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**Pēteris Zikmanis · Ramona Krūče · Lilija Auziņa**

# An elevation of the molar growth yield of *Zymomonas mobilis* during aerobic exponential growth

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**Abstract** Elevated values of molar growth yield ($Y_{x/s}$ = 14–26 g $mol^{-1}$) were obtained during exponential growth ($\mu > 0.4$ $h^{-1}$) of *Zymomonas mobilis* ATCC 29191 by using reduced concentrations of glucose (6.25–100 mM) and increased oxygen supply ($E_h > 300$ mV) in the growth medium, as compared to the $Y_{x/s}$ of anaerobic exponential growth (8–10 g $mol^{-1}$). Aerobically grown cells showed an increased maximum growth rate ($\mu_{max}$), and a reduced specific glucose consumption rate ($q_s$), and specific ethanol formation rate ($q_p$), thus demonstrating a more pronounced energy-coupling growth under oxic conditions. These results can be neither explained by the concept of a solely operating Entner-Doudoroff pathway as an ATP source in aerobically growing cultures of *Z. mobilis* nor considered to be consistent with existing data on the lack of the Pasteur effect in this bacterium. Therefore, the results rather give evidence for the essential contribution of aerobic ATP generation under the reported conditions.

**Key words** *Zymomonas mobilis* · Biomass yield · Aerobic growth · Anaerobic growth · Ethanol formation · Pasteur effect

## Introduction

The presence of a respiratory electron transport chain in the fermentative bacterium *Zymomonas mobilis* (Belaich and Senez 1965; Pankova et al. 1985; Strohdeicher et al. 1990) together with the ability of aerobic ATP generation by nongrowing cells on nonfermentable substrates (Dawes and Large 1970; Kalnenieks et al. 1993, 1995; Zikmanis et al. 1995) demonstrate a significant potential of this bacterium to perform, at least in principle, an aerobic energy-yielding metabolism. Such a possibility, however, is strongly contradicted by observations of the actual performance of growing cultures of *Z. mobilis* under oxic conditions. Thus, the absence of the Pasteur effect (Belaich and Senez 1965), lowered or unaffected biomass yield and growth rate (Bringer et al. 1984; Pankova et al. 1985, 1988; Vore and Talbrut 1993), and observed specifity of the NAD(P)H dehydrogenase reaction (Kim et al. 1995) may be considered to be convincing evidence in favor of the Entner-Doudoroff pathway as the sole ATP source, even during aerobic growth. However, the existing data on the aerobic growth of *Z. mobilis* are limited and are not comparable because of very different growth conditions (Doelle et al. 1993).

It should be noted in this respect that

1. Energetic advantages of an aerobic ATP generation can be realized only by co-ordination of the amount of ATP required for cellular growth, the cellular potential for the aerobic energy generation, and the oxygen supply (Oura 1972).

2. The efficiency of aerobic metabolism may be dependent on both the oxygen and the glucose available in the growth medium (Stanbury and Whitaker 1984).

3. A positive relationship exists, in general, between the growth rates and the growth yields of micro-organisms (Forrest 1967; Pirt 1975).

Therefore, the relatively high (20–100 g $l^{-1}$) glucose concentrations, the moderate values of $pO_2$ (13–20% of saturation ) and $E_h$ (140 mV) in the growth medium, and the low dilution rates (0.05–0.13 $h^{-1}$) used for aerobic cultivation of *Z. mobilis* (Bringer et al. 1984; Pankova et al.1985, 1987; Doelle et al. 1993) indicate a possible limitation of aerobic metabolism and cell growth.

This study represents an attempt to examine the anabolic and catabolic parameters of *Z. mobilis* during anaerobic and aerobic growth under conditions beyond the previously reported range. The following approaches were used to avoid possible limitations of aerobic growth of *Z.*

P. Zikmanis (✉) · Ramona Krūče · Lilija Auziņa
Institute of Microbiology & Biotechnology, University of Latvia, Rātsupītes Street 1, LV 1067 Riga, Latvia
Tel. +371-2-427923; Fax +371-2-428039
e-mail: root@muter.vernet.lv

*mobilis*: (1) an elevated oxygen transfer rate and reduced concentration of glucose in the growth medium, and (2) a cultivation mode directed toward "steady-state" conditions and maximal growth rate, achieved by continuous cultivation in a fermenter at a dilution rate close to the growth rate of an aerobic exponentially growing starter culture or, to a certain extent (Schlegel 1985), by subsequent transfer of exponentially growing cells into fresh growth medium.

## Materials and methods

### Strain and culture conditions

*Zymomonas mobilis* ATCC 29191 was maintained and cultivated in the standard culture medium (Bringer et al. 1984) except that 2.5 g $l^{-1}$ of Bacto yeast extract (Difco, Detroit, Mich., USA) was added and glucose concentrations were 6.25–100 mM. Aerobic growth was attained by incubating cultures in 0.75-l flasks containing 0.05 l medium with shaking on a reciprocal shaker (190 rpm) at an oxygen transfer rate of about 45 mmol $O_2$ $l^{-1}$ $h^{-1}$, determined by the sulfite oxidation technique (Stanbury and Whitaker 1984). Alternatively, cultures were incubated in an MBR fermenter (Witzekon, Switzerland) with a working volume of 1.4 l, a stirrer speed of 300 rpm, and an air flow of 60 l $h^{-1}$ ($pO_2$ = 51 ± 0.5%, $E_h$ = 385 ± 2 mV). Anaerobic growth was achieved by continuous flushing of flasks with pure nitrogen before inoculation and by nitrogen flow (60 l $h^{-1}$) instead of air during continuous growth in the fermenter ($E_h$ = –140 ± 3 mV); the working volume and stirrer speed as were the same in the aerobic cultivation.

Starter cultures containing 100 mM glucose in the growth medium were prepared by inoculating colonies from the nutrient agar at an initial cell concentration of 0.10 ± 0.01 g $l^{-1}$. Cultures were then grown anaerobically at 30° C for 7–8 h until the cell density reached 0.5–0.6 g $l^{-1}$ and the growth rate was 0.35–0.40 $h^{-1}$ (exponential phase). Cells were recovered by centrifugation (5,500 × *g*, 10 min, 20° C), washed with the glucose-free standard medium, and resuspended to the original cell density in fresh medium supplemented with glucose to continue exponential growth. For the inoculum for aerobic cultivation, this step was repeated subsequently under oxic conditions, and harvested cells were then transferred into fresh medium with 6.25–100 mM glucose, as for anaerobic growth.

### Analytical determinations

For glucose and ethanol determinations, duplicate samples were taken from growing cell suspensions and fixed in $HClO_4$ (200 mM final concentration), neutralized by KOH, and centrifuged. Glucose was determined using the dinitrosalicylic acid reagent (Miller 1959) or the hexokinase-glucose-6-P dehydrogenase (Sigma, St. Louis, Mo., USA) assay (Bergmeyer et al. 1981); the results obtained with the different assays were similar. The ethanol concentration was assayed enzymatically (Bernt and Gutmann 1981) with yeast alcohol dehydrogenase and $NAD^+$ (Sigma, St. Louis, Mo., USA). Measurements of oxygen consumption and ATP content of anaerobically and aerobically grown cells were performed as reported earlier (Zikmanis et al. 1995) except that a nonstarved cell suspension was used in the glucose-free standard medium and respiration was initiated by addition of the substrate solution in the same medium (6.25–100 mM glucose final concentration).

The biomass concentration was determined spectrophotometrically (recording spectrophotometer UV-260; Shimadzu, Kyoto, Japan) by measuring the $OD_{550}$. A calibration curve, which was used for calculations of dry cell mass was obtained for the strain under study during aerobic or anaerobic exponential growth. Dry mass was routinely determined with cells washed twice in distilled water and dried at 105° C for 24 h.

### Data processing and analysis

The values of kinetic and yield parameters were calculated from the concentrations of biomass, glucose, and ethanol (Pirt 1975; Stanbury and Whitaker 1984) determined during exponential growth at 1–h intervals. Data from independent series of experiments were combined and processed by conventional methods of regression and variance analysis, and influences of factors (initial glucose concentration, oxic/anoxic conditions, time) were evaluated using the F-test and the Student's *t*-test. A value of $1 - P \leq 0.01$ was considered to be significant. Data in the text, tables, and figures are given as the mean ± SE.

## Results and discussion

Double-reciprocal plots of growth rates of *Zymomonas mobilis* versus initial glucose concentrations of the growth medium showed that under oxic conditions, growth rates were significantly higher ($\mu_{max}$ = 0.53 $h^{-1}$) than under anoxic conditions ($\mu_{max}$ = 0.44 $h^{-1}$) (Fig. 1). Such a hyperbolic type of growth dependence on the initial substrate concentrations reflects, in many cases, the mechanism of substrate uptake in micro-organisms (Posten and Cooney 1993). In this respect, the estimated values of saturation constants of glucose consumption during aerobic and anaerobic growth ($K_s$ = 3.7 and 5.9 mM, respectively) were close to the range of $K_m$ (5–15 mM) reported for the glucose transport system of *Z. mobilis* (DiMarco and Romano 1985) and most probably reflect an operation of glucose transport by facilitated diffusion, i.e., by a low-affinity, high-velocity system.

The specific rates of glucose consumption ($q_s$) and ethanol formation ($q_p$) correspond to the amount of glucose consumed and ethanol produced per unit of biomass per hour; they are considered to be suitable parameters for the evaluation of the influence of cultivation conditions on the performance of catabolism in micro-organisms (Pirt 1975; Stanbury and Whitaker 1984). The effect of

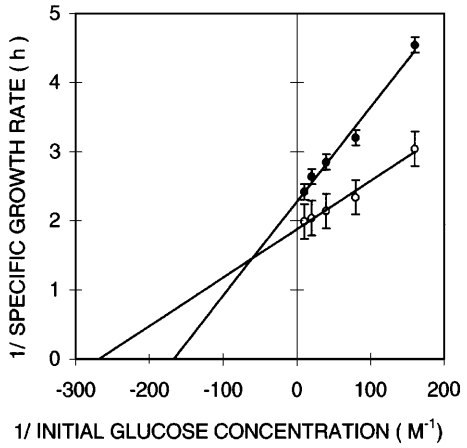


**Fig. 1** Effect of the initial glucose concentration on the specific growth rate of *Zymomonas mobilis* ATCC 29191 presented in a Lineweaver-Burk plot. ○ Aerobic exponential growth, ● anaerobic exponential growth. Data from three independent experiments performed in shaking flasks as described in Materials and methods. Values shown as the mean ± SE

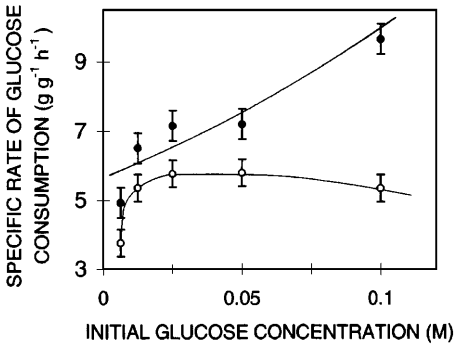


**Fig. 2** Effect of the initial glucose concentration on the specific rate of glucose consumption of *Zymomonas mobilis* ATCC 29191. ○ Aerobic exponential growth, ● anaerobic exponential growth. Data from three independent experiments performed in shaking flasks as described in Materials and methods. Values shown as the mean ± SE

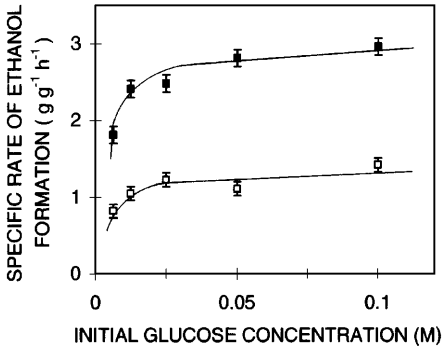


**Fig. 3** Effect of the initial glucose concentration on the specific rate of ethanol formation of *Zymomonas mobilis* ATCC 29191. □ Aerobic exponential growth, ■ anaerobic exponential growth. Data from three independent experiments performed in shaking flasks as described in Materials and methods. Values shown as the mean ± SE

initial concentrations of glucose in the cultivation medium and the presence of oxygen were reflected differently in the pattern of the corresponding curves (Figs. 2, 3). All of the curves represented nonlinear regressions ($1 - P = 0.01$). The $q_s$ values of anaerobically cultivated cells significantly ($1 - P = 0.01$) exceeded the specific rate of glucose consumption for aerobically grown cells and increased almost linearly with increasing initial glucose concentraions (Fig. 2). In contrast, under oxic conditions, an increase in the specific rate of glucose consumption was stopped above 25 mM and even reduced at 100 mM of initial glucose.

In a similar way, the values of $q_p$ (Fig. 3) for anaerobically grown cells significantly exceeded those obtained in the aerobic cultivation of *Z. mobilis*. When linearized ($1 - P = 0.01$) against the reciprocal values of initial glucose concentration, both curves showed a significantly higher slope value for aerobically grown cells and, therefore, a more pronounced response of the aerobic ethanol formation rate to the changes of initial concentration of glucose was confirmed. The values of ethanol yield per unit of glucose consumed ($Y_{p/s}$) or per unit of biomass formed

**Table 1** Oxygen consumption rate and ATP content in *Zymomonas mobilis* ATCC 29191 cells removed from medium during aerobic and anaerobic exponential growth in shaking flasks as described in Materials and methods

| Parameters | Growth | |
|---|---|---|
| | Aerobic | Anaerobic |
| Oxygen consumption rate[a] [nmol $min^{-1}$ (mg dry wt)$^{-1}$] | 130.0 ± 2.2 | 79.2 ± 2.6 |
| ATP content [nmol (mg dry wt)$^{-1}$] | | |
| Growing cells[b] | 2.59 ± 0.84 | 2.39 ± 0.39 |
| Upon glucose addition[a] | 1.63 ± 0.44 | 1.86 ± 0.10 |

[a] Initiated by glucose (6.25–100 mM) addition to the suspension of removed cells in glucose-free medium
[b] Directly sampled from the growth medium

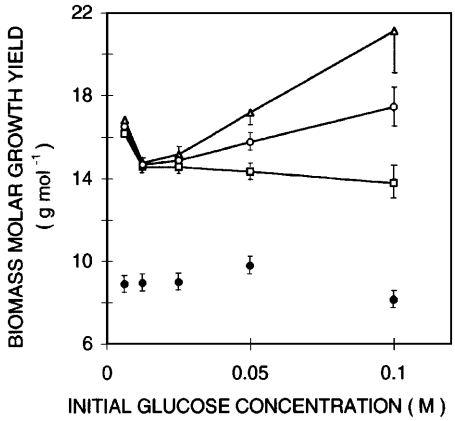


**Fig. 4** Changes of the molar growth yield of *Zymomonas mobilis* ATCC 29191 upon initial glucose concentration. △ Oxic conditions, during first hour of exponential growth; □ oxic conditions, during first two hours of exponential growth; ○ oxic conditions, average value; ● anaerobic exponential growth, average value. Data from three independent experiments performed in shaking flasks as described in Materials and methods. Values shown as the mean ± SE

($Y_{p/x}$) varied acording to the initial concentration of glucose; however, the values showed no significant regression. The mean values of $Y_{p/s}$ and $Y_{p/x}$ under anoxic growth conditions (0.36 ± 0.01 g $g^{-1}$ and 7.42 ± 0.15 g $g^{-1}$, respectively) were significantly higher than those during aerobic growth (0.22 ± 0.01 g $g^{-1}$ and 2.48 ± 0.10 g $g^{-1}$, respectively).

The observed reduction of $q_s$ and $q_p$ during aerobic exponential growth of *Z. mobilis* is of essential importance because oxidative inhibition of glucose consumption and ethanol formation are generally assumed to be indicators of the Pasteur effect, i.e., an activation of sugar catabolism by anaerobiosis (Aisenberg 1961; Lagunas 1986). The ratio between the $q_s$ values (Fig. 2) of anaerobically and aerobically grown cells varied between 1.22 and 1.81 over the entire range of increasing glucose concentrations under study. Therefore, strong evidence was obtained on the capability of exponentially growing *Z. mobilis* cells to vary the rate of sugar catabolism depending on the presence or absence of oxygen at reduced concentrations of

**Table 2** The effect of elevated glucose concentration on kinetic and yield parameters of *Zymomonas mobilis* ATCC 29191 during aerobic exponential growth in shaking flasks as described in Materials and methods

| Parameters | Glucose concentration (M) | |
|---|---|---|
| | 0.1 | 0.3–0.5 |
| Specific rate of glucose consumption, $q_s$ (g $g^{-1}$ $h^{-1}$) | 4.31 ± 0.20 | 11.04 ± 2.17 |
| Specific rate of ethanol formation, $q_s$ (g $g^{-1}$ $h^{-1}$) | 1.23 ± 0.11 | 1.54 ± 0.15 |
| Ethanol yield, $Y_{p/s}$ (g $g^{-1}$) | 0.28 ± 0.04 | 0.14 ± 0.02 |
| Ethanol yield per unit of biomass, $Y_{p/x}$ (g $g^{-1}$) | 3.06 ± 0.28 | 3.88 ± 0.35 |
| Molar growth yield, $Y_{x/s}$ (g $mol^{-1}$) | 16.75 ± 0.73 | 6.47 ± 1.29 |

**Table 3** Kinetic and yield parameters of *Zymomonas mobilis* ATCC 29191 during continuous growth in fermenter as described in Materials and methods

| Parameters | Continuous growth | |
|---|---|---|
| | Aerobic | Anaerobic |
| Glucose in growth medium (M) | 0.100 | 0.100 |
| Dilution rate, D ($h^{-1}$) | 0.410 ± 0.002 | 0.470 ± 0.002 |
| Specific rate of glucose consumption, $q_s$ (g $g^{-1}$ $h^{-1}$) | 2.86 ± 0.20 | 8.44 ± 0.19 |
| Specific rate of ethanol formation, $q_s$ (g $g^{-1}$ $h^{-1}$) | 0.84 ± 0.03 | 2.55 ± 0.03 |
| Ethanol yield, $Y_{p/s}$ (g $g^{-1}$) | 0.29 ± 0.03 | 0.30 ± 0.01 |
| Ethanol yield per unit of biomass, $Y_{p/x}$ (g $g^{-1}$) | 2.05 ± 0.06 | 5.42 ± 0.07 |
| Molar growth yield, $Y_{x/s}$ (g $mol^{-1}$)[a] | 25.78 ± 1.73 | 10.02 ± 0.22 |

[a] Calculated as the mean of $OD_{550}$ and direct dry mass measurements

glucose in the growth medium. This finding is apparently not consistent with the proposed generalization (Belaich and Senez 1965; Doelle et al. 1993) on the absence of the Pasteur effect in *Z. mobilis*.

The aerobically cultivated cells exhibited a significantly higher respiratory activity (Table 1) over the entire range of initial glucose concentrations, whereas the ATP content and the ATP formation capability did not vary under various cultivation conditions. However, the aerobically grown cells showed a significantly higher variance of ATP content, perhaps because of a more rapid decrease of ATP at higher initial concentrations of glucose (data not shown), thus reflecting a possible shift of the balance between the supply of energy from catabolism and its utilization for anabolic processes in *Z. mobilis* cells during aerobic growth (Forrest 1967).

An increase in the specific growth rate (Fig. 1), when observed together with a decrease in the specific rate of glucose consumption (Fig. 2), indicated a lower expense of glucose per unit of biomass formed, i.e., the higher biomass yield ($Y_{x/s}$) per unit of glucose consumed under oxic growth conditions. The pattern of corresponding curves (Fig. 4) reflected significant differences in this anabolic parameter within the entire range of initial glucose concentrations. It is noteworthy that the cultivation time appeared to be a significant factor with respect to the $Y_{x/s}$ at a higher (100 mM) glucose concentration, where biomass yield significantly decreased during the second hour of exponential growth and remained almost unchanged at a lower (6.25 mM) glucose concentration. Such a pattern of changes most probably reflects an influence of some inhibitory metabolite(s) that accumulate during growth depending on the initial glucose concentrations.

In order to evaluate the influence of higher initial concentrations (300–500 mM) on the values of $Y_{x/s}$ and other parameters, an independent series of experiments with aerobic cultivation was performed (Table 2). A decrease of biomass yield and the shifts of other parameters towards the values more typical of anaerobic growth (Figs. 2–4) were observed, thus confirming the significance of a reduced concentration of glucose to obtain elevated $Y_{x/s}$ values during aerobic exponential growth.

Continuous cultivation of *Z. mobilis* under steady-state conditions in a fermenter at high dilution rates resulted in practically the same values of kinetic and yield parameters (Table 3) under oxic and anoxic conditions as observed during exponential growth in flasks (Figs. 2–4; Table 2). Therefore, an independent additional support for the aforementioned results was achieved under more exactly defined growth conditions.

It should be noted that glucose catabolism in *Z. mobilis* solely follows the Entner-Doudoroff pathway, which is not very efficient since only 1 mol of ATP is synthesized per mol of glucose catabolized (Doelle et al. 1993). On the other hand, microbial biomass production per mol glucose catabolized is generally correlated with ATP availability (Stouthamer and Van Verseveld 1985). The reported values for molar growth yield of *Z. mobilis* fall in the range of $Y_{x/s}$ = 3.5–9.3 and apparently reflect the poor ability of *Zymomonas* to convert substrate into cellular material, i.e., the low efficiency of the catabolic pathway (Montenecourt 1985; Doelle et al. 1993). Therefore, the observed increase of $Y_{x/s}$ above this range of values can be explained by an additional ATP gain (Schlegel 1985) from pathways other than the Entner-Doudoroff pathway. Taking into account the aforementioned potential of *Z. mobilis* to perform an aerobic energy-yielding metabolism, a contribution of oxidative phosphorylation seems to be most probable under the given experimental conditions. Further work in this area will likely contribute to a better understanding of the molecular basis of energy metabolism in *Z. mobilis*.

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