CURRENT MICROBIOLOGY Vol. 43 (2001), pp. 418–423
DOI: 10.1007/s002840010331

Current Microbiology
An International Journal

The Product of the *cysK* Gene of *Bacillus stearothermophilus* V Mediates Potassium Tellurite Resistance in *Escherichia coli*

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Received: 28 March 2001 / Accepted: 17 April 2001

Abstract. The nucleotide sequence of a 4,539 bp fragment of *Bacillus stearothermophilus* V mediating tellurite resistance in *Escherichia coli* was determined. Four ORFs of more than 150 amino acids encoding polypeptides of 244, 258, 308, and 421 residues were found in the restriction fragment. *E. coli* cells harboring a recombinant plasmid containing the Te^r determinant express, when challenged with tellurite, a 32 kDa protein with an amino terminal sequence identical to the ten first residues of the 308 ORF. This ORF shows great similarity with the cysteine synthase gene (*cysK*) of a number of organisms. Recombinant clones carrying the active *cysK* gene have minimal inhibitory concentrations to K_2TeO_3 that were tenfold higher than those determined for the host strain or that of clones carrying ORFs 244, 258, and 421. Introduction of the *B. stearothermophilus* V *cysK* gene into a *cysK* strain of *Salmonella typhimurium* LT2 resulted in complementation of the mutation as well as transfer of tellurite resistance.

As a group, bacteria have evolved resistance to nearly all the metal ions which are considered toxic to the environment including, among others, Ag^+, AsO_2^-, AsO_4^-, Cd^{2+}, Co^{2+}, CrO_4^{2-}, Cu^{2+}, Hg^{2+}, Ni^{2+}, Sb^{3+}, TeO_3^{2-}, TeO_4^{2-}, and Zn^{2+}. Although low concentrations of some of these elements are important to maintain certain cellular metabolic processes, these metal ions can be strongly toxic when present at higher concentrations. Despite the increasing amount of literature published in this field, the biochemical and genetic mechanisms underlying the resistance phenomena are far from being well understood [14].

It has been suggested that the oxyanions of Te, tellurites and tellurates, exert their toxic effects through their strong oxidant properties [16]. It has been recently proposed that tellurite toxicity could be due to the replacement of sulfur and or selenium in various cellular functions [5].

Many efforts have been made to understand how bacterial cells counteract the toxic effects of potassium tellurite. Several Te^r determinants have been localized in plasmids [1] or in the bacterial chromosome [19]. The information currently available reveals that there is a great diversity both in the structure and organization of the genes involved in bacterial resistance to tellurite. However, the precise mechanism(s) involved in tellurite resistance still remains elusive [18].

Our group has been interested in studying tellurite resistance in bacteria for several years. Initially, we focused on thermophilic Gram negative rods of the genus *Thermus* [2, 3] and later on a thermotolerant Gram positive bacterium isolated from a soil sample [9]. In both cases we were able to demonstrate the existence of cellular reductases that converted tellurite to elemental tellurium at the expense of NAD(P)H [3, 9]. We recently communicated the cloning of a TeO_3^{2-} resistance determinant from *Bacillus stearothermophilus* V into *E. coli* and described the identification and characterization of the putative Te^r determinant [21]. Here we report that tellurite resistance of the *B. stearothermophilus* V determinant is found within a chromosomal DNA fragment of 4.5 kb. This fragment contains the *cysK* gene coding for the enzyme cysteine synthase that is responsible for mediating tellurite resistance in *E. coli* and *Salmonella typhimurium* LT2.

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Table 1. Oligonucleotides used in primer extension, DNA amplification, and cloning

Primer	Orientation	5′ → 3′ Sequence	PCR
O_1	Forward	CATG**CCATGG**CTTTTGTGTTAGATGTTGGCAACACGAATACG	ORF258
O_2	Reverse	GCCGAC**GTCGAC**TATCATTGTTTTTTATCTACATTTTTCTCATACAA	ORF258
O_3	Forward	CATG**CCATGG**GAGCGATGTTAAAAGGCGATGAAACATTAACG	ORF244
O_4	Reverse	CGC**GGATCC**CTATTATGCTTTTTTCGCATCTGCAAGCTGCTTCAG	ORF244
O_5	Forward	CATG**CCATGG**CGAGAACAGTAAACTCCATCACGGAATTA	ORF308
O_6	Reverse	CGAC**GTCGAC**TATTAGTCTTCGAATTGGTAAAGCGGCGTGCT	ORF308
O_7	Forward	CATG**CCATGG**AACAAAAGCGAAAAAGGAAGAGGCGGACAGTTTCT	ORF421
O_8	Reverse	GCCGAC**GTCGAC**TATTACCAAAGTTGAACCAAAATCAGGAATTCCAT	ORF421
O_A	Forward	CGC**GGATCC**ATGGCGAGAACAGTAAACTCCATC	Clone A
O_B	Forward	CGC**GGATCC**GGAAACAAATTCGATAAAATTAAT	Clone B
O_C	Forward	CGC**GGATCC**AAACATGGCGAGAACAGTAAACTC	Clone C
O_D	Forward	CGC**GGATCC**ATTAAGCCAATAATTGATACATTG	Clone D
O_E	Forward	CGC**GGATCC**AAATGATTGACAATTAAGCCAATA	Clone E
$O_{3'}$	Reverse	GCG**GAATTC**TTAGTCTTCGAATTGGTAAAGCGG	Clones A–E
O_{PE}	Forward	CTTCCTGGGTTCATAAACTCAAGTTTTAGATAGACATCG	Primer Extension

Materials and Methods

Strains and growth conditions. *E. coli* cells were grown in Luria broth [13] at 37°C with shaking and cells of the *cysK*$^-$ derivative of *S. typhimurium* LT2 (Mst 2383, *cys KAM* 1586::MudP, B orientation, 50 min) were grown at 37°C in Vogel and Bonner [22] minimal media containing 1 mM sodium sulphite and supplemented with 0.2% glucose. Solid media contained 2% agar (DIFCO) and ampicillin at 100 μg/ml was added when required. MIC determinations for tellurite were performed in liquid media after 48 h of growth as previously described [2].

Plasmid constructions and genetic manipulations. The DNA fragments used to clone the ORFs of 244, 258, 308, and 421 amino acids of *B. stearothermophilus* V in pET21d were synthesized by PCR using DNA of pTel [21] as the template. The oligonucleotides used in this study are shown in Table I. Primers were designed to introduce an *Nco*I restriction site at the 5′ end and a *Sal*I site at the 3′ end of the PCR fragments. Cloning of ORF244 involved the introduction of a *Bam*HI restriction site in the O_1 reverse primer (Table 1) as the cloned insert contains an internal *Sal*I site. Standard molecular biology procedures such as cloning, restriction endonuclease digestion, ligation, and transformation were performed essentially as described [13].

Mutagenesis of the *cysK* promoter. DNA fragments of *B. stearothermophilus* V containing deletions in the upstream region of the *cysK* gene were generated by PCR using the primers shown in Table 1 and cloned into the *Bam*HI/*Eco*RI sites of pBluescript-SK. Derivatives included plasmid pBS-A that does not contain nucleotide sequences upstream the ATG initiation codon, plasmid pBS-B that lacked the -10 region, plasmid pBS-C that lacked the -35 region, plasmid pBS-D that did not contain sequences upstream the Shine-Dalgarno (SD) element and plasmid pBS-E with an intact *cysK* promoter. Cells of *E. coli* JM109 harboring each of these plasmids are referred to as clones A, B, C, D, and E (Table 1), respectively.

Preparation of bacterial extracts and detection of recombinant proteins. Cell pellets were resuspended in 50 mM Tris-HCl buffer, pH 7.5, and disrupted by sonication. Cell debris was discarded and aliquots of the resulting lysates were fractionated by SDS-PAGE in 12% polyacrylamide gels. Proteins were visualized by Coomassie Blue staining or transferred electrophoretically to nitrocellulose filters for immunodetection. Antibodies against the CysK enzyme of *B. stearothermophilus* V were prepared using a partially purified recombinant protein. Extracts of *E. coli* cells expressing the recombinant enzyme were used in preparative SDS-PAGE and slices of Coomassie Blue stained polyacrylamide gels containing the 32 kDa protein band were crushed and inoculated in rabbits as reported [6].

In vitro assay for cysteine synthase. The cysteine synthase activity present in cell-free extracts was determined at 50°C by measuring the disappearance of 5-thio-2-nitrobenzoic acid (TNB) at 412 nm as previously described [17].

DNA sequencing, primer extension, and amino-terminal amino acid determinations. Both strands of the 4.5 kb DNA fragment from *B. stearothermophilus* V containing the cloned Te^r determinant were sequenced entirely. The GenBank accession number for the sequence of the 4.5 kb fragment reported in this communication is AF198621.

Primer extension involved RNA extraction from *E. coli* JM109 cells carrying pTel grown with or without 5.0 μg/ml of potassium tellurite using the RNeasy mini kit (Qiagen). DNA synthesis was performed with reverse transcriptase and [^{32}P]-labelled oligodeoxinucleotide O_{PE} (Table 1). The resulting fragment was fractionated on a 7% polyacrylamide gel containing 7M urea. To determine the transcriptional start site of the *cysK* gene, a sequence ladder obtained with the same primer and pTel as the template was coelectrophoresed on the same gel.

Sequential Edman degradation of the 32 kDa protein was performed as follows. The protein was separated by SDS-PAGE (12%) and electroblotted onto PVDF membranes. The membranes were then washed in deionized water, stained with Coomasie Blue R-250, destained, dried, and stored at −20°C. Strips of PVDF membranes containing the 32 kDa protein were cut and used for amino terminal sequence determination (Centro de Síntesis y Análisis de Biomoléculas, Universidad de Chile, Santiago, Chile).

Results and Discussion

Induction of a 32 kDa protein upon tellurite challenge. We previously reported the cloning of a 7 kb DNA fragment from *B. stearothermophilus* V in pBluescript-SK and demonstrated that the resulting plasmid

Table 2. Minimal inhibitory concentrations (MICs) to potassium tellurite determined for the *E. coli* and *S. typhimurium* cells included in this study

Strain	Plasmid	MIC K_2TeO_3 (μg/ml)	Source or Reference
E. coli JM109	None	2	Vásquez et al. (1999)
	pBluescript-SK	2	This study
	pTel	25	Vásquez et al. (1999)
	pTel4.5	25	This study
	pTel2.4	2	This study
	pBS-A	2	This study
	pBS-B	2	This study
	pBS-C	2	This study
	pBS-D	2	This study
	pBS-E	25	This study
E. coli BL21 (DE3)	None	ND	
	pET21d	2	This study
	pET21d/258	2	This study
	pET21d/244	2	This study
	pET21d/308	25	This study
	pET21d/421	2	This study
S. typhimurium LT2 (*cysK*$^-$)	None	ND	S. Maloy
	pET21d	5	This study
	pET21d/308	50	This study

ND, not determined. The numbers are the mean of three independent determinations.

pTel conferred tellurite resistance to *E. coli* JM109 [21]. No differences between the MICs determined in LB or in glucose-supplemented minimal media were observed. This observation differs from that of others who reported that tellurite resistance is dependent on the culture media [23].

To better identify the DNA region responsible for tellurite resistance the recombinant plasmid pTel was digested with *Eco*RI and the gene mediating K_2TeO_3 resistance was localized on the 4.5 kb fragment [21] by subcloning (Table 2). *E. coli* JM109 cells harboring pTel4.5 and grown in the presence of tellurite express a 32 kDa protein as detected by SDS-PAGE. Edman degradation analysis of the 32 kDa protein revealed the aa sequence MARTVNSITE that is 100% identical to the first ten amino terminal residues of the ORF of 308 amino acids predicted from the nucleotide sequence (see below).

Analysis of the 4.5 kb *Eco*RI fragment of *B. stearothermophilus* V. The 4,539 bp *Eco*RI fragment exhibits four ORFs higher than 150 aa and they are found in the left to right orientation. These ORFs have the same transcription orientation and their polypeptide products are referred to as P_{244}, P_{258}, P_{308}, and P_{421} according to their aa number (Fig. 1a). ORF244 displays a 69% of identity (85% similarity) with a replication protein of 31.8 kDa whose gene is located in the *ftsh-cysK* intergenic region of *B. subtilis* [11]. The ORF258 showed 72% identity (83% similarity) with a 26.2 kDa replication protein coded by the same genomic region of *B. subtilis*. The aa sequence predicted for P_{308} showed identities of 79% and 71% (similarities of 81% and 78%) with the cysteine synthase (CysK) from *B. thermoleovorans* and *B. subtilis* [11], respectively. The *B. stearothermophilus* V CysK exhibits the piridoxal-phosphate-binding heptapeptide SVKDRIA which is well conserved among other cysteine synthases. The product of ORF421 showed a 51% of identity (67% similarity) with the p-aminobenzoate synthase component I (or A subunit) of *B. subtilis* [15].

Cloning and expression of P_{244}, P_{258}, P_{308}, and P_{421}. To investigate which of these proteins can be associated with the transfer of tellurite resistance to *E. coli* each of the four ORFs were amplified by PCR using appropriate primers (Table 1) and cloned separately in pET21d. Interestingly, only the *E. coli* clone carrying the *B. stearothermophilus* V *cysK* gene (ORF 308) displays tellurite resistance (Table 2). In addition, a thermostable cysteine synthase activity was appreciably detected in bacterial extracts of cells expressing P_{308} (not shown). Because ORF308 was the most likely candidate of mediating tellurite resistance further studies on the organization of the *cysK* gene were performed.

Analysis of the *cysK* gene of *B. stearothermophilus*. The upstream region of the *cysK* gene contains promoter

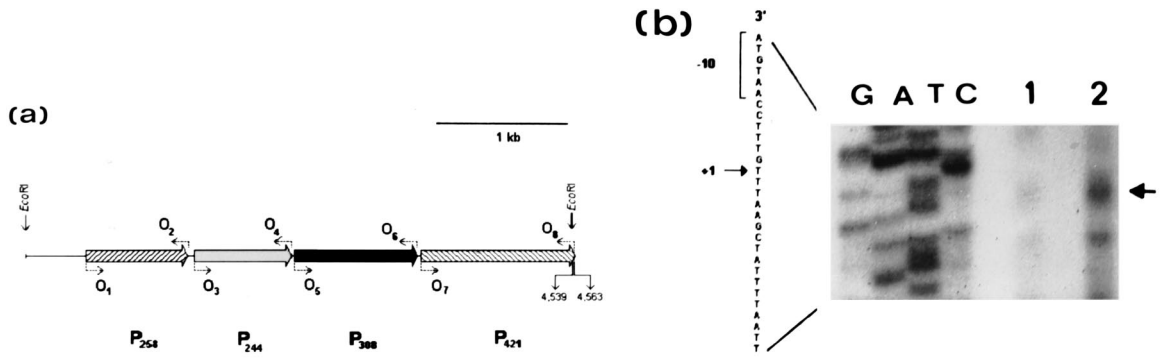

Fig. 1. Analysis of the ORFs contained within the 4.5 kb *Eco*RI fragment of *B. stearothermophilus* V. **(A)** Schematic representation of the ORFs greater than 150 aa found in the 4.5 kb *Eco*RI fragment of *B. stearothermophilus* V cloned in pBluescript-SK. The pairs of oligonucleotide (O) primers used to PCR and clone each of the ORFs to generate the proteins of 244 (P_{244}), 258 (P_{258}), 308 (P_{308}), and 421 (P_{421}) aa are illustrated. Transcription of the four ORFs is from left to right as indicated by the big arrows. The stop codon of ORF421 is located 44 nt downstream the *Eco*RI site as determined by additional DNA sequencing. **(B)** Determination of the start point at the *cysK* promoter region of *B. stearothermophilus* V. RNA extraction and primer extension were performed as described in Materials and Methods. Lane 1, *E. coli* JM109 cells carrying pTel and grown without potassium tellurite; lane 2, *E. coli* JM109 cells carrying pTel and grown in the presence of 5.0 μg/ml of K_2TeO_3. The sequence pattern of a dideoxinucleotide reaction (fmol Sequencing kit, Promega) performed using pTel as template is shown on the left.

elements that exhibit a high degree of homology with others reported in literature [12]. For instance, the hexanucleotides **TT**G**ACA** and **TA**C**ATT** match the -35 and -10 consensus sequences at the most conserved positions (bold). A putative ribosome binding purine-rich sequence GAGG is located 11 nucleotides upstream of the proposed ATG translational start codon. The transcriptional start site of the *cysK* gene was identified by primer extension analysis (Fig. 1b) using primer O_{PE} (Table 1). Interestingly, the RNA transcript was detected almost only in RNA preparations obtained from tellurite-stressed cultures.

To further assess the functionality of the *cysK* promoter sequences *in vivo*, a set of mutants lacking the -10, -35, and SD sequences was generated by PCR and cloned back into pBluescript-SK. *E. coli* JM109 cells were transformed with each of these recombinant plasmids and challenged with potassium tellurite. Tellurite resistance was only achieved with a clone carrying ORF308 preceded by a DNA segment containing the -35, -10, and SD promoter elements (clone E). MICs determined for clone A (lacking all three elements), clone B (lacking -10), clone C (lacking -35), and clone D (lacking SD) were almost indistinguishable from that of the host transformed with pBluescript-SK alone (Table 2). These results indicate that an intact promoter is required to express the *B. stearothermophilus* V *cysK* gene in *E. coli*.

When cell extracts prepared from clones A–E grown under permissive concentrations of K_2TeO_3 were subjected to SDS-PAGE, the 32 kDa protein band was appreciably detected only in clone E (not shown).

Complementation of a *cysK*$^-$ mutant of *Salmonella typhimurium* LT2. Transfer of the *cysK* gene of *B. stearothermophilus* V in a *cysK*$^-$ auxotrophic strain of *S. typhimurium* LT2 resulted in recovery of the prototrophic phenotype and heterologous expression of the thermophilic *cysK* gene as evidenced by SDS-PAGE (Fig. 2a) and immunoblot analysis using rabbit polyclonal antibodies raised against the *B. stearothermophilus* V cysteine synthase (Fig. 2b). In addition, *S. typhimurium* LT2 cells transformed with pET21d/308 and grown in minimal media showed a tenfold increase in the MICs to tellurite (Table 2). pET21d/308 was recovered from a number of Te^r clones of *S. typhimurium* LT2 and used to transform *E. coli* BL21Gold (DE3). Studies performed on these transformed cells revealed that they not only acquired resistance to ampicillin but exhibited increased levels of tellurite resistance as well (not shown).

The *cysK* gene has been associated with Te^r determinants in other microorganisms. Two loci that are involved with tellurite resistance in *R. sphaeroides* have been identified [10]. One of such loci contains the genes *tgrAB* that confer an increased tolerance to tellurite when transferred to *Paracoccus denitrificans*. Disruption of the *cysK* gene, located downstream of the *tgrAB* genes, results in reduction of the TeO_3^{2-} resistance levels suggesting that an intact cysteine metabolic pathway may be needed for high level resistance to K_2TeO_3 in *R. sphaeroides* [8, 10]. Interestingly, an association between the cysteine residues of the *E. coli* TehB determinant and tellurite resistance has been recently communicated [4].

It is also likely that tellurite can cause inactivation of vital cellular components by oxidation of essential reduced groups. It has been shown that tellurite-dependent thiol oxidation occurs in *E. coli* cells expressing several K_2TeO_3 resistance determinants [20]. In addition, Lloyd-

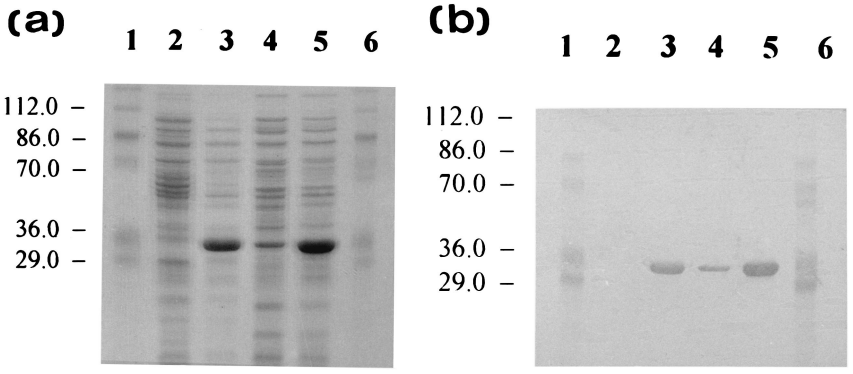

Fig. 2. Expression of the cysteine synthase of *B. stearothermophilus* V in a *cysK*$^-$ strain of *S. typhimurium* LT2. **(A)** Coomasie Blue stained proteins. **(B)** Immunoreactivity with a rabbit antiserum to the cysteine synthase. Cells of *S. typhimurium* LT2 harboring plasmid pET21d/308 were grown as described in Materials and Methods. Lane 2, *E. coli* JM109 harboring pTel and harvested after IPTG induction; lane 3, *E. coli* BL21 (DE3) harboring pET21d/308 and induced with IPTG; lanes 4 and 5 were loaded with cell extracts of cultures of *S. typhimurium* LT2 harboring plasmid pET21d/308 and harvested before and after IPTG induction, respectively. Prestained protein molecular weight standards (kDa) are shown in lanes 1 and 6.

Jones *et al.* [7] have reported that *E. coli* cells expressing a pMER610-derived Te^r determinant undergo TeO_3^{2-} specific reduction only when -SH groups are maintained in their reduced state. Experiments to determine whether the expression of the *cysK* gene of *B. stearothermophilus* V in *E. coli* correlates with a certain level of -SH protection *in vivo* are in progress in our laboratory. Preliminary results suggest that tellurite-stressed cells exhibit decreased levels of gluthatione and total thiols, an observation that is in agreement with those reported by Turner *et al.* [20] for the expression of a number of Te^r determinants in *E. coli*.

Although transfer of the *B. stearothermophilus* V *cysK* gene resulted in high level expression of the recombinant cysteine synthase in *E. coli*, a concomitant increase of intracellular cysteine concentration was not observed. This observation could be explained if cysteine exerts an inhibitory effect on its own biosynthetic pathway. Preliminary results obtained in our laboratory support this idea (Vásquez, unpublished observations).

In conclusion, we have cloned and expressed the *cysK* gene from *B. stearothermophilus* V in *E. coli* and *S. typhimurium* LT2 and demonstrated that expression of the *cysK* gene alone is responsible for the acquisition of resistance to potassium tellurite in both microorganisms.

ACKNOWLEDGMENTS

We are grateful to Dr. Sanley Maloy, University of Illinois, Urbana, USA, for providing the *cysK*$^-$ derivative of *S. typhimurium* and Gino Corsini, Universidad de Chile, for assistance with the primer extension experiments. This work received financial support from Fondecyt grants 1990917 and 799055, and from Dicyt.

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