. The early exponential phase is typically quite short and occurs at a time when the biomass is below the level of sensitivity of the measurement method, meaning that few data points are collected and those data points that are collected typically have large relative errors in them. Therefore it is virtually impossible to obtain a reliable fit of the early exponential phase, and therefore impossible to obtain a reasonable estimate of μ to insert into the equation for the deceleration phase. This problem was apparent in the various profiles analyzed in the present work, and therefore no attempt was made to fit the exponential equation to the first phase. In fitting the second phase the parameters μ and L were estimated as a single lumped parameter, μL, which represents the specific growth rate at the instant that the deceleration phase begins. Secondly, the logistic equation describes an asymptotic approach of the biomass concentration to X_m, such that the growth profile appears flat in the later stages of the fermentation. However, in some cases, even though the logistic equation describes the data adequately, the biomass or measured component decreases steadily during the later stages of the fermentation presumably due either to death and autolysis of the biomass or endogenous maintenance metabolism (Fig. 5).

The analyses of the data of Durand and Chereau *(55)* raise two important points about analyses of kinetics when growth is estimated indirectly by a biomass component that is also present in the substrate (Fig. 6). They used protein as an indirect indicator of growth, and the logistic equation does not adjust well to the raw data, the fit giving a maximum protein content (X_m) of almost 100 % of the dry weight of the sample (Table 6), which is clearly impossible, since the protein will constitute only around 50 % of the dry weight of the biomass.

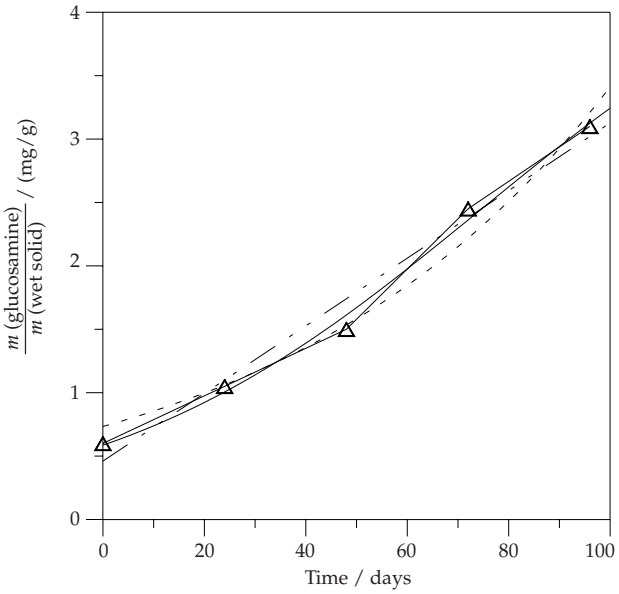

Fig. 2. A kinetic profile in which the lack of an adequate number and distribution of data points means that more than one equation can give an adequate fit. Curves of best fit for the exponential equation (—), linear equation (— – - -) and logistic equation (- – -). Data of Al-Asheh and Duvnjak *(66j).*

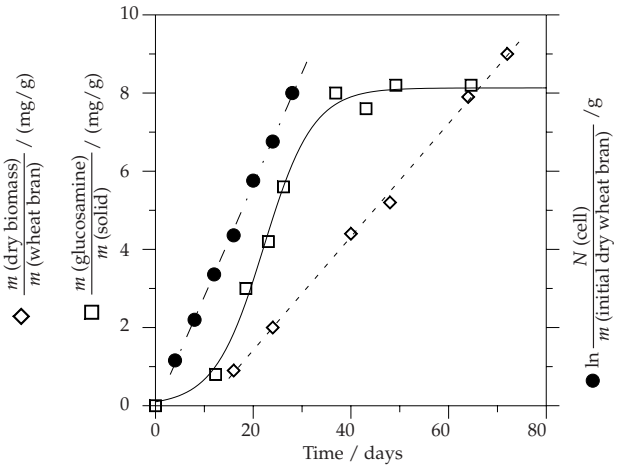

Fig. 3. Growth profiles that are described well by the various empirical equations: (—) logistic equation fitted to data of Kim *et al. (38(a))*; (— ·—) linear equation fitted to data of Kumar and Lonsane *(37)*; and (- – -) exponential equation, on a logarithmic scale, fitted to the data of Ramesh *et al. (26(a)).*

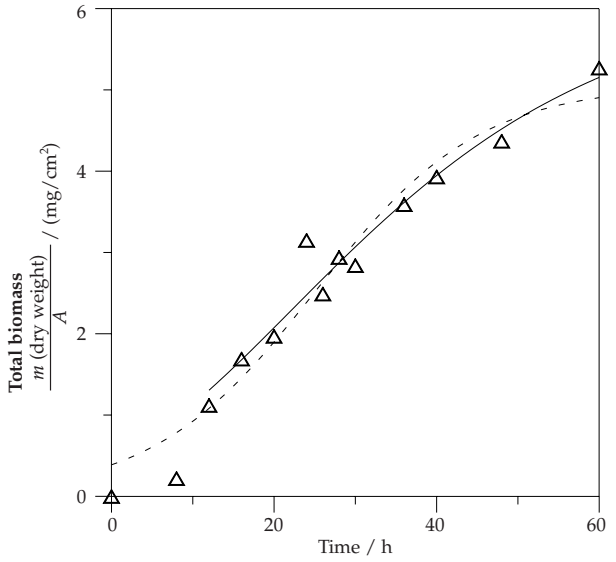

Fig. 4. A growth profile in which there is a short period of rapid acceleration followed by a long period during which the growth slowly decelerates, showing the fit of the logistic equation (- – -) and the two phase model (—) to the data. Data of Ikasari *et al. (18).*

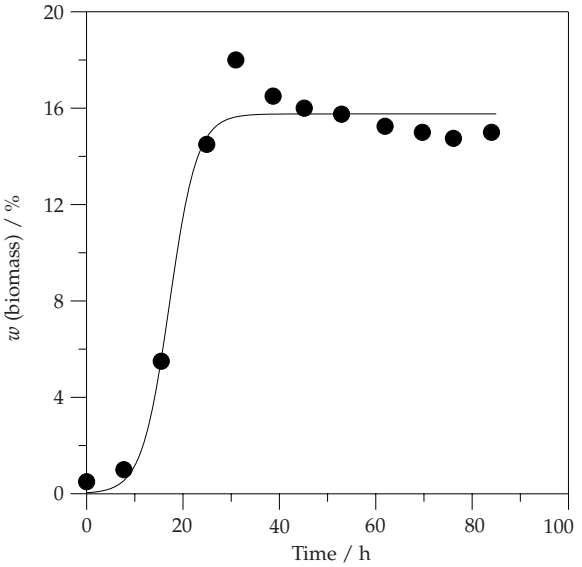

Fig. 5. A situation in which the logistic equation gives an adequate fit, but there is a systematic deviation later in the fermentation due to a decrease in the biomass concentration. Data of Tao *et al. (57(a)).*

However, the substrate contained protein even before it was inoculated, and since this protein is not biomass protein it should not be included in the estimate of the initial biomass concentration. The authors did not provide a measurement of the protein content of the uninoculated substrate, so an arbitrary value of 10 % (w/w) dry basis was assumed, since their zero time data point was 10.84 % (w/w) dry basis. This value of 10 was subtracted from all the data points. In this case the fit of the logistic model was much better, giving a more reasonable value for X_m of 14.5 % (w/w) dry basis. However, there is a further concern. Presumably the fungus was able to metabolize the protein in the substrate, and therefore the shape of the protein profile against time is the result of two opposing processes: the consumption of substrate protein and the production of biomass protein. From a simple curve of total protein versus time, it is not possible to say what the contribution of these opposing processes is, and therefore it is not possible to use these data to determine the growth kinetics in themselves. Therefore, although an empirical equation can be fitted to the data, it is not necessarily the growth itself

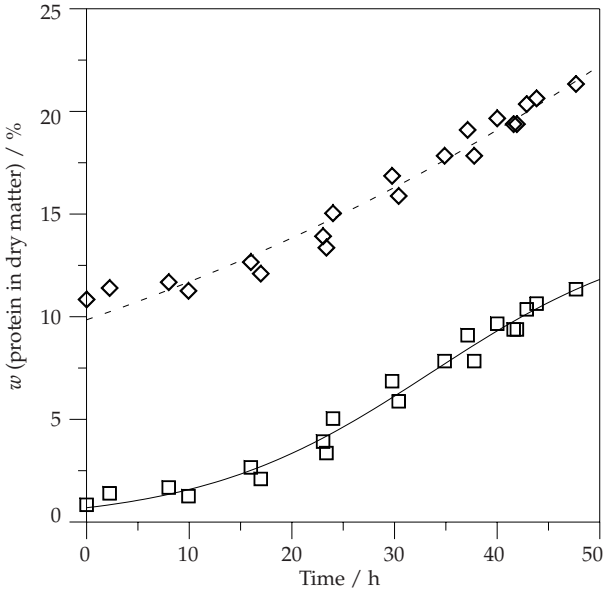

Fig. 6. The problem of fitting the logistic equation that can occur when the component used to measure the biomass is also originally present in the substrate: (- – -) fit of the logistic model to the original data of Durand and Chereau *(55)*; (—) fit of the logistic model to the data after subtraction of 10 from each protein data point.

that is being analyzed. Great care must therefore be taken in interpreting kinetic data when the indicator of the biomass is also present in the substrate and is potentially consumed during the fermentation.

It is clear that, given the complexity of different SSF systems, consisting of different microorganisms and substrates, and in which the limiting phenomena are different, no one empirical equation will ever be able to describe all the growth profiles well. Therefore the researcher must choose one empirical equation from amongst several possibilities. Obviously the equation to be chosen is that which most adequately describes the data. Since the equations are all empirical, there is no theoretical basis for preferring one over the other.

The logistic equation does give an adequate fit for a large proportion of the available growth profiles. If it adjusts well to the whole growth profile, which occurs in a reasonable number of cases, then it brings the added advantage of simplicity, since a single equation is used, whereas for the linear and exponential models the lag, growth and stationary phases will require different equations (typically $dX/dt = 0$), and the two phase model also requires more than one equation to describe the whole growth cycle.

Future Needs in Kinetic Modeling for SSF Bioreactor Models

The current attempt to analyze growth kinetics in SSF systematically has highlighted several issues that need to be resolved in the future in order to improve the performance of the kinetic submodels of bioreactor models. These are discussed below.

Inclusion of the effects of variations in environmental parameters on growth

The above kinetic analyses represent situations in which the environmental conditions are relatively constant during the whole growth phase. However, typically within SSF bioreactors it is almost impossible to avoid significant variations in key environmental variables *(4)*. If a mathematical model is to describe bioreactor performance successfully, then the kinetic submodel must describe how the growth kinetics of the microorganism vary with these variations in the environmental variables. The environmental variables for which it is most desirable to incorporate the effects are the temperature and the water activity of the substrate, since it is possible to influence these two variables in the manner in which the bioreactor is operated. A bioreactor model in which the growth kinetic model described the influence of these variables would be a useful tool in optimizing the operation of the bioreactor *(4)*.

Currently, the typical manner in which the effects of these environmental variables are incorporated into the growth kinetic equations is to express the parameters of the kinetic equations not as constants, but rather as functions of the environmental variables. The equations and their parameters are typically determined in what can be called »constant-condition« experiments. For example, in the use of this approach to determine the effect of temperature, the growth kinetic analysis is repeated by incubating the cultures within various constant temperature incubators covering the temperature range over which it is desired to know the effect of temperature. Small substrate masses are used to ensure that the temperature within the substrate bed remains at the temperature of the incubator throughout the entire growth cycle. The empirical growth equation is fitted to each growth profile. For example, in the case of the logistic equation, such a strategy gives a range of μ values corresponding to different temperatures and a range of X_m values corresponding to different temperatures. Empirical equations are then used to describe the relation between each growth parameter and the temperature. This approach has been used in the establishment of bioreactor models by various workers. For example, in applying this approach using the logistic equation, Saucedo Castaneda *et al. (76)* arrived at the following equations for two parameters of the equation:

$$\mu = \frac{A_1 e^{\left(\frac{-A_2}{RT}\right)}}{1 + A_3 e^{\left(\frac{-A_4}{RT}\right)}} \qquad /9/$$

and

$$X_m = B_o + B_1 T + B_2 T^2 + B_3 T^3 + B_4 T^4 \qquad /10/$$

where R is the universal gas constant and the various A and B symbols with subscripts represent the parameters that are adjusted in order to fit the equation to the data.

In the way that these equations were used in the dynamic model of bioreactor operation, at any instant the value of the parameter depended only on the temperature at that instant. This makes sense for the specific growth rate constant (μ), but the logic of this approach

is not so clear in the case of the maximum biomass X_m. If the final temperature returns to the optimum temperature for growth, then the model predicts that the biomass will reach the optimum value for X_m and therefore the variations in X_m with temperature during the fermentation simply serve to modify the instantaneous growth rate (described by equation /3/).

A similar approach can be used to determine the effect of water activity on the parameters of the kinetic equation, incubating a range of cultures in controlled humidity atmospheres. In fact these types of studies of the effect of temperature and water activity (or water content) on the growth rate have often been undertaken from in food microbiology studies, in an attempt to understand the effects of these environmental variables on food spoilage. Unfortunately, in the case of fungi it is the colony radial growth rate that is plotted against the environmental variable. Such data do not necessarily reflect the overall growth rate in the situation in SSF, in which the inoculum is spread across the whole surface, and the microcolonies that arise very quickly cover the whole substrate surface, such that the majority of the growth phase involves an increase in density of biomass within an area already colonized. In comparison, in experiments for the measurement of colony radial growth rates, the edge of the colony expands into an uncolonized medium.

The constant-condition approach to determining and modeling growth kinetics has the assumption, often not stated explicitly by the authors, that the growth depends solely on the current conditions and is not affected by the past history of the organism. Such a situation seems unlikely. For example, consider an organism that grows optimally at 37 °C and for which growth is deleteriously affected at 50 °C. It seems logical that if the organism were incubated initially at 37 °C and then shifted to 50 °C, the growth rate would be different from the growth rate of a culture incubated at 50 °C from the start of the fermentation, at least for several hours. Further, when the culture was returned to 37 °C, it seems logical that deleterious effects suffered during the time at 50 °C would prevent the organism from immediately resuming its optimal growth rate. In fact, such a situation was mimicked by Ikasari *et al. (18)*, who transferred cultures from a 37 °C incubator to a 50 °C incubator for 10 hours and then returned the culture to 37 °C. On returning to 37 °C from 50 °C the culture took 20 hours to resume the growth rate shown by the culture held at 37 °C throughout the whole growth cycle.

The mathematical description of the effects of temporal changes in temperature and water activity on the growth rate has not received any attention in the SSF literature. An insight into how such a model might be developed can be obtained from studies that have been made in the area of food microbiology. Bovill *et al. (77)* used a model in which the physiological state of the cell was represented by a variable Q, which varied according to the following equation:

$$\frac{dQ}{dt} = \mu Q \qquad /11/$$

where μ is a function that depends on the environmental conditions. Growth is then given by:

$$\frac{dX}{dt} = \mu X\left(1-\frac{X}{X_m}\right)\left(\frac{Q}{1+Q}\right) \qquad /12/$$

Such an approach enables the history of environmental conditions to affect the current growth rate, since the history will affect the value of $Q/(1+Q)$. The growth rate also depends on the current environmental conditions through the parameter μ.

This model describes non-lethal effects of unfavorable conditions. It would also be desirable to model death kinetics, although this has received little attention to date in SSF, with workers usually preferring to describe overall biomass profiles rather than to distinguish between living and dead cells. Part of the difficulty is that many SSF processes involve filamentous fungi, for which it is much more difficult to study death kinetics than is the case for unicellular organisms, with which total and viable counts can be used to distinguish dead and living cells.

Accounting for the changing biomass composition when indirect measurements are used

The biomass is a key variable in fermentation studies, since typically metabolic activities such as substrate consumption and product formation are strongly related to either or both of the growth rate and the actual biomass present. However, as mentioned previously, it is very often necessary to use indirect methods of determining biomass in SSF, such as the measurement of cell components, this being especially true for those processes involving fungi.

Unfortunately, the composition of the biomass typically varies during the fermentation. At present the only method available to take this into account is to determine the variations as a function of time in an artificial system that allows biomass determination, such as membrane filter culture, and to presume that the same variation occurs in the real system. Such an approach was taken in use of glucosamine to determine biomass by Nagel *et al. (10)* who arrived at the following equation for the glucosamine content of the biomass (G_x, mg-glucosamine mg-dry-biomass^{-1} as a function of time:

$$G_x = 44.61 + \frac{43.65}{\left(1+\exp\left(\frac{(t-\lambda)-61.70}{12.34}\right)\right)} \qquad /13/$$

where λ is the lag time (h).

Such a strategy allows glucosamine measurements to be converted into biomass measurements, however, the question remains as to whether the temporal variations in composition in the artificial and real systems are the same. The more closely the growth conditions provided by the artificial system mimic those experienced in the real system, the more likely this is to be the case, but it is never possible to be completely certain.

In the future it might be possible to develop structured growth models that explicitly describe the measured component as one of the variables, although this will require detailed knowledge about the various factors that control the cell composition.

Conclusions

Empirical models still have an important place within mathematical models of SSF bioreactors, although until now relatively little systematic effort has been made to analyze the kinetics even empirically. The analyses done here show that the logistic equation gives the most adequate fit in the majority of cases, but it obviously cannot be simply regarded as the universal equation of solid-state fermentation.

This review shows that, if it is intended to characterize growth kinetics for the purpose of modeling bioreactors, then more care needs to be taken in the experimental design, to ensure that sufficient samples are removed, and that they are distributed well enough to characterize the various phases of the growth curve.

There are still many areas in which further work is needed in order to make these empirical growth models truly useful within bioreactor models. More work needs to be done to understand how best to convert indirect measurements into estimates of the biomass, and more work needs to be done to characterize the effect of varying environmental conditions on the growth kinetics.

Symbols

Note that the symbol X may potentially be expressed in different units, depending on how the experiment was done. The units used for X affect the units of various other parameters. In this symbol list the units of X are taken as mg dry biomass/(mg initial dry substrate.h), and the units of the other parameters are written to be consistent with this. In the case that other units are to be used for X, the units of various other parameters must also be changed to maintain consistency.

K linear growth rate (mg dry biomass/(mg initial dry substrate.h))

k first order decay constant in the second phase of the two phase model (h^{-1})

L the fraction of hyphal tips surviving the entry into the second phase in the two phase model (dimensionless)

t time (h)

t_a the time at which there is a switch from the first to the second phase in the two phase model (h)

X biomass concentration (mg dry biomass/mg initial dry substrate)

X_o initial biomass concentration (mg dry biomass/mg initial dry substrate)

X_m maximum possible biomass concentration (mg dry biomass/mg initial dry substrate)

μ specific growth rate constant (h^{-1})

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Analiza profila kinetike rasta pri fermentaciji na suhoj podlozi

Sažetak

Matematički modeli što se danas predlažu pri opisu procesa u bioreaktorima, u kojima se provodi fermentacija na suhoj podlozi, koriste jednostavne empirijske jednadžbe za kinetiku rasta. Međutim, do sada nije bila provedena sistematska analiza profila rasta u sustavima fermentacije na suhoj podlozi. U radu su razne empirijske jednadžbe, uključujući linearne, eksponencijalne i logističke, bile prilagođene profilima dobivenim iz literature. Logistička jednadžba uglavnom daje adekvatan opis cijeloga profila rasta. U mnogima opis nije potpun jer dolazi do sistematskih devijacija od logističke krivulje koja bi najbolje odgovarala. Prema prilagođenoj krivulji osobito se smanjuje koncentracija biomase u kasnijim stadijima fermentacije, a podcijenjena je ili precijenjena koncentracija početne biomase. Iako se logistička krivulja općenito koristi u matematičkim modelima rada bioreaktora, ne može poslužiti kao univerzalno primjenjiva jednadžba u sustavima fermentacije na suhoj podlozi. Utvrđena su i razmatrana različita poboljšanja potrebna da bi se empirijske jednadžbe rasta u cijelosti mogle primijeniti.