Biosynthesis of Bacterial Glycogen: Primary Structure of *Salmonella typhimurium* ADPglucose Synthetase as Deduced from the Nucleotide Sequence of the *glgC* Gene

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The nucleotide sequence of a 1.4-kilobase-pair fragment containing the *Salmonella typhimurium* LT2 *glgC* gene coding for ADPglucose synthetase was determined. The *glgC* structural gene contains 1,293 base pairs, having a coding capacity of 431 amino acids. The amino acid sequence deduced from the nucleotide sequence shows that the molecular weight of ADPglucose synthetase is 45,580. Previous results of the total amino acid composition analysis and amino acid sequencing (M. Lehmann and J. Preiss, J. Bacteriol. 143:120-127, 1980) of the first 27 amino acids from the N terminus agree with that deduced from nucleotide sequencing data. Comparison of the *Escherichia coli* K-12 and *S. typhimurium* LT2 ADPglucose synthetase shows that there is 80% homology in their nucleotide sequence and 90% homology in their deduced amino acid sequence. Moreover, the amino acid residues of the putative allosteric sites for the physiological activator fructose bisphosphate (amino acid residue 39) and inhibitor AMP (amino acid residue 114) are identical between the two enzymes. There is also extensive homology in the putative ADPglucose binding site. In both *E. coli* K-12 and *S. typhimurium* LT2, the first base of the translational start ATG of *glgA* overlaps with the third base TAA stop codon of the *glgC* gene.

ADPglucose synthetase (EC 2.7.7.27) is an allosteric enzyme in the glycogen biosynthetic pathway of eubacteria (23, 24). Among the enteric bacteria, ADPglucose synthetase is activated by glycolytic intermediates with fructose 1,6-bisphosphate as the activator and AMP, ADP, and P_i as inhibitors (23). The enzyme catalyzes the synthesis of ADP glucose from glucose 1-phosphate and ATP in the reaction glucose 1-phosphate + ATP ⇄ ADPglucose + P_i. This reaction is the first unique step in bacterial glycogen biosynthesis.

In *Escherichia coli*, the structural genes for ADPglucose synthetase (*glgC*), glycogen synthase (*glgA*), and branching enzyme (*glgB*) are flanked by the *asd* (aspartic semialdehyde dehydrogenase) and *glpD* (glycerol phosphate dehydrogenase) genes (1). Okita et al. (20) have cloned the structural genes of *Salmonella typhimurium* genes *glgC* and *glgB* from a genomic library of *E. coli* K-12 into the *PstI* site of pBR322, and the nucleotide sequences of the *glgC* (2), *glgB* (3), and *glgA* (10) have been determined. *Salmonella typhimurium*, being closely related to *E. coli*, shows a lot of similarities in glycogen biosynthesis (12). The ADPglucose synthetases of *E. coli* and *S. typhimurium* are similar in that (i) they have similar subunit and native molecular weights; (ii) they have the same spectrum of activators and inhibitors; (iii) they have immunological cross-reactivity; (iv) the first 27 amino acids of the N terminus 25 are identical; (e) genetically, the *glg* genes of both are clustered around 75 units on their genetic maps and are cotransducible with *asd* and *glpD* genes (28). Recently, we have cloned the *glgC* and *glgA* genes from *S. typhimurium* (14). This paper is a report of the nucleotide sequence, the deduced amino acid sequence, and codon usage pattern of ADPglucose synthetase from *S. typhimurium*. Its deduced amino acid sequence and amino acid composition are compared with those of *E. coli* ADPglucose synthetase.

**MATERIALS AND METHODS**

**Bacteria, phage strains, and plasmids.** The bacteria, phage strains, and plasmids used in this study are as follows: *E. coli* K-12 JM101 [supE thi Δ(lac-proAB) F' traD36 proAB lacIq ΔM15], *E. coli* K-12 JM103 [supE thi Δ(lac-proAB) strA endA sbcA hsdR F' traD36 proAB lacIq ΔM15]; bacteriophages M13 mp8, 9, 10, and 11 (17); and plasmid pPL301, which contains the *S. typhimurium* *glgC* and *glgA* genes on a 5.8-kilobase-pair insert on the *SalI* site of pBR322 (14).

**Media, commercial enzymes, and chemicals.** Luria broth, YT medium, and YT soft agar were prepared as described previously (14, 18). Ampicillin was added at 25 μg/ml (final concentration) for the maintenance of plasmid pPL301.

**Restriction endonucleases Clal, Ddel, HindIII, HinfI, PstI, and PvuII** are from Bethesda Research Laboratories, Inc., as were T4 DNA ligase and the large fragment of DNA polymerase I. T4 polynucleotide kinase was from Pharmacia Fine Chemicals and P-L Biochemicals, Inc., calf intestine alkaline phosphatase was from Boehringer Mannheim Corp., and restriction enzyme *BsHII* was from New England Biolabs. All enzymes were used as recommended by the manufacturers.

**Isopropyl-β-D-thiogalactopyranoside** was from Sigma Chemical Co., and 5-bromo-4-chloro-3-indolygalactoside was from Bethesda Research Laboratories, Inc. Radioactive nucleotides [γ-32P]ATP (>5,000 Ci/μmol) and [α-32P]dTATP (>800 Ci/μmol) were from Amersham Corp.

**DNA sequencing.** DNA fragments containing the *S. typhimurium* *glgC* gene were purified from plasmid pPL301 (14) as described previously (2). DNA sequencing was done by...
FIG. 1. DNA sequencing strategy of the S. typhimurium LT2 glgC gene. Restriction endonucleases cleavage sites are represented by short vertical arrows on a thin line. The arrows beneath the line indicate the direction and extent of the sequence. The physical locations of glgC and glgA genes are represented in the box.

FIG. 2. Complete nucleotide sequence of the antisense strand and deduced amino acid sequence of the S. typhimurium glgC gene. The DNA sequence was determined from a 1.4-kilobase pair fragment of pPL301 as described in Materials and Methods. The box indicates the potential ribosome binding site. The deduced amino acid sequence of the glgC structural protein is shown below the DNA sequence. ** indicates the end of the glgC structural protein. The ATG start codon of the glgA structural protein is underlined.

RESULTS AND DISCUSSION

Nucleotide sequence of S. typhimurium glgC gene. The nucleotide sequence of a 1.4-kilobase-pair fragment containing the structural gene of S. typhimurium ADPglucose synthetase was determined. The sequencing strategy is shown in Fig. 1. More than 90% of the sequence was determined by the method of Maxam and Gilbert (17), and about 40% was determined by the method of Sanger et al. (26), allowing sequencing of both the sense and antisense strands with considerable overlapping. The fragments that were cloned into M13 phages for sequencing were PvuII-PstI (cloned into M13 mp11), PvuII-HindIII (cloned into M13 mp10), HindIII-PstI (cloned into M13 mp8 and mp9), and PstI-Sall (cloned into M13 mp8). The complete nucleotide sequence of the S. typhimurium glgC structural gene is shown in Fig. 2. It contains 1,293 base pairs and has the coding capacity for a protein of 431 amino acids. The calculated molecular weight of the method of Maxam and Gilbert (17) and the method of Sanger et al. (26), and the sequencing strategy is shown in Fig. 1. DNA fragments were cloned into M13 mp8 phases as described by Messing (18).

610 620 630 640 650 660

TTT GCG AAA GCG GGC CTA CCT CCA CAG CGG CGC AGT

Phe Val Glu Leu Pro Ala Pro Pro Met Leu Gly Asp Asp Lys Leu Ala Ser

670 680 690 700 710 720

ATG GGC ATT TCC GTG TGC AAC GCC AAC TAT CGT TAC CTA GAA

Met Glu Tyr Leu Leu Pro Asp Tyr Leu Tyr Glu Leu Ala Asp Asp Lys

730 740 750 760 770 780

GAT GGC ATT TCC GTG TGC AAC GCC AAC TAT CGT TAC CTA GAA

Asp Asp Leu Ser His Tyr Glu Leu Ala Pro Asp Asp Lys

790 800 810 820 830 840

GAT GGC ATT TCC GTG TGC AAC GCC AAC TAT CGT TAC CTA GAA

Asp Leu Tyr Ala His Pro Pro Pro Leu Ser Asp Pro Glu Glu Pro

850 860 870 880 890 900

TAC CCG CAT GTA GCT CGG CGA GGC ATT GCC TGG TYR

Tyr Try Arg Val Tyr Glu Leu Ala Tyr Tyr Lys Asn Asp Arg

910 920 930 940 950 960

GTC GGC CTC CGA CAG GTC AGG TTA CTA GAA

Val Val Gly Leu Leu Pro Met Tyr Asp Tyr Ala GAA

970 980 990 1000 1010 1020

CAG CGG CCG AAG CAC CGT CAT GAT GGC GAT CCC GGC

Asn Arg Arg Asp Asp Ala Pro Ala Thr Glu

1030 1040 1050 1060 1070 1080

TAC GGC TGC AGA GGC AGT TGC GGC CGG TGC

Val Thr Pro Glu Leu Thr Asp Tyr Gln Glu

1090 1100 1110 1120 1130 1140

CAG CCG CGA CCC CCC GCC CCC CCG CCC CCG CCG CCG

Val Arg Arg Leu Ser Ser Ser Ser Ser Ser Ser Ser

1150 1160 1170 1180 1190 1200

GAT GGC ATT TGG TGG GAT GGC ATT GCC TGG TRY

Asp Glu Arg Cys Arg Leu Arg Cys Tyr Glu

1210 1220 1230 1240 1250 1260

GAT GGC ATT TGG TGG GAT GGC ATT GCC TGG TRY

Asp Glu Arg Cys Arg Leu Arg Cys Tyr Glu

1270 1280 1290 1300 1310 1320

GAT ATT GTA GCT GTA GCT GTA GCT GTA GCT GTA GCT

Asp Asp Tyr Tyr Tyr Tyr Tyr Tyr Tyr Tyr

1330 1340 1350 1360 1370 1380

TA ATT GTA GCT GTA GCT GTA GCT GTA GCT GTA GCT

Asp Asp Tyr Tyr Tyr Tyr Tyr Tyr Tyr Tyr

1390 1400 1410

GAT GTC ATA GCG TGC CCT CGG CAG

Asp Val Ile Glu Ala Pro Ala Arg
of the glgC gene product is 45,580 and is in accordance to the value of 48,000 reported by Lehmann and Preiss (12).

The amino acid sequence of ADPglucose synthetase was deduced from the nucleotide sequence data (Fig. 2). Previous results of amino acid sequencing of the first 27 amino acids from the N-terminus agree with predictions from nucleotide sequencing data. The total amino acid composition determined from the deduced amino acid sequence (Table 1) is in accordance with the total amino acid composition data determined by acid hydrolysis and reported by Lehmann and Preiss (12). Most of the deduced values are within 1 to 2 standard deviations or identical to the observed value. The only striking difference is with serine, where there can be an overestimation in amino acid analysis data. Of the 431 amino acids of ADPglucose synthetase, 15.1% are basic amino acids, 12.8% are acidic amino acids, 28.5% are polar uncharged amino acids, and 43.6% are nonpolar amino acids.

Nucleotide sequence analysis. There is a potential Shine-Dalgarno sequence (27) of AGGAG at 11 bases upstream from the translational start site of glgC. Deduced amino acid sequence data, which agree with the C-terminal analysis of the S. typhimurium ADPglucose synthetase (11) and the N-terminal amino acid sequence data of the E. coli glycosyl synthase (6), indicate that the translational start of glgA follows immediately after the glgC translational stop support the genetic mapping results reported by Steiner and Preiss (28).

The G+C content of the S. typhimurium glgC gene is 52% and is in accordance with the average value of G+C content of 50 to 53% of the enteric bacteria and the average value of G+C value of 52% of the total S. typhimurium genome reported by Normore and Brown (19).

Codon usage. The codon usage of the S. typhimurium glgC gene is shown in Table 2. The codon usage is not random. There are preferences of GTG over CTA, TGT over CCA, GAA over ACT, ACC, and ACA for threonine; CCG over CCT, CCC, and CCA for proline, AAA over AAG for lysine; CAG overCAA for glutamine; GAA over GAG for glutamic acid; and GCC and GCG over GCT and GCA for alanine. Pyrimidine nucleotides are preferred at the wobble position of isoleucine, arginine, and glycine; G is preferred at the wobble position of leucine, valine, threonine, and glutamine; and G and C are preferred at the wobble position of valine and alanine. Besides, for isoleucine ATA is used only once, whereas ATT and ATC are used at approximately the same frequency. Similar codon usage pattern have been reported in the araB, araA, and araC genes of S. typhimurium LT2 (15, 16). Grogan and Fiers (4) suggested a general rule of codon usage in frequently expressed genes and rarely expressed genes in E. coli. It is correlated with the abundance of transfer RNA species and the occurrence of the respective codons in the structural genes (7, 8).

Interestingly, codons that were used only once, CGG for arginine, AGA for arginine, and ATA for isoleucine, are all clustered in amino acids residues 353 to 356. Moreover, CTC for isoleucine, which is used only twice, is at amino acid residue 350. The clustering of these rarely used codons around a certain area of the protein may serve to regulate the expression of the protein at the translational level. The relative abundance of these tRNA species may reflect the metabolic condition of the cell and hence may be a signal governing the expression of the protein.

Comparison of nucleotide sequences and deduced amino acid sequences of S. typhimurium and E. coli glgC genes. There is 80% homology in nucleotide sequence between E. coli and S. typhimurium glgC genes, showing that they have very similar codon usage. Moreover, it is interesting to note that in both bacteria the first base of the translational start of glgA (ATG) overlaps with the third base of the translational stop (TAA) of glgC (Fig. 2).

The deduced amino acid sequences of the S. typhimurium and E. coli glgC genes are compared in Fig. 3. There is 90% homology in their deduced amino acid sequence, and most of the changes are conservative. Of 45 differences in their amino acid sequences, 16 involve only one base change, 25 involve two base changes, and only 4 of them involve three base changes. Lehmann and Preiss (12) reported that ADPglucose synthetases from E. coli and S. typhimurium differ in their first 27 amino acid residues in the N terminus at residues 9 and 10. There was some uncertainty about residue 17 because gas chromatography and thin-layer chromatography indicated that it is glutamic acid, whereas back-hydrolysis of the phenylthiohydantoin derivative showed that it may be glutamic acid or proline (12). Our results from nucleotide sequencing showed that amino acid residue 17 is proline in the S. typhimurium enzyme. The two differences in amino acid residues 9 and 10 among ADPglucose synthetase are histidine in E. coli to arginine in S. typhimurium at

\[ \begin{array}{|c|c|c|}
\hline
\text{Amino acid} & \text{E. coli (deduced from DNA sequence)} & \text{S. typhimurium} \\
\hline
\text{Arg} & 32 & 31.6 ± 1.7 \\
\text{Lys} & 20 & 21.3 ± 1.7 \\
\text{His} & 10 & 8.2 ± 0.1 \\
\text{Cys} & 9 & 10.4 \\
\text{Asp} & 29 & 45.2 ± 3.3b \\
\text{Asn} & 19 & 13 \\
\text{Glu} & 29 & 43.6 ± 2.6c \\
\text{Gln} & 13 & 17 \\
\text{Thr} & 13 & 15.5 ± 0.4 \\
\text{Ser} & 30 & 39.4 ± 1.1 \\
\text{Pro} & 21 & 19.6 ± 0.6 \\
\text{Gly} & 27 & 31.0 ± 1.6 \\
\text{Ala} & 29 & 37.1 ± 2.7 \\
\text{Val} & 35 & 34.0 ± 1.5 \\
\text{Met} & 14 & 12.3 ± 0.7 \\
\text{Ile} & 24 & 26.3 ± 0.4 \\
\text{Leu} & 37 & 35.9 ± 1.6 \\
\text{Tyr} & 15 & 15.1 ± 0.9 \\
\text{Phe} & 15 & 13.2 ± 0.3 \\
\text{Trp} & 6 & 5.6 ± 0.3 \\
\hline
\end{array} 
\]

\* Determined in reference 12.
\* Number of Asp and Asn residues.
\* Number of Gln and Glu residues.

\( \begin{array}{|c|c|}
\hline
\text{Amino acid} & \text{Deduced from DNA sequence} \\
\hline
\text{Arg} & 32 \\
\text{Lys} & 20 \\
\text{His} & 10 \\
\text{Cys} & 9 \\
\text{Asp} & 29 \\
\text{Asn} & 19 \\
\text{Glu} & 29 \\
\text{Gln} & 13 \\
\text{Thr} & 13 \\
\text{Ser} & 30 \\
\text{Pro} & 21 \\
\text{Gly} & 27 \\
\text{Ala} & 29 \\
\text{Val} & 35 \\
\text{Met} & 14 \\
\text{Ile} & 24 \\
\text{Leu} & 37 \\
\text{Tyr} & 15 \\
\text{Phe} & 15 \\
\text{Trp} & 6 \\
\hline
\end{array} \)
residue 10. The change in amino acid character is conservative because both arginine and histidine are basic amino acids and both leucine and valine are nonpolar in nature. It therefore retains the ionic character and hydrophobicity in this portion of the enzyme. Moreover, the change from leucine to valine involves only one base change, from TTA to GTA.

The deduced amino acid sequences of ADPglucose synthetase from *E. coli* and *S. typhimurium* are also compared with respect to their allosteric sites. Previous studies in the *E. coli* enzyme (9, 21, 22) showed that pyridoxal phosphate can be specifically reduced onto lysine residue 39 and that this phosphoryl oxylation increases the enzymatic activity in the absence of the allosteric activator fructose bisphosphate in the reaction mixture, therefore suggesting that the lysine residue constitutes at least a portion of the activator binding site. Since fructose bisphosphate is the physiological activator of both the *E. coli* and *S. typhimurium* ADPglucose synthetase, it is not surprising that the lysine residue is retained in the same position of the primary structure of the enzyme. Moreover, the conservation of basic amino acid residues in the vicinity of lysine residue 39, especially arginine residues in position 29, 32, and 40, may be involved in the ionic interaction with the phosphorylated activators of ADPglucose synthetase as suggested by Haugen et al. (5), Parsons and Preiss (21, 22), and Kappel and Preiss (9). The similar features in the primary structure of ADPglucose synthetase in *E. coli* and *S. typhimurium* suggest that their mechanism in fructose bisphosphate activation is very similar if not identical.

Inhibitor and substrate binding sites in the *glgC* enzyme were also studied with azido-AMP and azido-ATP analogs (11) and was shown to involve specifically tyrosine residue 114. This tyrosine residue is also conserved in the *E. coli* and *S. typhimurium* enzymes. Moreover, the amino acid sequence upstream and downstream from the tyrosine residue is highly conserved without a single change in amino acid sequence.

Lysine residue 195 of the *E. coli* ADPglucose synthetase was shown to be an ADPglucose-protected site of the enzyme from inactivation by reductive phosphoryl oxylation by Parson and Preiss (21). Modification by pyridoxal phosphate on the lysine residue was blocked by incubation with the substrate ADPglucose. Therefore, this region was suggested to be involved in the binding of ADPglucose or ATP. This lysine residue is also conserved in the *S. typhimurium* enzyme. Comparison of the deduced amino acid sequence of ADPglucose synthetase of *E. coli* and *S. typhimurium* shows that the allosteric sites, fructose bisphosphate-, AMP-, ATP-, and ADPglucose-protected sites, are all conserved and thus suggest that the reaction mechanisms in the

### Table 2. Codon usage of the *S. typhimurium* glgC gene

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</table>
VOL. 169, represented by the one-letter amino acid code.

and that of the S. typhimurium enzyme is the synthetase of E. coli K-12 and amino acid ADPglucose synthetases sequence of E. coli ADPglucose synthetase is shown in the indicates the end of sequence. The amino *
tase. coli of 05520 and Al 22835 Grosjeans, 3. Baecker, P. A., E.

LITERATURE CITED
