

## Metabolism of reserve saccharides in the industrial strains of baker's yeast

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**Summary.** The cells of several industrial strains of yeast *Saccharomyces cerevisiae* grown under laboratory conditions into stationary growth phase in semi-synthetic medium with glucose had markedly lower content of glycogen and trehalose than the commercially produced yeast in yeast plant on the basis of one of these production strains. The yeast cells with low content of reserve saccharides were able to increase their content of both glycogen and trehalose if they were incubated for several hours under non-growing conditions with the presence of glucose or maltose. In contrast to accumulation, more days were needed to marked decrease of the content of reserve saccharides in the cells of commercial yeast incubated under similar conditions, however, without of carbon source. A marked decrease was observed under the conditions of starvation even in fermenting activity in dough whereas this activity was not causally related to the total content of glycogen or trehalose in baker's yeast.

The reserve saccharides of yeast are represented by non-reducing disaccharide trehalose ( $\alpha$ -D-glucopyranosyl-(1-1)- $\alpha$ -D-glucopyranosid) and by polysaccharide glycogen. The data of their content are very different. The measured values for trehalose are between 0.5 to 15% of the dry weight of the cells and for glycogen between 5.5 to 12.1% [1]. Other authors report more wider range for both saccharides — less than 1% and more than 23% of the dry weight of the cells [2—6]. These variations in glycogen and trehalose content of yeast suggest that reserve saccharides play important role during the yeast life cycle.

The synthesis of reserve saccharides in yeast cells represents a process dependent on the cell cycle phase, on the presence of nutrients and the degree of

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aeration during cultivation [6—9]. The biosynthesis of glycogen in yeast has a similar mechanism than that in animal cells [10—11]. It is carried out on protein-carrier with the participation of the following enzymes: synthetase initiating the glycogen production, glycogen synthetase (UDP-glucose: glycogen-glycosyltransferase, EC 2.4.2.11) and glycosylbranching  $\alpha$ -glucantransferase (EC 2.4.1.18) [11, 12]. The increase of glycogen content in yeast during growth is partially connected with glycogen synthetase activation, probably by means of protein kinase and partially with the increase of the total content of glycogen synthetase in the cell [13]. The recessive mutations in the regulatory gene *GLC 1* [14] can induce a defect in activation of glycogen synthetase and cause a deficiency in glycogen [5]. Such pleiotropic mutations [14], besides glycogen, affect also the trehalose metabolism, particularly the inability to accumulate trehalose under non-growing conditions or during growth on glucose [9, 15]. This defect of mutants in trehalose production can be avoided by growing their cells on maltose if they simultaneously contain the constitutive allele of *MAL* gene [9] which indicates the existence of two distinct systems in trehalose biosynthesis [15, 16, 17].

System I is catalyzed by trehalase-6-phosphate synthetase (UDP-glucose: glucose-6-phosphate-glucosyltransferase, EC 2.4.1.15.), which is probably a gene product of *SST1* locus [16]. System II is specified for maltose, it proceeds in the cells only during growth on maltose and does not require the product of the defective *SST1* gene. Under non-growing conditions trehalose is not produced from glucose by this system [9, 16].

The degradation of reserve saccharides takes place usually after exhaustion of exogenous carbon sources. The enzyme  $\alpha$ -1,4-glucan: orthophosphatglucosyltransferase (EC 2.4.1.1) participates in glycogen degradation [10]. Trehalose is hydrolyzed by trehalase (EC 3.2.1.28) to glucose [10]. It should be noted that whereas trehalose is localized in cytosol, enzyme trehalase occurs in vacuole [18]. The cryptic form of trehalase can be changed to a highly active one in the presence of ATP and cAMP, probably by protein kinase [19].

The different course of accumulation and utilization of glycogen and trehalose indicate that both saccharides play a different role in the yeast life cycle [6, 18]. It is presumed that glycogen serves as the source of carbon and energy at the respiratory adaptation or starvation. The participation of trehalose is only connected with the process of cell starvation and it is not excluded in cell osmoregulation [18]. The content of reserve saccharides is in close correlation with the yeast durability reflected both in the activity and viability of its cells during storage [20—24].

With respect to the fermenting activity of yeast in dough the work concentrates on the study of the dynamics of changes in the content of reserve saccharides in the cells of the production strain of baker's yeast in Trenčín yeast plant.

## Materials and methods

The following industrial strains of baker's yeast were used in this work: *S. cerevisiae* Fett D/80 (Slovlik, n. e. Trenčín), *S. cerevisiae* OOSF-RH (Slovlik, n. e. Trenčín), *S. cerevisiae* VU5 (isolated from Belgian commercial yeast), *S. cerevisiae* VU6 (isolated from Hungarian commercial yeast) and *S. cerevisiae* (isolated from Dutch commercial yeast). The yeast produced on the basis of VÚ 8 the production strain *S. cerevisiae* OOSF-RH was supplied by the yeast plant Slovlik, n. e. Trenčín.

The yeast cells were growing aerobically on semisynthetic medium [25] containing glucose (5 g, or 100 g/l), maltose (20 g/l) or sucrose (20 g/l) as a source of carbon and energy at 30°C from the initial concentration of  $5 \times 10^4$  cells/ml.

Accumulation of reserve saccharides under non-growing conditions in the yeast cells grown on semisynthetic medium with glucose (5 g/l) was carried out by their aerobic incubation at 30°C in phosphate buffer solution (100 mmol/l) pH 6 containing the yeast cells (3 mg of dry weight/ml) and glucose (10 g/l) or maltose (10 g/l) as the carbon source.

Degradation of reserve saccharides during starvation was followed at 30°C by incubation the compact pressed yeast or by incubation of the suspension of pressed yeast (3 mg of dry weight/ml) in phosphate buffer solution (100 mmol/l) pH 6 while shaken.

The extraction and determination of trehalose in yeast was carried out according to the method of Trevelyan and Harrison [26]. The suspension of yeast with the content of  $750 \times 10^6$  cells was cooled with the addition of icy distilled water and washed twice. The cells sediment was twice extracted by 4 ml of trichloroacetic acid (0.5 mol/l) during 40 minutes at laboratory temperature. The collected supernatants after filling the water to 20 ml were used to determine glucose by anthrone method. To 2.5 ml of cooled fresh anthrone reagent (2 g of anthrone solved in 1 l of sulfuric acid diluted in ration 5 : 2 by distilled water) 0.5 ml of trehalose extraction was added, the content of tubes was mixed and boiled for 10 minutes in water bath in sealed tubes. The intensity of arising green colour was measured spectrophotometrically at wave length 620 nm.

For extraction and determinati of glycogen in yeast the method of Becker [27] was used and modified. The suspension with the content of  $3 \times 10^8$  cells was centrifuged, the sediment was shifted to a calibrated tube and filled up to 1 ml with the solution of  $\text{Na}_2\text{CO}_3$  (0.25 mol/l). Glycogen was alkaline extracted during 90 minutes on boiling water bath in tubes with cooled closures. After cooling the extract was neutralized with 0.1 ml of acetic acid (3 mol/l) and filled to the volume of 5 ml by Na-acetate buffer solution (0.2 mol/l) pH 4.8. Glycogen was hydrolyzed by amyloglucosidase solution from *Aspergillus*

*niger* (18 U/mg; SERVA), purified by dialysis: 1 ml of amyloglucosidase solution (10 mg/ml) was dialyzed at 4°C against 500 ml of Na-acetate buffer solution (10 mmol/l). Then 10  $\mu$ l of amyloglucosidase solution (1.8 I. U) was added to 1 ml of extract with glycogen and hydrolysis lasted for 2 hours at 37°C on a water bath. The comparative solution was processed in the same way containing Na-acetate buffer solution instead of suspension after alkaline extraction. After the completed glycogen hydrolysis the content of tubes was neutralized by 30  $\mu$ l of buffer solution of KOH [Tris-HCl (1 mol/l): KOH (10 mol/l): acetic acid (1 mol/l) = 3:0.8:0.2] and it was filled to the volume of 1.5 ml by distilled water. Glucose resulting from glycogen hydrolysis was determined enzymatically using the commercial BIO-Lachema test.

Fermenting activity of yeast in dough was determined by the method of Burrows and Harrison [28]. The dough composition was as follows: 100 g of flour T 650, 1.5 g of NaCl, 0.8 to 1.4 g of dry weight of yeast-cells in 50 ml of H<sub>2</sub>O and 2 g of sucrose. The dough preparation and fermenting activity determination was performed in conditioned room at 30°C. The dough components conditioned to 30°C were mixed in mixer, then doughed intensively for 5 minutes and used per 50 g in parallel determinations. The dough shaped like a thin snake was put into infusion bottle and connected by means of metal tube with the second infusion bottle containing water. The increasing amount of CO<sub>2</sub> in the second bottle was driving out the water by tube into calibrated vessel, in which every 30 minutes during 3 hours the water volume driven out by gases arising at dough fermentation was measured. After calculation to 1.2 g of dry weight of yeast the fermenting activity was expressed, as ml of CO<sub>2</sub>/100 g dough which corresponds to the volume of CO<sub>2</sub> in ml liberated by fermentation of 100 g of dough (containing 1.2 g of dry weight of yeast) at 30°C.

## Results and discussion

The first part of our work was oriented to the selection and optimization of the method of determining the reserve saccharides, especially glycogen. Many works, devoted to the study of metabolism of glycogen and trehalose in yeast, apply the method of Trevelyan and Harrison [26] for determination of these saccharides. The above method consists of the chemical fractionation of cells and of the subsequent determination of total saccharides in isolated fractions. This method can be fully applied for determining the trehalose content, however, the values measured for glycogen content can be even 10 times higher than when applying specific enzymatic methods [6, 29] due to the inclusion of the part of polysaccharides of cell wall into glycogen fraction.

In our work the enzymatic method was used for glycogen determination in whole cells without the previous desintegration of the cell wall [27]. Reproducibility of the analysis by the above method was, however, obtained only after dialysis of the commercial amyloglucosidase of the firm Serva whose additives interfered with the colour reaction of the enzyme test of the firm Lachema n. e. for glucose determination.

The content of reserve saccharides determined by the above mentioned methods in the production strains of the yeast *S. cerevisiae* of different provenience, grown into the stationary phase of growth on semisynthetic medium with glucose, is given in Table 1. It indicates that, in spite of the different origin among the studied strains, no substantial differences have been detected in the content of reserve saccharides or in the fermenting activity measured in dough for common bakery goods with the addition of exogenous sucrose.

The determination of the content of glycogen and trehalose in the samples of pressed and dried commercial yeast (Tab. 2) has shown that the commercial yeast has a much higher content of reserve saccharides than the same production strain grown under laboratory conditions which is evidently connected with the different cultivation conditions. The results indicated further on that whereas in winter season no differences were found between the samples of dried and pressed yeast in the composition of reserve saccharides, a marked difference was manifested in the samples of pressed yeast analyzed during winter and summer periods. The decrease in the content of reserve saccharides, first of all glycogen, in summer period may be attributed to the extreme external temperatures affecting the yeast during expedition from the producing plant. In spite of the low content of reserve saccharides its fermenting activity in dough did not drop.

In order to explain the effect of cultivation conditions and the growth phase on the content of glycogen and trehalose in yeast, their content was estimated even after the growth of cells in semisynthetic media, where the source of carbon and energy was represented by maltose, sucrose, or by glucose in low or very high concentration (Table 3). It was found that in the studied industrial strains a synthesis of trehalose and glycogen takes place under the given condition even in the late exponential phase of growth of culture whereas a more marked accumulation of reserve saccharides was observed in the media with maltose as a substrate. The analysis of fermenting activity in dough, designated for common bakery goods, with the yeast biomass grown under different conditions have indicated that the highest activity was detected in cells after growing into stationary phase of growth under derepression conditions with glucose or with maltose as the substrates. Similarly, like in commercial yeast, the correlation between the total content of reserve saccharides and fermenting activity in dough was not observed.

Table 1. Content of reserve saccharides and fermenting activity in dough for common bakery goods of the industrial strains of bakers's yeast grown in semisynthetic medium with glucose (5 g/l)

	Glycogen	Trehalose	Fermenting activity (ml CO <sub>2</sub> /100 g of dough/90 min)
	(g/100 g of dry weight)		
<i>S. cerevisiae</i> Fett D/80	0,09	2,3	350
<i>S. cerevisiae</i> OOSF-RH	0,13	1,5	335
<i>S. cerevisiae</i> VU 8	0,22	1,4	375
<i>S. cerevisiae</i> VU 5	0,10	1,7	382
<i>S. cerevisiae</i> VU 6	0,18	1,6	345

Table 2. Content of reserve saccharides and fermenting activity in dough for common bakery goods of commercial yeast — production strain *S. cerevisiae* OOSF-RH

Yeast from Trenčín (calendar month)	Time after expedition	Glycogen	Trehalose	Fermenting activity (ml CO <sub>2</sub> /100 g of dough 90/min)
		(g/100 g of dry weight)		
Dried (february)	3 months	4,50	11,7	—
Pressed (February)	4 days	4,25	11,4	340
Pressed (July)	4 days	0,27	7,2	415

Table 3. Influence of carbon source on the content of reserve saccharides and fermenting activity in dough for common bakery goods in industrial yeast strains grown in semisynthetic medium

Strain	Carbon source (g/l)	Cultivation time (h)	Glycogen	Trehalose	Fermenting activity (ml CO <sub>2</sub> /100 g of dough/90 min)
			(g/100 g of dry weight)		
<i>S. cerevisiae</i> Fett D/80	glucose (5)	24	—	2,5	350
	glucose (100)	24	—	2,5	120
	maltose (20)	24	—	6,8	315
	sucrose (20)	24	—	5,4	290
<i>S. cerevisiae</i> OOSF-RH	glucose (20)	16	0,12	2,7	250
	maltose (20)	16	0,51	3,4	225
<i>S. cerevisiae</i> VU 6	glucose (20)	16	0,09	2,7	340
	maltose (20)	16	0,14	3,0	395

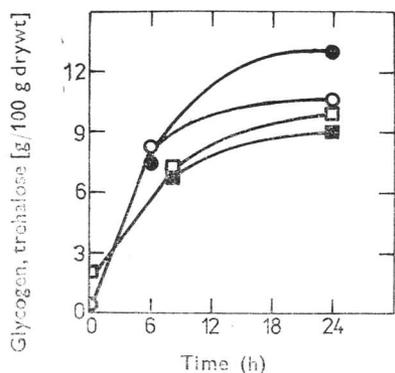


Figure 1. Accumulation of glycogen (○, ●) and trehalose (□, ■) in cells of the production strain *S. cerevisiae* OOSF-RH grown in semisynthetic medium with glucose (5 g/l) during incubation under non-growing conditions with the presence of glucose (10 g/l) (○, □) or maltose (●, ■).

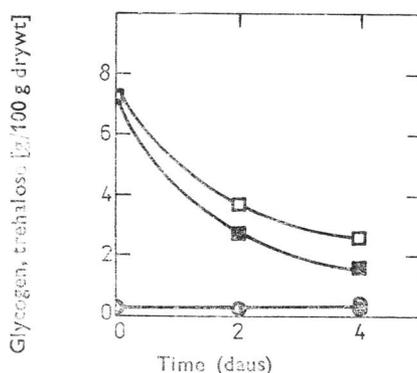


Figure 2. Degradation of glycogen (○, ●) and trehalose (□, ■) during yeast starvation in compact sample (○, □) and in suspension (●, ■).

The content of reserve saccharides of baker's yeast can be properly changed by the changes of external conditions. As seen from Figure 1, the cells of the production strain of Trenčín yeast plant, the yeast *S. cerevisiae* OOSF-RH incubated under non-growing conditions with the presence of carbon source were able to increase the content of their reserve saccharides several times. The accumulation kinetics of glycogen and trehalose under the above experimental conditions was not markedly dependent on the type of carbon-source, glucose or maltose. The maximum amount of trehalose accumulated during 24 hours represented approx. 10% of dry weight of cells and it corresponded to the trehalose content in the cells of commercial yeast. In glycogen accumulation the values measured after 24 hours represented almost 12% of dry weight of cells which are much higher values than those measured in the commercial baker's yeast. Under similar experimental conditions other strains of the yeast *S. cerevisiae* accumulated after 17 hours trehalose and glycogen in the quantities being 14% of dry weight in fortrehalose and 22% of dry weight, for glycogen [6].

There are considerable differences in the published data concerning the content of reserve saccharides in yeast [1—6]. For example, in the samples of yeast from 5 Czechoslovak yeast plants the difference stated in the content of trehalose is more than two-fold [30]. In the fresh pressed yeast from the national enterprise Labena in Krásne Březno the content of trehalose represented 9 %

of dry weight and the glycogen content was 10% of dry weight of yeast whereas after 4 days of starvation at 35°C and pH 5.5 their content dropped approx. to 1% of dry weight [31].

These results support the fact that the content of reserve saccharides of the cells is strongly dependent not only on the conditions of yeast cultivation but also on the conditions of their storage.

The literature includes the articles observing the changes of the level of reserve saccharides at the storage of baker's yeast in compact pressed yeast or in yeast suspension under the conditions which should accelerate the degradation processes [31—33]. In our experiments with the commercial yeast the course of changes in reserve saccharides was observed during starvation of cells in both variants, i. e. in pressed yeast at 30°C, as well as in the suspension of cells of pressed yeast in phosphate buffer solution with pH 6 at 30°C, incubated aerobically on shaker (Fig. 2, Fig. 3A).

It was found that the course of degradation of reserve saccharides is affected by the changes performed in yeast already during expedition. Thus, already at the beginning of the experiment the content of trehalose and especially glycogen was markedly lower in yeast samples from summer period (Fig. 2) than in samples from winter period (Fig. 3). The yeast incubation with the absence of exogenous nutrients, however, caused further decrease in the content of reserve saccharides of cells. The degradation speed of glycogen and trehalose was the highest in the first two days of starvation. In the pressed yeast the course of degradation was somewhat slower than in suspension which may be caused by easier transport of degradation substances in suspension. Degradation of glycogen and trehalose in cell suspension was, apart from aerobic conditions, observed also under anaerobic conditions under the presence of nitrogen. A significant difference in the rate or intensity of degradation processes was, however, not detected.

Fermenting activity in dough is one of the most important properties of baker's yeast. The study of its changes with respect to the content of glycogen and trehalose during starvation has shown that the cell starvation results in decrease of fermenting activity in dough regardless the fact whether the cells had a high or low content of reserve saccharides at the beginning (Fig. 3). The course of decrease of the fermenting activity in commercial yeast with a high content of reserve saccharides (Fig. 3A) was similar as the drop of fermenting activity in the cells of the same production strain of the yeast *S. cerevisiae* OOSF-RH grown on semisynthetic medium with maltose (20 g/l), though their content of glycogen and trehalose was low (Fig. 3B).

The results of our work suggest that the content of reserve saccharides in baker's yeast is quite dependent on cultivation conditions, whereas it can be raised to the values corresponding to more than 10% of dry weight of cells by

their incubation under non-growing conditions with the presence of carbon and energy source.

Fermenting activity of baker's yeast in dough for common bakery goods does not represent the function of the cell content of glycogen or trehalose. Though by starvation (storage) of yeast its content of reserve saccharides as well as the fermentating activity in dough decreases, still it seems that there does not exist a mutual causal relation among the changes of the above properties. It is also confirmed by fermenting activity in the cells of the production strain *S. cerevisiae* OOSF-RH grown into stationary stage of growth on semisynthetic medium with glucose (5 g/l) which, in spite of having the low content of trehalose and glycogen, was losing the fermenting activity in dough by starvation much slower than in the commercial yeast (Fig. 3C).

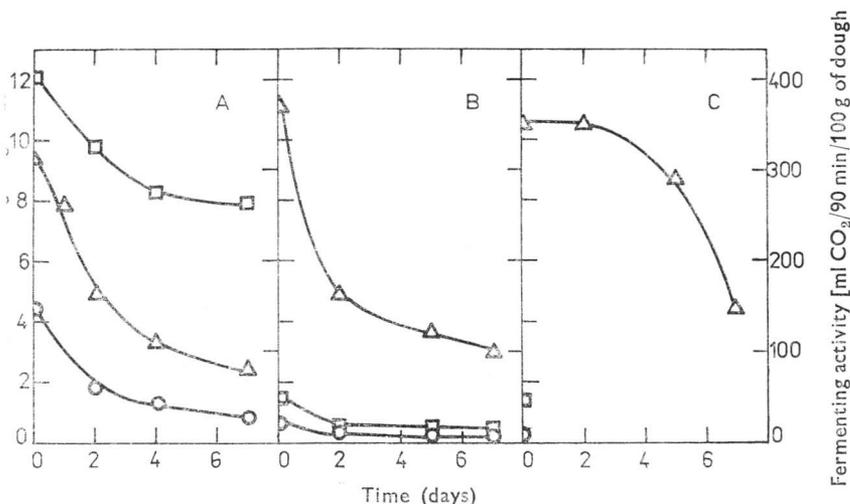


Figure 3. Changes in the content of glycogen (o), trehalose (□) and fermenting activity in dough for common bakery goods in the sucrose presence (Δ) during starvation of the cells of production strain of yeast *S. cerevisiae* OOSF-RH grown in yeast plant on molasses (A), in laboratory under aerobic conditions in semisynthetic medium with maltose (20 g/l) (B) or with glucose (5 g/l) (C).

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## Обмен веществ запасных сахаридов промышленных штаммов хлебопекарных дрожжей

### Резюме

Клетки многих промышленных штаммов дрожжей *Saccharomyces cerevisiae*, выросших в лабораторных условиях до стационарной фазы роста в полусинтетической среде с глюкозой, содержали значительно меньше гликогена и трегалозы, чем коммерческие дрожжи, производимые на дрожжевом заводе на базе одного из этих производственных штаммов. Клетки дрожжей с низким содержанием запасных сахаридов были способны в несколько раз повысить содержание гликогена и трегалозы после инкубации в течение нескольких часов в условиях вне роста в присутствии глюкозы или мальтозы. В отличие от аккумуляирования требовалось несколько дней для того, чтобы в клетках коммерческих дрожжей, подвергающихся инкубации в подобных условиях но без источника углерода, отчетливо понизилось содержание запасных сахаридов. Отчетливое снижение при данных условиях голодовки наблюдалось так же в бродильной активности в тесте, причем эта активность не была в причинной связи с общим содержанием гликогена и трегалозы хлебопекарных дрожжей.

## Metabolizmus zásobných sacharidov priemyselných kmeňov pekárskych kvasiniek

### Súhrn

Bunky viacerých priemyselných kmeňov kvasiniek *Saccharomyces cerevisiae* vyrastených laboratórne do stacionárnej fázy rastu v polosyntetickej pôde s glukózou mali podstatne nižší obsah glykogénu a trehalózy ako komerčné droždie vyprodukované v droždiarni na báze jedného z týchto produkčných kmeňov. Bunky kvasiniek s nízkym obsahom zásobných sacharidov mali schopnosť viacnásobne zvýšiť svoj obsah glykogénu i trehalózy ak sa inkubovali niekoľko hodín za nerastových podmienok v prítomnosti glukózy alebo maltózy. Na rozdiel od akumulácie viac dní bolo potrebných k tomu, aby sa v bunkách komerčného droždia inkubovaných za podobných podmienok ale bez zdroja uhlíka obsah zásobných sacharidov výrazne znížil. Výrazný pokles sa pozoroval za týchto podmienok hladovania aj v kvasnej aktivite v ceste, pričom táto aktivita nebola v príčinnej súvislosti s celkovým obsahom glykogénu ani trehalózy pekárskych kvasiniek.