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Isolation and Expression of the *catA* Gene Encoding the Major Vegetative Catalase in *Streptomyces coelicolor* Müller

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We isolated the *catA* gene for the major vegetative catalase from *Streptomyces coelicolor* Müller. It encodes a polypeptide of 488 residues (55,440 Da) that is highly homologous to typical monofunctional catalases. We investigated *catA* expression by analyzing both *catA* mRNA and catalase activity. *catA* expression was increased by H_2O_2 treatment but did not increase during stationary phase. A putative catalase (CatB) cross-reactive with anti-CatA antibody appeared during stationary phase and in the aerial mycelium.

Catalase is an oxidoreductase which transfers two electrons to H_2O_2, decomposing it into O_2 and H_2O. Most of the catalases characterized so far can be classified into one of two types based on their enzymological properties (reference 15 and references therein): monofunctional (typical) catalases and bifunctional catalase-peroxidases. Multiple catalases have been found in organisms such as *Escherichia coli* (5, 6), *Bacillus subtilis* (16), *Streptomyces coelicolor* (13, 14), *Saccharomyces cerevisiae* (19, 20), and *Aspergillus nidulans* (17). The role of each enzyme in different stages of the growth of these organisms is not well understood.

In *S. coelicolor* Müller, multiple catalases exist in late phases of growth in liquid culture or after the onset of differentiation on surface culture (4, 14). The major catalase (Cat4) is a typical catalase which consists of four identical subunits of 56 kDa and is expressed at a rather constant level throughout the different growth phases (14). A similar catalase has been reported in *S. coelicolor* A3(2) by Walker et al. (23). The involvement of H_2O_2 or reactive oxygen species in signaling for cell development has been suggested from studies in many systems (3, 10, 18). In this respect, the role of each catalase in growth and differentiation deserves systematic investigation. As an initiating effort toward this goal, this paper describes the isolation and characterization of the *catA* gene for the major vegetative catalase Cat4, whose expression is induced by H_2O_2 but not during the stationary phase of growth, unlike other major catalases in *E. coli* and *B. subtilis* (2, 12).

Cloning and sequence analysis of the *catA* gene. The compilation and alignment of amino acid sequences from typical monofunctional catalases enabled us to design PCR primer pairs with which to isolate a catalase gene from *S. coelicolor* Müller (ATCC 10147) (see Fig. 1). A single PCR product of 276 bp was produced whose deduced amino acid sequence closely matched the conserved amino acid residues of typical catalases. Genomic Southern hybridization with this PCR fragment revealed a single prominent band from each restriction digest tested. There was also a minor hybridizing band which might bear a related gene. We screened a phage library of *S. coelicolor* Müller DNA to isolate the clone carrying the template gene (*catA*) for the PCR product. A 4.5-kb insert from one phage clone containing the *catA* gene was further characterized, and the nucleotide sequence of the internal 2.0-kb *Sal*I-*Ava*I fragment was determined (Fig. 1). The sequence reveals a single open reading frame (ORF) encoding a polypeptide of 488 residues with a deduced molecular mass of 55,440 Da. A putative ribosome binding site ((GAGGAG) was located 6 nucleotides upstream from a putative initiation codon, UUG. The deduced gene product is almost the same size as the subunit of the major catalase Cat4 purified from *S. coelicolor* Müller, which is about 56 kDa as judged by its electrophoretic mobility (14). The *catA* ORF contained all the partial peptide sequences from the Cat4-like catalase purified from *S. coelicolor* A3(2) by Walker et al. (23) with a few differences. The comparison of amino acid sequences revealed significant homology between the deduced *catA* gene product and large regions of numerous typical catalases. Nearly all the residues important for catalytic activity and heme binding are conserved (8).

Expression of the *catA* gene in *E. coli* and *Streptomyces lividans* TK24. In order to verify the *catA* gene product, we expressed this gene on multicopy plasmids in both *E. coli* and *S. lividans. E. coli* cells containing the *catA* gene on pUC18 exhibited much higher levels of catalase activity (20-fold) than cells containing the parental vector (Fig. 2A, lanes 1 and 2). The overproduced CatA catalase of *E. coli* comigrated with the *S. coelicolor* Cat4 enzyme on native gels (data not shown). When the *catA* gene was introduced on pIJ702, *S. lividans* TK24 cells produced two times more catalase activity, which again comigrated with Cat4 (data not shown). The identity of CatA with the major catalase Cat4 was confirmed by Western blot analysis with anti-Cat4 antibody (Fig. 2A, lanes 3 and 4). A single polypeptide of about 56 kDa was detected in extracts of *E. coli* cells harboring the *catA* gene.

Determination of the transcription start site of the *catA* gene. We determined the transcription start site for *catA* by S1 nuclease mapping of RNAs from cells grown to mid-exponential phase (Fig. 2B). The probe used generated a single species of protected band and assigned the 5′ end of the *catA* mRNA to the G residue 27 nucleotides upstream from the initiation codon. RNAs isolated from *E. coli* cells containing the *catA* gene also generated the same protected band, implying that the same promoter was utilized in both *E. coli* and *S. coelicolor*. Putative promoter elements were identified which closely match the consensus *S. coelicolor* Eσ^{hrdB} promoters (TTGCCT-N_{16}-TAGGGT versus TTGACN-N_{16-18}-TAGAPuT) (Fig. 1) (22). Since this promoter resembles *E.*

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GTCGACGCCGGTGGACCGGGAGTGGGGCACCGCCTGGTCGGCCGCGTTCAGGTCCTTGAC    60
GACCTGCGAGCCGATCAGCCCCGTCCCGCCGATGACCGCGATCTTCATGCGCACGCTCTC   120
TTCCTTCCGGAGCCGGGTGGCTCAGGAACCACTGTGTCGGTGTGCGCGGAGGACGGCGCT   180
CTGAACGCCCCCGAAGGGATGAGAACGGCCCGGTCCGGGGTGCCGGAACGCCGGAGTGGC   240
CGACGCTGTCGCTCCCGCCCCCGGCAGGGCGCGGCACCCCAGCAGGCTTCGGCATCAATT   300
CAAGAGCGAATATTGCTCTAGATGTCGCCTTGCCTTAGATCCTGTCCAAGGTAGGGTGGT   360
                    -35                  -10
GGCTGCGAAGAACCACACCGAGGAGCAAGCCTTGCCTGAGAACAACCAGAAGCCGCTGAC   420
                          M  P  E  N  N  Q  K  P  L  T
CACGGTCGCCGGTCCGCCGGTTCCCGACAACCAGAACTCCCTGACCTCCGGCCCGCGCCG   480
 T  V  A  G  P  P  V  P  D  N  Q  N  S  L  T  S  G  P  R  R
CCCGATGCTCCTGCAGGACGTGTGGTTCCTGGAGAAGCTCGCGCACTTCGACCGGGAGGT   540
 P  M  L  L  Q  D  V  W  F  L  E  K  L  A  H  F  D  R  E  V
CATCCCGGAGCGCCGGATGCACGCCAAGGGGTCGGGGCTGTTCGGCACTTTCACGGTCAC   600
 I  P  E  R  R  M  H  A  K  G  S  G  L  F  G  T  F  T  V  T
TCACGACATCACCCGGTACACCAGCGCGAAGATCTTCTCCGAGATCGGCAAGAAGACCCC   660
 H  D  I  T  R  Y  T  S  A  K  I  F  S  E  I  G  K  K  T  P
GCTGTTCACCCGGTTCTCCACCGTCGCCGGTGAGCGCGGTGCCGCCGACGCCGAGCGCGA   720
 L  F  T  R  F  S  T  V  A  G  E  R  G  A  A  D  A  E  R  D
CATCCGCGGCTTCGCCGTGAAGTTCTACACGGACGAGGGCAACTGGGACCTGGTCGGAAA   780
 I  R  G  F  A  V  K  F  Y  T  D  E  G  N  W  D  L  V  G  N
CAACACCCCGGTCTTCTTCTTCCGCGACCCGCTGAAGTTCCCGGACCTCAACCACGCGGT   840
 N  T  P  V  F  F  F  R  D  P  L  K  F  P  D  L  N  H  A  V
GAAGCGCGACCCGCGCACCAACCTGCGCAACGCCGAGAACAACTGGGACTTCTGGACCAA   900
 K  R  D  P  R  T  N  L  R  N  A  E  N  N  W  D  F  W  T  N
CCTCCCCGAGGCCCTGCACCAGGTCACGATCGTGATGTCGGACCGCGGCATCCCGGCCTC   960
 L  P  E  A  L  H  Q  V  T  I  V  M  S  D  R  G  I  P  A  S
CTACCGGCACATGCACGGGTTCGGCTCGCACACGTACAGCCTGATCAACGCCGAGGGCGA  1020
 Y  R  H  M  H  G  F  G  S  H  T  Y  S  L  I  N  A  E  G  E
GCGGTTCTGGGTCAAGTTCCACCACCGCACCCAGCAGGGCATCAAGAACCTCACCGACGC  1080
 R  F  W  V  K  F  H  H  R  T  Q  Q  G  I  K  N  L  T  D  A
CGAGGCCGAGGCCCTGGTCGGCAAGGACCGCGAGTCCCACCAGCGCGACCTCTTCGACGC  1140
 E  A  E  A  L  V  G  K  D  R  E  S  H  Q  R  D  L  F  D  A
GATCGAGGACGGCGACTTCCCGAAGTGGAAGCTGTTCATCCAGGTCATGCCGGAGGCCGA  1200
 I  E  D  G  D  F  P  K  W  K  L  F  I  Q  V  M  P  E  A  D
CGCGGAGAACTACCGCTTCCACCCCTTCGACCTCACCAAGGTCTGGTCGAAGAAGGACTA  1260
 A  E  N  Y  R  F  H  P  F  D  L  T  K  V  W  S  K  K  D  Y
CCCGCTGATCGAGGTCGGCGAGTGGGAGCTCAACCGCAACCCCGACAACTACTTCGCGGA  1320
 P  L  I  E  V  G  E  W  E  L  N  R  N  P  D  N  Y  F  A  D
CGTGGAGCAGGCCGCCTTCAGCCCGGCCAACGTGGTCCCGGGCATCGAGGCTTCCCCCGA  1380
 V  E  Q  A  A  F  S  P  A  N  V  V  P  G  I  E  A  S  P  D
CCGGATGCTGCAGGGCCGCCTCTTCTCCTACGGCGACGCCCAGCGCTACCGCCTCGGCGT  1440
 R  M  L  Q  G  R  L  F  S  Y  G  D  A  Q  R  Y  R  L  G  V
CAACCACCACCACCAGATCCCGGTCAACGCCCCGAAGAACCCGGTGAACTCCTACCACCG  1500
 N  H  H  H  Q  I  P  V  N  A  P  K  N  P  V  N  S  Y  H  R
CGACCCGGCCATGCGCGTCGACGGCAACCAGGGAGCCACCCCGGGCATCGAGCCCAACTC  1560
 D  P  A  M  R  V  D  G  N  Q  G  A  T  P  G  I  E  P  N  S
CTACGGCCGCTGGCAGGAGCAGCCGGCCTACCGCGACCCGGCCCAGGCCGTGGGCGCCGT  1620
 Y  G  R  W  Q  E  Q  P  A  Y  R  D  P  A  Q  A  V  G  A  V
CGCCGACCGGTTCAACTACCGCGAGGACGACGACAACTACTTCGAGCAGCCCGGCAACCT  1680
 A  D  R  F  N  Y  R  E  D  D  D  N  Y  F  E  Q  P  G  N  L
GTTCCGGCAGATGAGCCCGGAGCAGCAGCAGGTTCTGTTCGAGAACACGGCACGCGCCAT  1740
 F  R  Q  M  S  P  E  Q  Q  Q  V  L  F  E  N  T  A  R  A  I
CGACGGCGCCTCGGCGCAGACCATCGAGCGCCACATCGGCAACTGCACCCAGGCCGACCC  1800
 D  G  A  S  A  Q  T  I  E  R  H  I  G  N  C  T  Q  A  D  P
GGCCTACGGCGCGGGCGTCCGCAAGGCGATCGAGGCCCTGGCCGCCGGCAACCTCTGATC  1860
 A  Y  G  A  G  V  R  K  A  I  E  A  L  A  A  G  N  L  *
CGGCCGGTCAGCGACACACGCGGTACATCGCCTCGTACCGGCGCGGGCACCTCGGAGGTG  1920
CCCGCGCCGGTGCGCGGTACCGCCACGGAGAACTACTTCATGGACATGCACAACAGCGGG  1980
CGGACTGACTCCCGAG                                               1996
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FIG. 1. Nucleotide sequence of the *catA* gene. The transcription start site at nucleotide 365 (Fig. 2B) is indicated with a bent-end arrow, and the putative Shine-Dalgarno sequence is presented in boldface. Potential promoter sequences for $E\sigma^{hrdB}$ recognition are in boldface and underlined. The coding region starts at the TTG codon at nucleotide 392 and ends at the TGA codon at nucleotide 1855, thus encoding a polypeptide of 488 amino acids. The amino acid residues in boldfaced italics are those that are identical to previously reported peptide sequences (23). The two arrows indicate the regions that bind PCR primers (5′-TTCGACCGSGAGCGSATCCCSGAC-3′ and 5′-GATGAAGAA-GAYSGGSGTGTTGTT-3′, where S is G or C and Y is C or T).

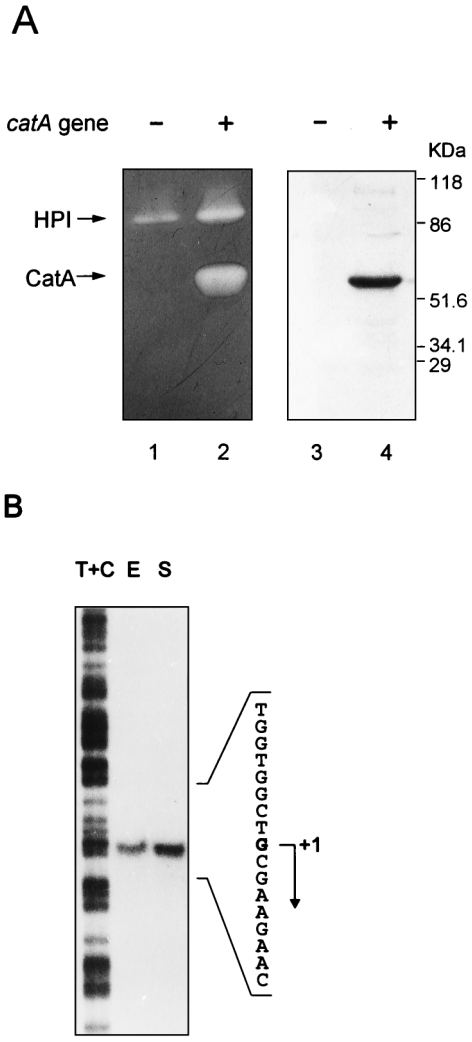

FIG. 2. Expression of the *catA* gene. (A) Catalase activity staining and Western blot analysis of the *catA* gene product expressed in *E. coli. E. coli* cells containing the *S. coelicolor catA* gene on plasmid pUC18 (lanes 2 and 4) or the parental vector (lanes 1 and 3) were grown to an optical density at 600 nm of 0.5. Cell extracts were prepared and analyzed for catalase activity on native 7% polyacrylamide gels as described by Clare et al. (7) (lanes 1 and 2) or by Western blotting on sodium dodecyl sulfate-polyacrylamide gels with anti-Cat4 antiserum (lanes 3 and 4). The size of the overexpressed CatA gene product was estimated as 56 kDa, the same as that of the purified Cat4 protein. The positions of molecular mass markers are shown on the right. (B) S1 nuclease mapping analysis of *catA* mRNA expressed in *E. coli* and *S. coelicolor*. RNAs were prepared from *E. coli* cells expressing CatA (lane E) or from *S. coelicolor* cells grown for 20 h (mid-exponential phase) (lane S) as described by Hopwood et al. (11). S1 nuclease mapping analysis was done with a 629-nucleotide *Sal*I-*Bgl*II fragment as a probe as described by Smith and Chater (21). The initiating G nucleotide is indicated with an arrow. T+C, Maxam-Gilbert sequencing ladder.

coli $E\sigma^{rpoD}$ promoters, it is most likely that the $E\sigma^{rpoD}$ holoenzyme recognized this promoter in *E. coli.*

Regulation of *catA* gene expression by H_2O_2 and growth phase. The total catalase activity in *S. coelicolor* in the presence or absence of H_2O_2 was measured at different growth phases. As shown in Fig. 3A, compared with the early exponential phase culture, the total catalase activity increased about sevenfold when cells were cultured until stationary phase in YEME liquid medium (11). In rapidly growing cells, 100 μM H_2O_2 induced catalase activity twofold. The inducibility by H_2O_2 decreased as cells entered stationary phase. We resolved different catalases in cell extracts by native polyacrylamide gel electrophoresis and examined the expression of each catalase under the same conditions (Fig. 3B). We observed that Cat4 (CatA) is the major catalase in rapidly growing cells, is induced by H_2O_2, and increases during exponential culture for up to 20 h. At late exponential phase (40-h culture), Cat4 decreased slightly but a new activity (Cat5) appeared, contributing to the increase in total catalase activity (Fig. 3B, lane 5). During stationary phase, we observed an emergence of high-molecular-weight catalase activity (Cat1) as well as an increase in the levels of activities comigrating with Cat4 and Cat5 (Fig. 3B, lane 7). The emergence of at least two catalases other than CatA contributed to the increase in total catalase activity at later phases of growth. However, the quantitative assessment of each individual catalase cannot be accurately achieved from this type of activity staining analysis.

We next monitored the changes in *catA* expression by measuring both its RNA and its protein product (Fig. 4). Northern

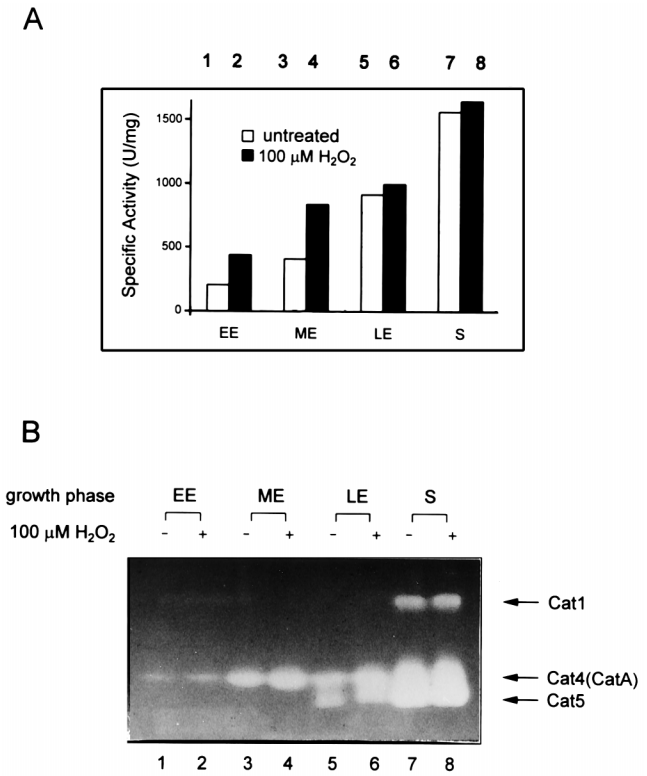

FIG. 3. Change in total catalase activity during growth and upon H_2O_2 treatment. Extracts were prepared from *S. coelicolor* cells grown for 10 h (early exponential [EE] phase [lanes 1 and 2]), 20 h (mid-exponential [ME] phase [lanes 3 and 4]), 40 h (late exponential [LE] phase [lanes 5 and 6]), and 100 h (stationary [S] phase) in YEME liquid medium (11), in which the doubling time was approximately 2 h. For H_2O_2 treatment, cultures were treated with either 100 μM (final concentration) H_2O_2 (lanes 2, 4, 6, and 8) or an equal volume of water as a corresponding control (untreated) (lanes 1, 3, 5, and 7) for 1 h. (A) Catalase activities in cell extracts were measured spectrophotometrically as described by Beers and Sizer (1) using 20 μg of total protein. (B) Proteins (20 μg) in cell extracts were electrophoresed on a native 7% polyacrylamide gel and stained for catalase activity. The positions of Cat1, Cat4 (CatA), and Cat5 are indicated (14).

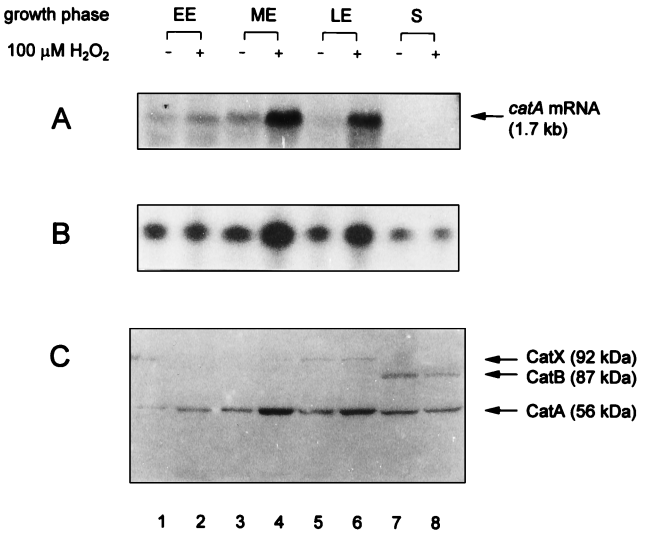

FIG. 4. Change in *catA* gene expression during growth and upon H_2O_2 treatment. Cell extracts and RNAs were prepared from the same cell cultures used for the experiment shown in Fig. 3. The level of *catA* transcript was assessed by Northern blot analysis (A) and S1 nuclease mapping (B). The amount of CatA polypeptide was estimated by Western blot analysis (C). Each sample contained 30 μg of RNA (A), 50 μg of RNA (B), or 50 μg of total protein (C). Northern analysis revealed a transcript of 1.7 kb, consistent with the predicted size of monocistronic *catA* mRNA. In Western analysis, two weak cross-reacting bands were detected beside the major 56-kDa CatA protein; they are indicated as CatX (92 kDa) and CatB (87 kDa).

analysis revealed a single mRNA species of 1.7 kb (Fig. 4A). This corresponds to the size of the *catA* ORF and implies that the message is monocistronic. The level of *catA* mRNA increased up to fourfold following H_2O_2 treatment during exponential phase (Fig. 4A). No full-length *catA* mRNAs were detected at stationary phase. However, it was extremely difficult to obtain intact RNAs, from cells at this growth phase, probably because of increased level of RNases. We therefore tried to detect a portion of *catA* mRNA near the 5′ end by S1 nuclease protection with the same probe used for the experiment shown in Fig. 2B (Fig. 4B). The results confirm the observation made after by Northern analysis that *catA* mRNA is induced by H_2O_2 until the late exponential (40-h) phase. Both Northern and S1 analyses demonstrated that the level of *catA* mRNA in the absence of H_2O_2 increases slightly between 10 and 20 h of culture but decreases as cells enter stationary phase. The level of CatA polypeptide was determined under the same conditions by using anti-Cat4 antiserum. The results, presented in Fig. 4C, demonstrate that the level of CatA polypeptide increased slightly from 10 to 20 h, consistent with the increase in RNA level, but remained almost constant from 20 to 100 h. The level of the CatA polypeptide in rapidly growing cultures also increased about twofold in the presence of H_2O_2.

In Western blot analysis, we observed the emergence of a ~87-kDa polypeptide (CatB) that cross-reacted with anti-Cat4 antibody during the stationary phase of growth. This polypeptide is likely to correspond to one of the catalases enhanced in 100-h cultures, either Cat1 or the increased catalase comigrating with Cat4 (Fig. 3B). Another cross-reacting band (CatX) that is weaker than CatB was also observed. The significance of these bands in relation to total catalase activity is not clear at this point. Cells were also harvested from solid medium at stages of substrate, aerial, and sporulated mycelia and analyzed for CatA protein by Western blotting. The level of CatA did not change significantly, consistent with the behavior of *catA* gene expression observed in liquid culture (data not shown). The presence of the CatB polypeptide was observed in the later stages of growth when aerial mycelium and spores were present, consistent with the result in the liquid phase.

The characteristics of the *S. coelicolor catA* gene product and its mode of regulation suggest that *S. coelicolor* CatA is different from vegetative catalases of *E. coli* (HPI) and *B. subtilis* (catalase 1) in gene regulation and/or biochemical aspects. *E. coli* HPI is an *rpoS*-controlled catalase-peroxidase whose level increases during stationary phase (5, 12). *B. subtilis* catalase 1 is controlled by *spo0A* and increases during stationary phase (2). Since the level of CatA gradually increases and is inducible by H_2O_2 during the exponential growth phase, it is likely that the transcriptional level of the *catA* gene reflects the intracellular concentration of H_2O_2 and/or the specific growth rate. As suggested for HPI of *E. coli*, it may play a major role in reducing the concentration of H_2O_2 inside the cell (9).

Nucleotide sequence accession number. The nucleotide sequence of the *catA* gene has been deposited in the EMBL/GenBank/DDBJ database (accession no. X96981).

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