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Phospho-β-glucosidases and β-Glucoside Permeases in *Streptococcus, Bacillus,* and *Staphylococcus*

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The presence of phospho-β-glucosidases and β-glucoside permeases was found in strains of *Streptococcus, Bacillus,* and *Staphylococcus.* In streptococci, the phospho-β-glucosidase activity depends on the antigenic group. The highest activity was found in strains of group D. In group D strains, phospho-β-glucosidase activity is induced by β-methyl glucoside and cellobiose but not by thiophenyl β-glucoside (TPG). With the exception of four strains isolated in Japan, all strains of *B. subtilis* tested possess an inducible phospho-β-glucosidase activity, β-methyl glucoside, cellobiose, and TPG acting as inducers. *S. aureus* strains possess phospho-β-glucosidase A but not phospho-β-glucosidase B, whereas most *S. albus* strains show no detectable phospho-β-glucosidase activity. The prompt fermentation of β-methyl glucoside by *S. aureus* strains could serve as an additional criterion for their differentiation from *S. albus.* A comparative investigation of the active uptake of ^{14}C-TPG showed that a *Streptococcus* group D strain and a *B. subtilis* strain possess two inducible permeases with characteristics similar to the β-glucoside permeases I and II of *Enterobacteriaceae.* In *S. aureus,* TPG is accumulated by a constitutive permease with high affinity for aromatic β-glucosides and glucose. The active uptake of TPG by *S. aureus* appears to depend on the activity of the phosphoenol pyruvate-dependent phosphotransferase system.

A study of strains belonging to several genera of *Enterobacteriaceae* (7, 8) indicated that β-glucosides are catabolized in a phosphorylated form by a system consisting of three permeases and two enzymes which hydrolyze only phosphorylated β-glucosides. It was found that the distribution and inducibility of individual elements of this system vary with the taxonomic group and could be of diagnostic significance. Studies on a wider range of bacteria could therefore be of interest from a biochemical and taxonomic point of view. β-Glucosides are fermented by a variety of gram-positive and gram-negative bacteria, but with the exception of *Enterobacteriaceae* there are no published data on their active uptake and only a few published reports on their enzymatic hydrolysis. The phosphorolysis of cellobiose by cellobiose phosphorylase has been reported for cellulolytic bacteria (1, 2), and the enzymatic hydrolysis of aromatic β-glucosides has been reported in *Mycoplasma* (3) and *Pseudomonas syringae* (9). To our knowledge there are no pertinent data for *Streptococcus, Bacillus,* and *Staphylococcus,* although strains of *Streptococcus* and *Bacillus* ferment β-glucosides (*Bergey's Manual of Determinative Bacteriology,* 7th ed.). By using a screening test similar to that employed for the detection of phospho-β-glucosidases in *Enterobacteriaceae,* an attempt was made to detect the presence of these enzymes in strains of the investigated gram-positive bacteria. The catabolism of β-glucosides in a phosphorylated form was found in strains of all three genera, and it appears that the hydrolysis of aromatic β-glucosides by phospho-β-glucosidases may be an important pathway for their utilization in *Eubacteriales.*

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MATERIALS AND METHODS

Strains. The present investigation includes 32 strains of *Streptococcus,* 28 strains of *Bacillus,* and 67 strains of *Staphylococcus.* The species and antigenic structures are indicated in the Results section. The strains were obtained from B. Beame, R. Gordon, M. McCarty, L. Mindich, R. Novick, M. Oichi, and from the collection of our Department.

Media. The strains were maintained on nutrient-agar slants, with the exception of *Streptococcus,* which was maintained on heart infusion-agar. The determination of enzymatic activity and active uptake was made with cells grown in LB broth (7). *Streptococcus* strains, with the exception of group D, were cultivated in LB broth with 0.3% glucose. The fermentation of

carbohydrates by strains of *Streptococcus* was tested in semisolid Thioglycollate Medium (Difco) with bromothymol blue as indicator. Fermentation by *Bacillus* was tested on semisynthetic agar plates (7) with 0.1% yeast extract and fermentation by *Staphylococcus* was tested in Phenol Red Broth (Difco) and on Phenol Red Agar. β-Methyl glucoside, cellobiose, salicin, and arbutin were used at a concentration of 0.5%.

Enzyme determinations. Screening for phospho-β-glucosidases was performed under the conditions described for *Enterobacteriaceae* (7). One unit of phospho-β-glucosidase activity corresponds to the liberation of 1 nmole of aglycone per min per mg (dry weight) of bacteria. The cultures to be used for the enzyme assay were incubated overnight at 35 C. The activity of representative strains from each group was also measured in logarithmic-phase cultures. The phosphotransferase of *Aerobacter aerogenes* was prepared as described previously (7). Extracts were prepared from cell suspensions equivalent to 50 mg (dry weight) in 0.05 M phosphate buffer (*p*H 7.3). Bacilli were subjected to two bursts of 30 sec each at 4 amp with a Branson Sonifier; streptococci and straphylococci were subjected to three 1-min bursts of sonic treatment. The activity of sonic extracts is expressed in nanomoles of aglycone per minute per milligram of protein.

Active uptake of ^{14}C-thiophenyl β-glucoside (TPG). The active uptake of ^{14}C-TPG was determined under conditions described previously (7, 8). Cells were grown in LB medium without inducer and with 2×10^{-2} M β-methyl glucoside, 2×10^{-2} M cellobiose, or 2×10^{-4} M TPG. At an optical density of 0.30 (560 nm, Coleman Junior spectrophotometer, 19-mm tubes), the cells were washed in 0.05 M phosphate buffer (*p*H 7.3) and suspended in the same buffer to a concentration of 0.5 mg (dry weight) of cells/ml. ^{14}C-TPG was added to a final concentration of 2×10^{-4} M (11,000 counts per min per ml). Nonradioactive phenyl β-glucoside, glucose, and lactose were added as indicated to a final concentration of 10^{-2} M.

RESULTS

A screening test similar to that employed for *Enterobacteriaceae* (7) was used for the detection of phospho-β-glucosidase activity in strains belonging to the genera *Streptococcus*, *Bacillus*, and *Staphylococcus*. The interpretation of the results is analogous to that proposed for *Enterobacteriaceae* and is based on the assumption of an overall similarity of the substrate specificity of β-glucoside permeases and phospho-β-glucosidases. As there are no published data on the active uptake of β-glucosides by gram-positive bacteria, the results of the screening test were compared with the results of active uptake experiments performed with representative strains of the three genera.

Streptococcus. Determination of the phospho-β-glucosidase activities of 32 *Streptococcus* strains belonging to the antigenic groups A, B, C, D, E, F, G, L, and M indicated pronounced differences among the different groups. The results obtained with several strains of the antigenic groups B and D indicated a relatively high degree of similarity among strains belonging to the same antigenic group.

Intact cells of the group B strains O90R and 436 showed no detectable hydrolysis of *p*-nitrophenyl β-glucoside (PNP-glu; Table 1). Addition of glucose-6-phosphate (G-6-P) and GL-Phosphotransferase from *A. aerogenes* reveals the presence of a low cryptic phospho-β-glucosidase activity, which increases after growth in the presence of β-methyl glucoside and TPG. The two strains differ in their cryptic phospho-β-glucosidase B activity. Two additional strains of group B also showed a low cryptic phospho-β-glucosidase activity with no detectable hydrolysis of PNP-glu by intact cells. In contrast to the strains of group B, intact cells of the two group D strains, D 76 and C 1, showed a semiconstitutive hydrolysis of PNP-glu and salicin which is induced by β-methyl glucoside and cellobiose but not by TPG. Toluene treatment reduced the activity found in intact cells. The activity of toluenized cells increased upon addition of G-6-P and increased further after addition of G-6-P and GL-phosphotransferase. The hydrolysis of phosphorylated salicin paralleled the hydrolysis of phosphorylated PNP-glu. Three additional strains of group D showed an induction pattern similar to that of strains D76 and C1.

Active uptake experiments showed that uninduced cells of the group B strain O90R accumulate only 0.9 μmole of ^{14}C-TPG/g and also have a low affinity for phenyl β-glucoside and cellobiose. The accumulation of TPG did not increase after growth in the presence of β-methyl glucoside, cellobiose, and TPG. The low accumulation of TPG was consistent with the lack of phospho-β-glucosidase activity of intact cells of this strain. The uptake of ^{14}C-TPG by the group D strain D76 is illustrated in Fig. 1. The active uptake by uninduced cells and cells grown in the presence of TPG was similar, reflecting the lack of inducer activity of TPG for the hydrolysis of PNP-glu by intact cells. In both instances there was an initial peak in the accumulation of TPG. The addition of glucose and especially of cellobiose increased the accumulation of TPG whereas the addition of phenyl β-glucoside and lactose had no detectable effect. Induction by β-methyl glucoside produced an increase of only 30% in the accumulation of TPG. Cells grown in the presence of β-methyl glucoside differ from uninduced cells by a higher accumulation of TPG after addition of glucose and by the chasing of TPG by phenyl β-glucoside.

The permease activity induced by β-methyl glucoside resembles in this respect the β-glucoside permease I of *Enterobacteriaceae* (6, 7). The permease induced by cellobiose is characterized by a lack of the initial peak in the accumulation of TPG and chasing of TPG by phenyl β-glucoside, cellobiose, glucose, and to a lesser extent by lactose. By its affinity for both phenyl β-glucoside and cellobiose the permease induced in strain D76 by growth in the presence of cellobiose resembles the β-glucoside permease II of *Enterobacteriaceae* (7, 8).

The measurement of phospho-β-glucosidase activity of streptococci of other antigenic groups showed a lack of detectable activity in strains belonging to the antigenic groups A, L, and M and a low constitutive or semiconstitutive activity in strains belonging to groups C, E, and F. Among two strains of group G, one showed a low constitutive activity (3 units of PNP-glu/ml), and the other showed a high semiconstitutive activity (23 units PNP-glu/mg) which was further increased by growth in the presence of TPG. Two strains of group N showed a high semiconstitutive activity which increased by growth in the presence of β-methyl glucoside and cellobiose.

Bacillus. The present investigation includes 24 strains of *B. subtilis*, two strains of *B. cereus*, one strain of *B. megatherium*, and one strain of *B. licheniformis*. All *Bacillus* strains tested possess a semiconstitutive phospho-β-glucosidase activity. This activity is sensitive to toluene treatment and cannot be restored by addition of G-6-P. The addition of G-6-P and GL-phosphotransferase

TABLE 1. *Phospho-β-glucosidase activity of Streptococcus, Bacillus, and Staphylococcus strains*[a]

Organism	Inducer	Intact cells: PNP-glu[b]	Toluenized cells[c]			
			PNP-glu	PNP-glu + G-6-P	PNP-glu + G-6-P and phospho-transferase	Salicin + G-6-P and phospho-transferase
Streptococcus group B, O90R	None				2	3
	β-Methyl				9	3
	Cellob				2	4
	TPG				8	5
Streptococcus group B, 436	None				2	
	β-Methyl				3	
	Cellob				2	
	TPG				4	2
Streptococcus group D, D76	None	39	2	8	31	21
	β-Methyl	189	15	53	110	129
	Cellob	89	3	41	62	47
	TPG	47	2	7	32	27
Streptococcus group D, C1	None	28	2	4	34	15
	β-Methyl	201	56	102	118	109
	Cellob	121	31	52	84	51
	TPG	30	3	5	54	29
B. subtilis W23	None	5			40	12
	β-Methyl	29			47	51
	Cellob	15			62	14
	TPG	17			51	43
B. subtilis IAM 1212	None	7			17	2
	β-Methyl	8			20	2
	Cellob	12			29	3
	TPG	8			19	2
S. aureus 560	None	3	2		3	
	β-Methyl	5	2	2	6	
	Cellob	3		2	4	
	TPG	3		2	4	

[a] Phospho-β-glucosidase activity was tested with overnight cultures in LB medium, washed with 0.05 M phosphate buffer (*p*H 7.3), and suspended in 1.5 ml of phosphate buffer. Activity is expressed in nanomoles per minute per milligram (dry weight) of cells. Incubation was for 20 min at 35 C. β-Methyl, β-methyl glucoside; Cellob, cellobiose.

[b] Suspension of 0.2 ml of intact cells.

[c] Suspension of 0.2 ml of toluene-treated cells.

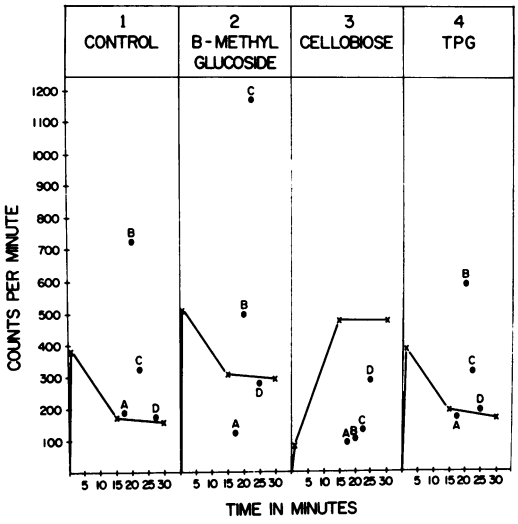

FIG. 1. *Uptake of ^{14}C-TPG by Streptococcus D-76. TPG was added at a final concentration of 2 × 10^{-4} M (11,000 counts/min) to a washed cell suspension of 0.5 mg (dry weight)/ml in 0.05 M phosphate buffer (pH 7.3). After the determination of the active uptake at 0 time, the suspension was divided into samples of 0.9 ml which were introduced into tubes containing 0.1 ml of water (controls) and tubes containing 0.1 ml of the nonradioactive compounds. Final concentration of the nonradioactive compounds, 10^{-2} M. The suspensions were incubated by shaking at 28 C, collected on 0.45-μm filters (Millipore) at the time intervals indicated in the graph, and washed with 4 ml of cold phosphate buffer. (1) LB medium without inducer; (2) LB medium with 2 × 10^{-2} M β-methyl glucoside; (3) LB medium with 2 × 10^{-2} M cellobiose; (4) LB medium with 2 × 10^{-4} M TPG. Symbols: ×, ^{14}C-TPG; A, ^{14}C-TPG + ^{12}C-phenyl β-glucoside; B, ^{14}C-TPG + ^{12}C-cellobiose; C, ^{14}C-TPG + ^{12}C-glucose; D, ^{14}C-TPG + ^{12}C-lactose.*

resulted in an activity which in most instances was higher than the activity found with intact cells. Similar results were also obtained with sonic extracts of four *B. subtilis* strains. The data obtained with two *B. subtilis* strains are shown in Table 1.

Intact cells of strain W23 hydrolyze PNP-glu semiconstitutively, but not after toluene treatment. The hydrolysis of PNP-glu by intact cells was induced by β-methyl glucoside, cellobiose, and TPG. The hydrolysis of salicin by intact cells paralleled that of PNP-glu. After addition of G-6-P and GL-phosphotransferase, the activity of toluenized cells became higher than that of intact cells. The hydrolysis of phosphorylated PNP-glu was induced by β-methyl glucoside, TPG, and to a higher degree by cellobiose, whereas the hydrolysis of phosphorylated salicin was induced by β-methyl glucoside and TPG but not by cellobiose. This difference in inducibility appears to indicate the presence of two distinct phospho-β-glucosidases. Logarithmic phase cells showed a similar induction pattern to that of overnight cultures; their basal activity, however, was approximatley three times higher. In contrast to strain W23, intact cells of strain IAM 1212 showed only a slight increase in activity after growth in the presence of cellobiose, and the rate of hydrolysis of salicin by intact and toluenized cells was very low. Among the *B. subtilis* strains, 20 strains showed the same induction pattern as strain W23 and four strains were similar to strain IAM 1212. All four strains with low phospho-β-glucosidase B activity were from a group of six strains isolated in Japan and received through the courtesy of M. Oichi Two strains of this group are similar to strain W23. Deoxyribonucleic acid isolated from strains with low phospho-β-glucosidase B activity has transforming activity for *B. subtilis* (M. Oichi, *personal communication*).

Determination of the accumulation of ^{14}C-TPG by strain W23 (Table 2) showed a maximal accumulation by uninduced cells of 4.8 μmoles/g. The maximal accumulation by uninduced cells was reached after an incubation of 30 min at 28 C. TPG was chased by phenyl β-glucoside and to a lesser extent by glucose. Growth in the presence of β-methyl glucoside increased the accumulation of TPG to 7.1 μmoles/g, whereas growth in the presence of TPG resulted in an accumulation of 13.9 μmoles/g. In both instances there was an initial peak in the accumulation of TPG, glucose increased the accumulation of TPG, and there was an increase in the affinity for phenyl β-glucoside. Cellobiose and lactose had no detectable effect on the accumulation of TPG. Growth in the presence of cellobiose did not produce an increase in the accumulation of TPG as compared with uninduced cells; however, in contrast to uninduced cells, TPG was chased by both phenyl β-glucoside and cellobiose. It appears, therefore, that β-methyl glucoside and TPG induce β-glucoside permease I and cellobiose induces β-glucoside permease II. Uninduced cells of strains IAM 1212 showed a maximal accumulation of 2.4 μmoles of TPG per g, with low affinity for phenyl β-glucoside, cellobiose, and glucose and no detectable affinity for lactose. The maximal accumulation of TPG occurred after an incubation of 30 min. Growth in the presence of β-methyl glucoside, cellobiose, and TPG had no detectable effect on the accumulation of TPG. This is consistent with the lack of induction of the hydrolysis of PNP-glu by intact cells.

Staphylococcus. The present study includes 19 coagulase-positive *S. aureus* strains and 48 coagu-

lase-negative *S. albus* strains; 42 of the latter were isolated from nutrient-agar plates exposed to the air. All *S. aureus* strains tested showed a relatively low constitutive or semiconstitutive hydrolysis of PNP-glu, with activities varying between 2 and 6 units/mg (dry weight). A common trait of all *S. aureus* strains is the inability to hydrolyze salicin (Table 1). Toluene treatment reduced the activity found in intact cells. The phospho-β-glucosidase activity is restored at different degrees, depending on the strain, by addition of G-6-P and G-6-P with GL-phosphotransferase. Efficient inactivation requires, for most strains, cell suspensions of 1 mg (dry weight) or less and toluene treatment for at least 30 min at 35 C. Sonic treatment was also less efficient than that observed with *Enterobacteriaceae*, *Streptococcus*, and *Bacillus*. In contrast to the *S. aureus* strains, only three of the *S. albus* strains showed a weak phospho-β-glucosidase A activity. The remaining 45 strains showed no detectable activity. This was reflected in the prompt fermentation of β-methyl glucoside by all *S. aureus* strains, whereas only four *S. albus* strains showed a delayed fermentation of β-methyl glucoside. Salicin, arbutin, and cellobiose were not fermented by the *S. aureus* and *S. albus* strains.

Two *S. albus* strains showed a maximal accumulation of 1.7 and 1.9 μmoles of TPG per g, which did not increase after growth in the presence of β-methyl glucoside, cellobiose, and TPG. The accumulation of ^{14}C-TPG by the *S. aureus* strains 560, 3811, 480 and 147BW showed the following features. The accumulation of TPG by uninduced cells varies between 7.9 μmoles/g for strain 560 and 22.4 μmoles/g for strain 147BW. The maximal accumulation occurs after an incubation of at least 30 min at 28 C. Depending on the strain phenyl β-glucoside chases 63 to 72% of the label and glucose chases 68 to 81%; cellobiose and lactose have no detectable effect (Table 2). Among inducers tested, only TPG produces a slight increase in the accumulation of TPG by strains 560 and 147BW, but not with the other strains. Growth in the presence of TPG does not affect the shape of the accumulation curve or the affinity to nonradioactive compounds tested. Because of the availability in *S. aureus* of mutants lacking components of the PEP-dependent phosphotransferase system (5), we decided to investigate whether, as found in *E. coli* and *A. aerogenes*, phosphorylation by the PEP-dependent phosphotransferase system is required for the accumulation of aromatic β-glucosides. Strain 700 A, received from M. Morse, is a pleiotrophic carbohydrate-negative mutant which lacks enzyme I of the PEP-dependent phosphotransferase system. We found that this mutant is also unable to ferment β-methyl glucoside and shows no detectable hydrolysis of PNP-glu. Strain 700 A showed a maximal accumulation of only 1.7 μmoles of TPG per g. Two carbohydrate-positive revertants of this strain, selected for the fermentation of lactose, accumulated 6.3 and 7.1 μmoles of TPG per g and had a phospho-β-glucosidase activity of 3 and 4 units/mg with PNP-glu as substrate. It appears, therefore, that as previously found in *Enterobacteriaceae* the activity of the PEP-dependent phosphotransferase system is required for the active uptake of β-glucosides by *S. aureus*.

TABLE 2. *Accumulation of ^{14}C-TPG by Streptococcus group D, Bacillus subtilis, Staphylococcus aureus, and Aerobacter aerogenes*[a]

Organism	Inducer[b]	Initial peak	Accumulation of TPG in the presence of:			
			Phenyl β-glucoside	Cellobiose	Glucose	Lactose
Streptococcus D76	None	+	105	403	187	97
	β-Methyl	+	40	162	365	95
	Cellob	−	21	23	29	59
	TPG	+	103	285	157	103
B. subtilis W23	None	−	58	105	67	109
	β-Methyl	+	38	102	155	98
	Cellob	−	52	58	53	96
	TPG	+	24	109	172	106
S. aureus	None	−	35	107	26	98
	β-Methyl	−	33	103	25	106
	Cellob	−	31	109	23	95
	TPG	−	34	97	22	97
A. aerogenes	None	−	75	108	78	91
	β-Methyl	+	28	105	141	96
	Cellob	−	33	21	43	97
	TPG	+	26	96	161	102

[a] The accumulation of ^{14}C-TPG after addition of nonradioactive phenyl β-glucoside, cellobiose, glucose, and lactose is expressed as per cent of the average value of the uptake of TPG alone at 15 and 30 min, which is considered as 100. The maximal difference between the internal concentrations of TPG at 15 and 30 min is 19% for *S. aureus* and between 8 and 15% for the other organisms. Experimental conditions were the same as for Fig. 1.

[b] β-Methyl, β-methyl glucoside; Cellob, cellobiose.

DISCUSSION

As in the *Enterobacteriaceae*, we have found that aromatic β-glucosides are catabolized in a phosphorylated form by strains of *Streptococcus*, *Bacillus* and *Staphylococcus*. It appears, therefore, that the phospho β-glucosidase system is a

major catabolic system for the utilization of β-glucosides by bacteria. In fungi, yeasts, higher plants, and animals, the main mechanism appears to be the hydrolysis of nonphosphorylated aromatic β-glucosides into glucose and aglycone, and to our knowledge no catabolic system similar to the β-glucoside system has been described in these organisms. As found in *Enterobacteriaceae*, the presence of the complete system in some taxonomic groups, and of only parts of the system in others, as well as differences in inducibility, could be used for purposes of differentiation. For gram-positive bacteria the catabolism of β-glucosides could be used as an additional criterion for the differentiation of *S. aureus* from *S. albus* and of some antigenic groups of *Streptococci*. Studies with additional strains are required for the determination of a possible correlation between the phospho-β-glucosidase B and permease activity of *B. subtilis* strains and their geographical distribution.

Similarities as well as differences in permease activity appear to make the β-glucoside system a useful object for comparative studies on active uptake. The intracellular concentration of β-glucosides is the result of an active entry reaction which can be considered as the trapping of β-glucosides in a phosphorylated form and an exit reaction of still unknown nature. The comparison of the absolute level of the accumulation of TPG by induced and uninduced cells is therefore only of limited value. The characterization of the active uptake of β-glucosides requires the introduction of additional criteria (6, 7) such as K_m value, temperature optimum, shape of the accumulation curve, effect of dinitrophenol and azide, and the chasing by nonradioactive carbohydrates. Among the additional criteria employed in the present investigation, the initial peak of the accumulation of TPG observed after induction of β-glucoside permease I reflects probably the difference in the initial velocity of the entry and exit reaction. The decrease of the accumulation of ^{14}C-TPG after addition of nonradioactive carbohydrates could be explained by the competition of these compounds for the entry reaction. The increase in the accumulation of TPG after the addition of glucose and cellobiose is more difficult to explain. It could result from competition for the exit reaction, as proposed by Hoffe, Englesberg, and Lamy (4) for the glucose permease.

A comparison of the active uptake of TPG by strains of *A. aerogenes*, *Streptococcus* group D, *B. subtilis*, and *S. aureus* is made in Table 2. With the exception of *Streptococcus*, uninduced cells show no initial peak in the accumulation of TPG, and the labeled compound is chased, at different degrees, by phenyl β-glucoside and glucose. Uninduced cells of the *Streptococcus* strain differ from uninduced cells of the above strains by the initial peak in the accumulation of TPG and an increase in the accumulation of TPG after addition of cellobiose and glucose. TPG and β-methyl glucoside in *A. aerogenes* and *B. subtilis* and only β-methyl glucoside in *Streptococcus* group D induce a permease with high affinity for aromatic β-glucosides but not for cellobiose. Common elements of this permease activity are an initial peak in the accumulation of TPG, chasing of TPG by phenyl β-glucoside, and an increase in the accumulation of TPG after addition of glucose. The degree of this increase in accumulation depends on the strain, but only in *Streptococcus* does the accumulation of TPG also increase after the addition of cellobiose. In the same bacteria, cellobiose induces a permease with high affinity for phenyl-β-glucoside, cellobiose, and glucose. The above data seem to indicate that, although there are individual differences in their characteristics, all three organisms possess inducible permeases which can be classified as β-glucoside permeases I and II. The active uptake of TPG by *S. aureus* shows several distinct characteristics. The permease found in uninduced cells has a high affinity for phenyl β-glucoside, comparable to that of induced cells of the other genera, and also a high affinity for glucose. Induction by TPG produces a slight increase in the active uptake of TPG but, unlike the other genera, the chasing by glucose remains unaffected. The relatively high accumulation of TPG by uninduced cells and the low phospho-β-glucosidase activity could suggest another primary function of the β-glucoside permease in *S. aureus*, possibly as a glucose permease.

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