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EXPERIMENTAL ARTICLES

Growth of the Thermophilic Bacterium *Geobacillus uralicus* as a Function of Temperature and pH: An SCM-Based Kinetic Analysis

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Abstract—The synthetic chemostat model (SCM), originally developed to describe nonstationary growth under widely varying concentrations of the limiting substrate, was modified to account for the effects of nontrophic factors such as temperature and pH. The bacterium *Geobacillus uralicus*, isolated from an ultradeep well (4680 m), was grown at temperatures ranging from 40 to 75°C and at pH varying from 5 to 9. The biomass kinetics was reasonably well described by the SCM, including the phase of growth deceleration observed in the first hours after a change in the cultivation temperature. At an early stage of batch growth in a neutral or alkalescent medium, bacterial cells showed reversible attachment to the glass surface of the fermentation vessel. The temperature dependence of the maximum specific growth rate (μ_m) was fitted using the equation $\mu_m = A\exp(\lambda T)/\{1 + \exp B[1 - C/(T + 273)]\}$, where A, λ, B, and C are constants. The maximum specific growth rate of 2.7 h^{-1} (generation time, 15.4 min) was attained on a complex nutrient medium (peptone and yeast extract) at 66.5°C and pH 7.5. On a synthetic mineral medium with glucose, the specific growth rate declined to 1.2 h^{-1}, and the optimal temperature for growth decreased to 62.3°C.

Key words: thermophilic microorganisms, *Geobacillus uralicus*, growth kinetics.

Thermophilic microorganisms attract much interest in connection with their biotechnological potential and the significant ecological functions they perform in natural and disturbed ecosystems [1–3].

The beneficial biotechnological features of this group of microorganisms are the following: (1) they exhibit a high rate of growth, which leads to shorter cultivation times; (2) the enzymes isolated from thermophilic organisms are more stable and active in a wider range of temperature and pH; and (3) because of their diverse biosynthetic activities, thermophiles are likely candidates for producing valuable metabolites for practical purposes [4, 5].

One of the authors of this work (N. Popova) isolated and described a thermophilic bacterium from a biofilm formed on the surface of a corroded pipeline in an ultradeep well drilled by the Urals geological prospecting expedition (the pipeline and well temperature was 40–72°C). Based on a combination of physiological, biochemical, and morphological features and on the results of 16S rDNA sequence analysis, this bacterium was assigned to the genus *Geobacillus* [6] and described as a new species, *G. uralicus* [7].

The goal of this work was to characterize the growth kinetics of the new bacterium in order to answer the three following questions. (1) Can the growth of thermophiles be adequately described by kinetic models originally developed for mesophilic organisms and, specifically, by the synthetic chemostat model (SCM), which describes a wide spectrum of stationary and nonstationary (transient) processes dependent on the current and previous concentrations of the limiting substrate [8]? (2) Can SCM be used to describe transient growth kinetics resulting from a change in nontrophic culture conditions (temperature and pH)? (3) How does the growth rate of *G. uralicus* depend on the composition of the nutrient medium (complex or synthetic), temperature, and pH?

MATERIALS AND METHODS

Organism and cultivation conditions. The bacterium *Geobacillus uralicus* was isolated from a biofilm that formed on the walls of a corroded pipeline [7].

The bacterium requires no growth factors and can grow aerobically on ribose, fructose, glycerol, maltose, mannitol, sucrose, xylose, galactose, succinate, and pyruvate. The most active growth was observed on glucose, which was used in further experiments as the sole source of carbon and energy.

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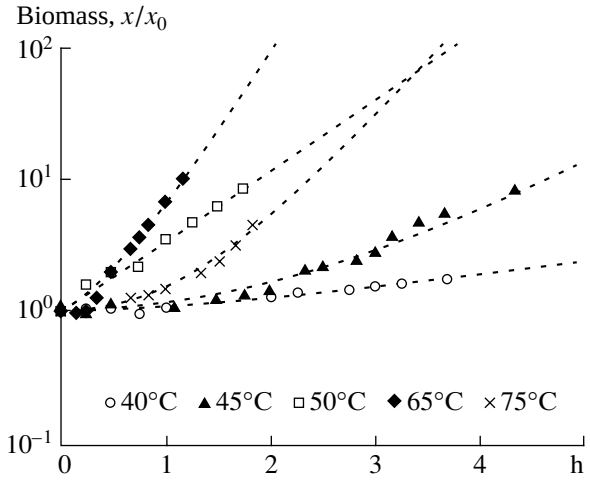

Fig. 1. Growth dynamics of bacilli on a complex medium at different temperatures. Readings of the optical density of bacterial suspension were normalized with respect to their initial level x_0 and plotted on a semilogarithmic scale. Dotted lines represent calculation by the SCM, equation (5).

The bacterium was maintained on agarized medium containing 2.5 g/l yeast extract (Oxoid) and 5 g/l tryptone (Oxoid) at 55°C; in the course of experiments, it was grown on complex and synthetic media. The complex medium was composed of yeast extract, 2.5 g/l, and tryptone, 5 g/l, pH 7.0. The synthetic medium was composed of (mg/l) glucose, 200; $(NH_4)_2SO_4$, 400; KH_2PO_4, 100; K_2HPO_4, 1000; $MgSO_4 \cdot 7H_2O$, 200; $CaCl_2 \cdot 2H_2O$, 40; $CuSO_4 \cdot 5H_2O$, 0.04; KI, 0.1; $FeCl_3 \cdot 6H_2O$, 0.4; $MnSO_4 \cdot 4H_2O$, 0.4; $Na_2MoO_4 \cdot 2H_2O$, 0.2; $ZnSO_4 \cdot 7H_2O$, 0.4; H_3BO_3, 0.5; and EDTA-Na, 5.0 [8].

The acidity of the medium was varied from 4.6 to 9.0 by adding different quantities of 1 N KOH or 0.5 N HCl. Bacteria were grown in a glass fermentation vessel (working volume, 100 ml) equipped with a water-jacket. The temperature was maintained in the range of 40–75°C to within ±0.5°C using an UH-4 ultrathermostat (Germany). The culture was stirred with a magnetic mixer (300 rpm) and aerated by a continuous flow of sterile air (membrane filter, 0.4 μm) at a rate of 0.3 l/min. To keep evaporation of the culture liquid to a minimum, the air was first moistened by passing it through sterile water having the same temperature. The biomass density was determined from its optical density measured on an SF-46 spectrophotometer at a wavelength of 540 nm.

The kinetics of batch growth was monitored in two variants of a short-term test. In the first variant, bacteria were grown in a fermentor with samples taken at regular intervals for optical density determinations. After 5–6 h, or when the optical density equaled 0.6 units (whichever came first), the measurements were stopped, 90% of the bacterial suspension was drained off, and the remainder was diluted with fresh nutrient medium; the incubation temperature was elevated or decreased; and the whole procedure was repeated. In the second test variant, the same inoculum was added to a series of flasks (10 vol %) in which the pH was adjusted to different values, and the incubation was carried out on a temperature-controlled shaker at 55°C with samples taken at regular intervals to determine optical density.

The parameter values of the mathematical models were determined by fitting the model to the obtained data and minimizing the mean square error of the fit with the aid of Solver, Excel, and Microsoft Office 2000. The parameter values were subject to additional constraints based on their biological meaning (nonnegativeness) and on preliminary kinetic observations (e.g., μ_m was assumed to fall within the interval 0 to 3 h^{-1}).

RESULTS AND DISCUSSION

The dynamics of bacterial growth with change of temperature. Curves obtained in the first variant of short-term experiments (see Materials and Methods) are shown in Fig. 1. The temperature in the fermentor was increased from 40 to 80°C in 5°C steps, and, at each step, the culture was diluted with fresh nutrient medium to induce bacterial growth. Each rise of the temperature by 5°C was accompanied by a short but clearly recorded lag phase or, to be more precise, a phase of temporary growth deceleration. The duration of this phase was shortest when bacteria were grown in the temperature interval of 50–60°C and increased both at lower and higher temperatures with a concurrent decrease in the growth rate after its stabilization.

To make the kinetics of the transient processes caused by abrupt temperature changes more evident, the specific growth rate (SGR) was plotted in Fig. 2 as a function of time. The values of SGR (not to be confused with the μ_m constant) were calculated using the following relationship:

$$\mathrm{SGR} = \frac{1}{x}\frac{dx}{dt} = \frac{d\ln x}{dt} \approx \frac{\ln(x_i/x_{i-1})}{t_i - t_{i-1}},$$

where x is the current biomass density, and the i and i–1 subscripts indicate the test data obtained at time t_i and at the preceding time t_{i-1}, respectively.

Figure 2 shows only part of the data obtained: four transient processes for the temperature interval 60–75°C. The arrows indicate instants when the cell suspension was diluted with fresh medium and the temperature was increased by 5°C. It is clearly seen that, at temperatures above 60°C, growth was immediately slowed down after stepwise elevations of temperature and then SGR gradually increased to the level corresponding to the new temperature. A similar transient kinetics resulted from temperature increases in the range 40–50°C (data not shown), except that the period of decelerated growth increased with the cultivation temperature.

Mathematical equations describing transient kinetics. The most straightforward mathematical model capable of predicting the lag phase is the so-

called synthetic chemostat model (SCM) [8]. The essence of this model is the notion that the current growth rate is determined not only by the given cultivation conditions but also by the physiological state of the cells and, above all, by the quantity of nonconstitutive cell components, whose content changes in response to changes in culture conditions, e.g., the concentration s of the limiting substrate. Such components were divided into two groups: P components, making the active growth of cells possible (enzymes of primary metabolic pathways and RNA and proteins of ribosomes), and U components, responsible for cell resistance to adverse environmental factors (many enzymes of secondary metabolism, protective pigments, alternative oxidase, etc.). For example, under chronic starvation ($s \longrightarrow 0$), the cellular content of P components declines and that of Ucomponents goes up, securing the viability of starving cells over a long period. Transfer of cells to a rich medium with surplus substrate ($s \gg K_s$) alters this ratio in favor of P components and increases the growth rate of cells to a maximum.

In the SCM, the vector of the component content in the biomass is expressed in terms of a scalar function of the physiological state r, reflecting the overall relative content of all P components,

$$r = \frac{P_1 - P_1^{\min}}{P_1^{\max} - P_1^{\min}} \approx \frac{P_2 - P_2^{\min}}{P_2^{\max} - P_2^{\min}} \approx \ldots \approx \frac{P_n - P_n^{\min}}{P_n^{\max} - P_n^{\min}} = \frac{s}{K_r + s}, \quad (1)$$

where $P_i^{\max}$ and $P_i^{\min}$ are, respectively, the lower and upper bounds of the variation of the ith P component; and n is the number of such components. The analysis of available data [8, 11] showed strong correlation of the contents of individual P components (as a result of coordination of cell autosynthesis). On these grounds, one function r can be used for all P biopolymers of the cell, at least as a good semiempirical approximation.

The dynamics of r is determined by the concentration of the limiting substrate with a lag, since cell mass is a slow-changing variable and its component content reflects not so much the current trophic state of the culture as past variations of the concentration of the limiting substrate. Specifically, a batch culture will show a lag phase if cells of the inoculum previously experienced a shortage of one or several substrates and the content of P components is insufficient to realize the maximum SGR. The lag phase duration is determined by the time needed to bring the intracellular contents of ribosomes and enzymes of primary metabolism to their maximum levels. The whole SCM is represented by the three following equations:

$$\frac{dx}{dt} = \mu(s, r)x, \quad \mu(s, r) = \mu_m r \frac{s}{K_s + s},$$

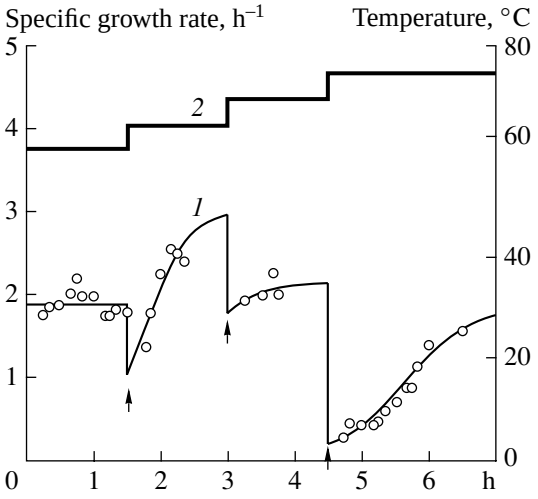

Fig. 2. Transient behavior of (*1*) the specific growth rate caused by stepwise increases in (*2*) the cultivation temperature. The curves were calculated using equation (6). The moments of cell suspension dilution with fresh medium are indicated by arrows.

$$\frac{ds}{dt} = \frac{\mu(s, r)x}{Y}. \quad (2)$$
$$\frac{dr}{dt} = \mu(s, r)\left(\frac{s}{K_r + s} - r\right),$$

where x, s, and r are, respectively, the cell biomass, the concentration of the limiting substrate, and the physiological state variable r; and μ_m, K_s, K_r, and Y are constants. The first two equations are simply expressions of the material balance between the biomass and the limiting substrate. The third equation for function r describes the rearrangement dynamics of the biomass component content (the relationship between P- and U-components). The pace of this rearrangement scales with $\mu(s, r)$ (the current SGR) and with the difference between the equilibrium and current values of r; this difference acts as a driving force for the adaptive rearrangement of metabolism.

If the substrate is not limiting, as in the tests described above ($s \gg K_s \approx K_r$), we have $\mu(s, r) = \mu(r) = \mu_m r$, and the second equation can be dropped. Then, instead of (2), we get

$$\frac{dx}{dt} = \mu_m r x, \quad \frac{dr}{dt} = \mu_m r(1 - r). \quad (3)$$

Up to this point, our treatment followed the basic SCM, formulated elsewhere with regard to the trophic factor of the medium—the concentration of the limiting substrate [8, 11]. Now, we will extend the model to cover other factors as well, such as the temperature and acidity of the medium. The first and most obvious

impact of these factors is their influence on the rates of metabolic processes, including the growth rate and its constant μ_m, which the maximum SGR attained under surplus substrate ($s \gg K_s$). Accordingly, a constant μ_m in equation (3) should be replaced by the function $\mu_m(T, \text{pH})$, which needs to be determined from experimental data. However, there is also another effect of nontrophic factors to be taken into account: if they are nonoptimal for growth but not lethal and if all required growth substrates are available in the medium, then cells will start synthesizing additional *P* components to maximize the growth rate under the given nonoptimal conditions. Note that a distinction should be made between growth and multiplication of cells under nonoptimal conditions and the ability of cells to resist adverse conditions. In the first case, such conditions are assumed to be much less severe than in the second case, and it is the *P* components that are needed by cells for faster growth and not *U* components. When growth conditions deteriorate even further, the metabolic control strategy will switch from growth to the preservation of viability.

The examples are heat shock proteins in overheated cells, desaturases in overcooled cells, components of additional ion-exchange channels in membranes of cells growing under nonoptimal pH, etc. The first to change in this case is the physiological state vector, and, in equation (1), we have $n + m$ components instead of n, where m is the number of additional *P* components, the expression of which is induced by cell transfer to nonoptimal conditions. At the transfer time, their content in cells is very small or zero, and this can be formally described as an abrupt fall of the initial value r_0 to some small value even if, until this point, the value of r was maximal ($r = 1$). Therefore, by taking into account the two outlined effects of nonoptimal nontrophic medium factors, we arrive at the following modification of equation set (3):

$$\begin{aligned} \frac{dx}{dt} &= \mu_m(T, \text{pH})rx, \\ \frac{dr}{dt} &= \mu_m(T, \text{pH})r(1-r), \quad r_0 < 1. \end{aligned} \tag{4}$$

A change in growth conditions is expected to cause an immediate drop of μ_m and r_0. This gives rise to a lag period, during which r increases asymptotically to its maximum value $r = 1$ and the specific growth rate increases to its highest value, $\text{SGR} = \mu_m(T, \text{pH})$, possible under the given conditions.

Equations (4) has a simple analytical solution for variable x and is given by

$$x = x_0\{1 - r_0 + r_0 \exp[\mu_m(T, \text{pH})t]\}. \tag{5}$$

The transient kinetics of SGR is also described by a simple relationship:

$$\text{SGR} = \frac{\mu_m(T, \text{pH})}{1 + (1/r_0 - 1)e^{-\mu_m(T, \text{pH})t}}. \tag{6}$$

It can readily be seen that (6) describes a smooth change of SGR from its initial value $\mu_m(T, \text{pH})r_0$ at $t = 0$ to its upper limit equal to $\mu_m(T, \text{pH})$ at $t \longrightarrow \infty$.

Let us return to the experimental data. As follows from Fig. 1, equation (5) is in good agreement with the growth dynamics data obtained at different temperatures. The errors of fit for transient processes caused by a temperature increase by 5°C were small. The variant with the maximum incubation temperature might be regarded as the only exception, but even in this case the relative squared error of fit (0.043) was smaller than the corresponding error of the experimental method (0.05). A comparison between the predicted and experimentally observed dynamics of SGR (Fig. 2) makes an even more stringent test of model adequacy, because growth rates are notably less sluggish than the respective values of biomass dynamics. As seen from Fig. 2, the SGR simulation errors were generally larger; however, they remained smaller than the random (experimental) error in SGR values computed by numerical differentiation of x data. Even so, the SCM in all cases could capture reasonably well the general trend of SGR kinetics, consisting in an abrupt fall of SGR upon change in temperature and in subsequent asymptotic rise of SGR to its new steady-state level. It is interesting that the study of SGR kinetics was able to bring to light some shortcomings of the experiment not obvious from the x kinetics. For example, the temperature transition from 60 to 65°C was not monitored to completion: it was interrupted at a point when the steady-state value of SGR had not yet been reached. Nevertheless, the maximum value of SGR at the given temperature could be reliably found by fitting the data to the model.

Analysis of the influence of temperature. Let us now consider the actual dependence of SGR upon temperature, represented by the function $\mu_m(T)$. It is seen from Figs. 2 and 3 that both SGR and r_0 attain their maximum values at temperatures between 60 and 70°C, which should be considered optimal. In order to determine the optimum temperature more accurately, one needs to fit the whole bundle of curves by a single mathematical equation that defines the dependence $\mu_m(T)$ over the entire temperature range including the region of growth slowdown at excessively high temperatures. Such an equation was found in the following relatively simple form [11]:

$$\mu_m(T) = \frac{A \exp \lambda T}{1 + \exp B\left[1 - \dfrac{C}{T + 273}\right]}, \tag{7}$$

where T is temperature, °C; and A, B, C, and λ are kinetic constants. The parameter A is equal to the growth rate at 0°C; λ and B characterize, respectively, the steepness of growth acceleration caused by temperature and the steepness of thermoinactivation; and parameter C is numerically equal to the temperature at which 50% of the cells are thermoinactivated (in practice, the value of C is close to the temperature maxi-

mum). The parameter values obtained for the bacteria studied are given in the table and in Fig. 3. The maximum growth rate of 2.5 h^{-1}, corresponding to the generation time of 15.4 min, was found to occur at 66.5°C.

The value of λ can be converted to the conventional temperature characteristic Q_{10}, which is how many times the process rate increases when the temperature is increased by 10 degrees. The obtained value of Q_{10} for our bacteria was 2.16, which falls within the recognized variation range of Q_{10} for biological objects [12]. It is important to remember that Q_{10} is applicable only within a limited temperature interval. At elevated temperatures, when thermoinactivation comes into play (formally speaking, when the denominator in equation (7) becomes notably different from unity), Q_{10} will no longer be constant and may decrease to negative values. Equation (4) is free from this limitation, and its parameters are constant in the entire temperature range.

The influence of the medium acidity. It was reliably established in second-type experiments (see Materials and Methods) concerned with pH growth profiles (Fig. 4b) that, during the initial 1–2 h of culture growth in a neutral or alkalescent medium, the density of the culture actually decreased rather than increased. For other organisms, such a reduction of optical density at the start of cultivation has been described in detail elsewhere [9, 10] and explained by the reversible adhesion of cells to the glass surface of the cultivator. Attachment of cells to the surface is a means of their adaptation to adverse environmental conditions and may increase as these conditions deteriorate. Adhesion is prevented by the so-called antiadhesins, which are exometabolites produced by bacteria during the first hours after passage to a new nutrient medium. Therefore, saturation of the new medium with antiadhesins is a key step in making it habitable. It is interesting that no attachment of cells was observed in our tests concerned with the influence of temperature. The explanation lies in the way our short-term experiments were arranged. Bacteria were cultured in the same fermentor; growth started after the cell suspension was diluted with fresh medium; and cells did not experience the transfer-induced stress, because the medium already contained antiadhesins of the previous fermentation at a concentration above critical. Therefore, no adhesion occurred. By contrast, in experiments concerned with the effect of pH, the same inoculum was simultaneously placed in a series of shake flasks containing fresh medium. Under such conditions, adhesion did occur and manifested itself as a decline of culture density during the first hours of the experiment.

In this work, no special determination of antiadhesins was carried out and the growth dynamics was mathematically represented by fitting equation (5) to the accumulated biomass curve at points outside the adhesion density gap. As a consequence, the specific maximum adhesion of cells a in different short-term test variants could be estimated from the difference

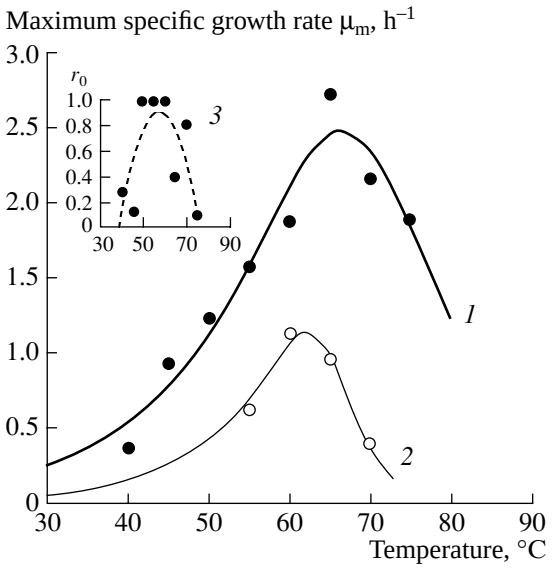

Fig. 3. Influence of temperature on the maximum specific growth rate of bacteria on (*1*) complex and (*2*) synthetic media. Inset: (*3*) temperature dependence of the initial value of the physiological state function r_0 on complex medium. Continuous curve represents calculation by equation (7); dotted line represents fitting by a second-degree polynomial.

between the obtained model curves and all experimental points,

$$a = (x_{min} - x^*)/x_0, \quad (8)$$

where x_0 is the cell suspension density at the time of inoculation ($t = 0$), x_{min} is the minimum density attained at a time $t = t^*$ (during the first 1–2 h of cultivation), and x^* is the estimated density at the time t^* in the absence of adhesion.

The calculation of culture density dynamics for one of the experiments at pH 9 is illustrated in Fig. 4a. It can be seen that curves can indeed be described by the SCM adjusted to account for cell adhesion at the start of growth. The results of all second-variant short-term tests in which the initial acidity of the medium was varied are shown in Fig. 4b. The most active growth was observed in neutral or alkalescent media (with a peak at pH 7.5), and the maximum adhesion occurred in alkalescent media. The curves of growth rate versus pH were similar for complex and synthetic media (data for the synthetic medium are not shown).

Parameter values in equation (5) describing growth rate of bacteria as a function of temperature

Parameter	Numeric value	Unit
A	0.025	h^{-1}
λ	0.077	$(°C)^{-1}$
B	57.5	Dimensionless
C	67.6	°C

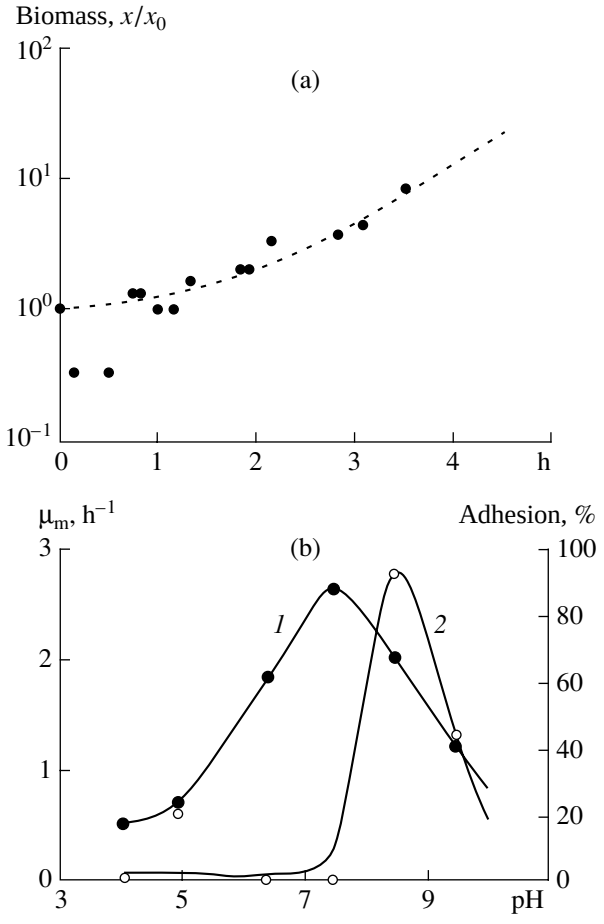

Fig. 4. Dependence of the growth of bacilli upon initial acidity of the medium. (a) Example of time variation of the optical density of a culture grown at pH 9. Dotted line is calculation by the SCM adjusted to account for cell attachment to vessel walls at the beginning of growth (equations (5) and (8)). (b) (*1*) SGR of bacilli and (*2*) cell adhesion to vessel walls as functions of the initial acidity of the culture liquid.

The influence of the nutrient medium. In this work, bacterial growth was compared on two media—a complex (yeast extract and peptone) and a synthetic one (glucose and mineral salts). No basic difference in the kinetics of batch growth on these media was observed. The biomass accumulation curves were exponential with a short lag phase that could be fairly well described by the SCM (Fig. 5, for growth at 60°C; no data for growth on the synthetic medium at other temperatures are reported because of their similarity with the results shown in Fig. 1). The difference between the results obtained on the two media was purely quantitative. First, the specific growth rate on the minimal medium was two times lower and amounted to 1.2 h^{-1} at the optimal temperature (generation time of 35 min). Second, the optimal temperature downshifted from 66.5°C (complex medium) to 62.3°C (synthetic medium). The first effect is widely known: more active growth on complex media is explained by savings in metabolic energy not spent on the synthesis of polypeptides and other cell components that are transported ready-made from the medium. The nature of the second phenomenon requires further study.

Let us consider a hypothesis based on Herbert's postulate [12] stating that the apparent growth rate of microorganisms recorded in experiment is, in fact, the difference between rates of true growth and endogenous decomposition,

$$\mu_{app} = \mu_{tru} - a. \quad (9)$$

Although both summands on the right-hand side (μ_{tru} and a) increase with temperature, the second one has a steeper slope, and at some critical temperature T^{max} they level and give the net zero growth rate. The inactivation is determined by the content of thermolabile components and should be roughly the same for any culture of the given species regardless of the medium—a complex or a synthetic one—on which it grows. Given that μ_{tru} is notably higher on a complex medium, the upper temperature limit T^{max} should also be higher on a complex medium than on a synthetic one. Experimental data provide clear-cut evidence for this conclusion. Thus, we failed to obtain stable growth of bacilli on the synthetic medium at temperatures above or equal to 70°C, whereas the growth rate on the complex medium at this temperature remained quite high and differed from the maximal one by less than 20%. It can be seen from Fig. 3 that the descending part of the temperature curve for the synthetic medium tends to cross the abscissa at a much lower temperature. Finally, we noted that the higher the T^{max} (the upper temperature limit), the higher the T^{opt} (temperature optimum) and vice versa. Then, if the T^{max} is determined by the relationship between μ_{tru} and a, the same reason can also explain the shift of T^{opt}.

Let us sum up our findings. The kinetic synthetic chemostat model, originally developed for mesophilic organisms, was shown to be fully applicable to thermophilic bacteria, enabling better understanding and quantitative description of their growth. The SCM was initially designed to account for the effect of the trophic factor, specifically, to describe stationary and nonstationary growth under wide variations of the limiting substrate concentration, both current and previous (the "memory" effect). In this work, the SCM was shown to apply also to transient processes caused by abrupt changes of nontrophic factors such as pH of the medium and cultivation temperature. This is hardly accidental because unbalanced and nonstationary microbial growth can always be attributed to a temporary lack of correspondence between the cell composition (which has notable inertia and depends upon culture history) and the current medium conditions. The

mechanism of transient growth consists in the adaptive rearrangement of the component content of cells triggered by information signals coming from the medium and proceeding most likely at the transcription level (derepression and induction of synthesis of nonconstitutive enzymes and other biopolymers, including rRNA). The modification of the component composition, e.g., the synthesis of heat shock proteins at elevated temperatures, is accompanied by acceleration of cell growth and follows the same kinetic pattern (see the *S*-shaped curves of the specific growth rate in Fig. 2) no matter what cultivation parameter suffered an abrupt change: the concentration of the limiting substrate (transition from starvation to nutrient surplus), the temperature, or pH.

Regarding the particular features of the new organism we studied, *Geobacillus uralicus*, the SCM made it possible to determine more accurately the important temperature characteristics and kinetic patterns of its growth in media of different acidity. It should be noted that, by fitting the model to the entire experimental curve, growth parameters could be determined with significantly higher accuracy than through simple visual examination. First, the computation of parameter values (T^{opt}, T^{max}, pH^{opt}, etc.) using equations such as (7) takes into account all experimental data points rather than just a few extremum points, where a chance outlier can be mistaken for a true extremum. Second, knowing the kinetic law of growth makes it possible to determine the true values of growth parameters that are often masked in an actual experiment by the influence of uncontrolled factors such as adhesion, shortage of O_2, unfinished transient process, etc. Finally, a comprehensive model can predict the behavior of the culture in a wide range of cultivation conditions. The bacterium *G. uralicus* is a genuine thermophile, growing at temperatures ranging from 40 to 75°C. The maximum specific growth rate of 2.7 h^{-1} (generation time, 15.4 min) was observed on a complex nutrient medium (peptone and yeast extract) at 66.5°C. On a synthetic medium (glucose and mineral salts), it declined to 1.2 h^{-1} with a corresponding downshift of the optimum temperature to 62.3°C. The optimal pH was 7.5. In alkalescent medium, adhesion of cells to the glass surface of the cultivator was noted.

It is worth noting that the temperature in the well from which this culture was isolated ranged from 40 to 72°C, while the pH of stratal waters and drilling fluid ranged within 7.5–8.0 and 7.0–7.75, respectively. Therefore, an amazingly close match was found between in situ growth conditions and the optimal growth conditions for laboratory cultures.

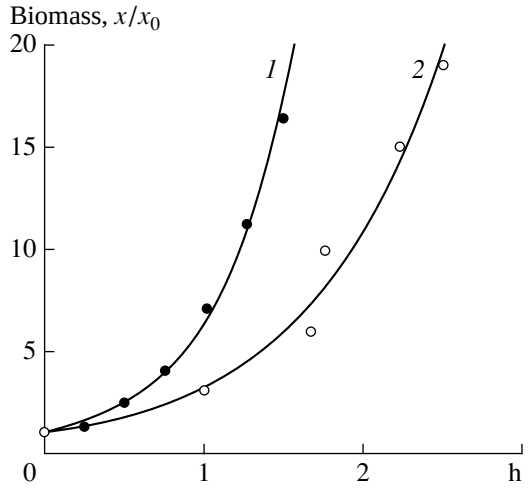

Fig. 5. Growth dynamics of bacilli on (*1*) complex and (*2*) synthetic media. Continuous curves represent calculations by the SCM, equation (5).

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