Genome-Wide Transcriptional Profiling of the *Escherichia coli* Responses to Superoxide Stress and Sodium Salicylate

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Escherichia coli responds to oxidative stress by activating sets of coregulated genes that help the cell to maintain homeostasis. Identified previously by genetic and biochemical approaches, the soxRS system mediates the induction of 18 of these redox-inducible genes (including the soxS gene itself). An overlapping set of genes is activated by an assortment of structurally unrelated molecules with antibiotic activities; many genes in this response are controlled by the marRAB system. The activation of either the soxRS or the marRAB system results in enhanced resistance to both superoxide-generating agents and multiple antibiotics. In order to probe the extent of these regulatory networks, we have measured whole-genome transcriptional profiles of the E. coli response to the superoxide-generating agent paraquat (PQ), an inducer of the soxRS system, and to the weak acid salt sodium salicylate (NaSal), an inducer of the marRA system. A total of 112 genes was modulated in response to PO, while 134 genes were modulated in response to NaSal. We have also obtained transcriptional profiles of the SoxS and MarA regulons in the absence of global stress, in order to establish the regulatory hierarchies within the global responses. Several previously unrelated genes were shown to be under SoxS or MarA control. The genetic responses to both environmental insults revealed several common themes, including the activation of genes coding for functions that replenish reducing potential; regulate iron transport and storage; and participate in sugar and amino acid transport, detoxification, protein modification, osmotic protection, and peptidoglycan synthesis. A large number of PO- and NaSal-responsive genes have no known function, suggesting that many adaptive metabolic changes that ensue after stress remain uncharacterized.

Escherichia coli responds to oxidative stress by modifying the expression of many genes. Early studies using two-dimensional gels to analyze variations in protein expression have shown that the synthesis of more than 80 proteins is activated in response to oxidative stress (19). Some of these induced proteins were identified as possessing fundamental antioxidant functions, e.g., superoxide dismutase and catalase. The search for mutants with altered antioxidant defenses led to the isolation and characterization of pleiotropic regulators that operate as redox-regulated genetic switches (3, 20, 42, 43, 45). The bestcharacterized pleiotropic regulators of the antioxidant responses are the OxyR and SoxR proteins (36). Both proteins have the remarkable ability of directly transducing oxidative signals to genetic regulation. Both proteins are expressed constitutively in an inactive state and are transiently activated in cells under specific types of oxidative stress. The activation of the OxyR and SoxR proteins results in the transcriptional enhancement of sets of genes (regulons) whose products relieve the stress by eliminating oxidants and preventing or repairing oxidative damage (36).

SoxR is a member of the MerR family of metal-binding transcription factors, and it exists in solution as a homodimer, with each subunit containing a [2Fe-2S] cluster. In nonactivated SoxR, these clusters are in the reduced state and their

oxidation activates SoxR as a powerful transcription factor (12, 16). Interestingly, SoxR can also be activated by nitric oxide (NO) by direct nitrosylation of the iron-sulfur clusters (11). The active (oxidized or nitrosylated) form of SoxR activates transcription of the soxS gene up to 100-fold. The soxS gene product, SoxS protein, belongs to the AraC/XylS family of DNA-binding transcription factors (3), but its activity seems to be regulated solely at the level of expression. Conventional analysis using limited proteomics and genetic approaches showed that SoxS activates the expression of 17 genes or operons. The known SoxS-activated genes are sodA (encoding Mnsuperoxide dismutase), fpr (NADPH-ferredoxin oxidoreductase), *micF* (antisense RNA, repressor of OmpF translation), ribA (cyclic GMP hydrolase), inaA (unknown function), fldA and *fldB* (flavodoxins A and B), *nfo* (endonuclease IV), marRAB (multiple-antibiotic-resistance operon), nfsA (also called *mdaA*, a nitroreductase), *zwf* (glucose-6-phosphate dehydrogenase), fur (an iron-binding repressor of iron uptake), fumC (fumarase C), acnA (aconitase), tolC (outer membrane protein), acrAB (drug efflux pump), and rimK (a modifier of ribosomal protein S6). Activating tolC, acrAB, micF, and rimK alters the sensitivity of E. coli and Salmonella enterica to a broad range of antibiotics (9, 10, 27, 33). SoxS is also a repressor of the soxS gene (34) and thus limits its own synthesis.

The diversity of genes activated by OxyR and SoxR illustrates the variety of cellular defense mechanisms against oxidative stress. Antioxidant mechanisms include the scavenging of reactive species (*sodA*, *ahpCF*), synthesis of reducing species (*acnA*, *zwf*), repair of oxidative damage (*nfo*, *fpr*), drug efflux (*acrAB*, *tolC*), reduction of cell permeability (*micF*), and replacement of redox-sensitive isozymes by redox-resistant isozymes (*fumC*). This variety is hardly surprising, given the

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large number of targets for oxidative damage; virtually all biological macromolecules can be damaged by oxidants. Particularly sensitive are electron-rich moieties, such as metal centers in proteins, unsaturated bonds in phospholipids, aromatic amino acids, and the double bonds of bases in nucleic acids (40). Oxidative stress has other, indirect effects, such as depletion of reducing power by consumption of NADH and NADPH in antioxidant reactions (40).

Interestingly, the induction of the marRAB regulon also results in enhanced resistance to oxidative agents and multiple antibiotics (3, 18). The genes of the marRAB regulon overlap significantly with those of the soxRS regulon (2, 5). This overlap evidently results from the structural similarity between the MarA and SoxS proteins and their respective DNA-binding sites (29, 30). Thus, two overlapping sets of genes are modulated by different signals sensed by different regulatory circuits. While the soxS gene is under the redox-regulated, positive control of SoxR, marA is under negative control by MarR, a repressor whose DNA-binding activity is regulated by the binding of small molecules with toxic effects (1, 31, 39). Among marRAB inducers are sodium salicylate (NaSal), the naphthoquinones menadione and plumbagin, and dinitrophenol. Although NaSal does not activate the soxRS regulon and although paraquat (PQ), a superoxide-generating agent, only marginally activates the marA regulon (30), the naphthoquinones activate both regulons (33). In contrast to PQ, menadione is a natural plant product. This fact has led to the hypothesis that the early evolution of the soxRS and marA regulons was shaped by the environmental stress mediated by naphthoquinones and other noxious xenobiotics from natural sources (33).

Although a complete profile of the cellular responses to oxidative stress has been lacking, the availability of the complete sequence of the *E. coli* genome now provides important tools for analyzing gene expression. The analysis of the variations of the "transcriptome," or transcriptional profiling, has already yielded abundant biological information in several organisms, including *E. coli* (4, 37, 44), *Bacillus subtilis* (14), *Caulobacter crescentus* (25), and *Saccharomyces cerevisiae* (15, 23).

Here we have determined genome-wide transcriptional profiles of *E. coli* cells exposed to the superoxide-producing agent PQ or to NaSal. We have also begun to dissect regulatory hierarchies within these responses by expressing, in the absence of stress, individual transcription factors that respond to environmental insult.

MATERIALS AND METHODS

Bacterial strains and plasmids. E. coli strain GC4468 (K-12 $\Delta lacU169 \ rpsL$) (19) was used as the wild type in all experiments. The GC4468 $\Delta soxRS$ derivative DJ901 (20) transformed with pJP105 (*placZ:soxS lacI* Ap^r) (35) was used in the SoxS expression experiment. The GC4468 $\Delta marRAB$ derivative MB106 was constructed for this study by transduction of the kanamycin-tagged 1.24-kb deletion spanning the *marRAB* operon from strain AG100/Kan (28) and was transformed with pMB102 (*placZ:marA lacI* Ap). Plasmid pMB102 was constructed by replacing the *robA* gene in plasmid pMB101 (6) with a PCR product containing the *marA* gene. The sequence of the cloned *marA* gene was confirmed at the Molecular Biology Core Facility of the Dana-Farber Cancer Center.

Culture growth and RNA isolation. Overnight cultures were diluted 1/100 in 15 ml of Luria broth contained in 125-ml Erlenmeyer flasks and were grown at 37° C and 250 rpm to an optical density at 600 nm (OD₆₀₀) of 0.5. At this point, the cultures were either left untreated or exposed to the different inducers for 45



FIG. 1. Growth of *E. coli* strain GC4468. OD₆₀₀ as a function of time for strain GC4468 was measured. The cultures were either left untreated (empty circles) or treated with 250 μ M PQ (filled circles). PQ was added to log-phase cultures (empty arrow), and cells were harvested after 45 min (filled arrow). For detailed culture conditions, see Materials and Methods.

min. The cells were harvested by centrifugation of 1.5-ml aliquots in a microcentrifuge for 30 s. An RNAeasy kit (Qiagen) was used to lyse the cells and extract total RNA. The RNA preparation obtained from the RNAeasy columns was extracted with phenol (pH 5.0) at 60°C, followed by extraction with a mixture of acidic phenol and chloroform and finally with chloroform alone. The RNA was precipitated with 90% ethanol and 3 M sodium acetate overnight at -20°C and was recovered by centrifugation for 10 min at 4°C. The RNA pellet was washed twice with cold 70% ethanol, dried in a Speed-Vac, and resuspended in diethylpyrocarbonate-treated water. The RNA was quantified by light absorption at 260/280 nm. Samples of the RNA were separated by electrophoresis in agarose gels and stained with ethidium bromide to verify the purity and integrity of the RNA preparation, using the 16S and 23S ribosomal bands as indicators. The absence of chromosomal DNA was verified by using the RNA preparations as the template in PCR amplifications. Briefly, ~100 ng of total RNA or ~20 ng of chromosomal DNA was incubated in PCR cocktails containing sodB-specific primers. While the reactions containing chromosomal DNA consistently yielded a DNA fragment of the expected size, the reactions containing RNA preparations always failed to yield a product.

cDNA synthesis. The RNA preparations from each sample were used as the template for cDNA synthesis by employing a commercial set of 4,290 open reading frame (ORF)-specific oligonucleotides (Sigma-Genosys) as primers. A total of 1 μ g of total RNA was incubated in reaction buffer with the ORF-specific oligonucleotides, dTTP, dATP, and dGTP, at 90°C for 2 min and was then cooled to 42°C at a rate of 2.4°C/min. Two hundred units of avian myeloma virus reverse transcriptase (Sigma-Genosys) was added to each reaction, together with 20 μ Ci of [³³P]dCTP (3,000 Ci/mmol). The mixture was incubated at 42°C for 2 h. Labeled products were purified on gel filtration columns (Sephadex G-50).

Hybridization. The Panorama gene arrays (Sigma-Genosys) are positively charged nylon membranes onto which ORF-specific PCR products have been spotted in duplicate. The arrays represent the complete set of known and predicted ORFs as deduced from the complete genomic sequence of the *E. coli* K-12 strain MG1655 (7). For all experiments, a pair of membranes was used: one was hybridized with cDNA synthesized from the untreated cell culture, and the other was hybridized with the cDNA synthesized from the treated cell culture. Hybridization and washing steps were carried out following the manufacturer's instructions. The nylon filters were prehybridized at 65°C for 1 h in cylindrical tubes containing 5 ml of hybridization solution (5× SSPE [1× SSPE is 0.18 M NaCl, 10 mM sodium phosphate, and 1 mM EDTA {pH 7.7}], 2% sodium dodecyl sulfate, 1× Denhardt's reagent, and 100 µg of sonicated salmon testes DNA/ml). The whole cDNA preparation was first denatured at 100°C in 3 ml of hybridization solution solution solution the tubes and replaced by the mix containing the labeled cDNA. The filters were hybridized for



FIG. 2. Scatter plot of expression levels for the *E. coli* genome: untreated and PQ-treated cells. The percent total intensity for each gene represented in the arrays is plotted on a log scale. A relatively small number of genes had associated signal intensities that were below average background levels. The subtraction of the background value from these signals resulted in a negative corrected value and therefore a negative percentage of total signal. These genes were given an arbitrary value of 0.000001% of total intensity.

~16 h at 65°C in a rotary oven. After this, the filters were rinsed with washing solution ($0.5 \times$ SSPE, 0.2% sodium dodecyl sulfate) twice at room temperature and three more times at 60°C. The filters were then air dried and wrapped in clear plastic film. Two series of experiments were performed using two different pairs of membranes. For each experimental series, the hybridized membranes were stripped and reprobed up to four times, following the procedures recommended by the manufacturer.

Array imaging and analysis. Phosphorimaging screens were exposed to the hybridized filters for 48 to 72 h at room temperature. The screens were scanned in a Storm 840 PhosphorImager (Molecular Dynamics) at a 50-µm resolution. The resulting files were analyzed by determination of pixel density using Arrayvision software, which determined the intensity of each duplicate spot, measured in arbitrary units. The background signal was determined for each filter by averaging the intensities of 42 spots that did not contain DNA. This average background was then subtracted from the intensity at each DNA spot, and the corrected intensity of each spot was expressed as a percentage of the sum of all intensities. This treatment allowed comparison between filters independently of total hybridization intensity. The corrected intensities of duplicate spots were averaged, and the untreated and treated intensities from two independent experiments were averaged. The expression ratio for each gene was calculated as the treated/untreated intensities. Thus, an expression ratio of 1 indicated an invariable level of a transcript, whereas expression ratios larger or smaller than 1 indicated up- or down-regulated levels of mRNA, respectively.

Two stringency criteria were applied to each data set. First, only those genes were further analyzed that had an expression level equal to the average background plus 3 standard deviations in at least one of the culture conditions in both duplicate experiments. This minimum expression threshold helped to discard genes with very low expression in control or experimental samples with a confidence of 99.9%. Second, only those genes for which the log of the expression ratio was equal to the mean plus or minus 2.5 standard deviations were considered activated or down-regulated, respectively. This statistical threshold provides ratios that are significantly different from the mean with confidence higher than 99%. Gene annotation. The expression values and ratios for each gene were transferred to Excel spreadsheets for statistical analysis and integration into updated, annotated databases (38), accessible online (http://genprotec.mbl.edu).

Web access. The complete data sets for all experiments are available online (http://www.hsph.harvard.edu/demplelab/genomics).

Gene probe synthesis and Northern blot analysis. The RNA samples used in the gene array experiments were also used in Northern blot experiments as an independent way to assess the quantitative validity of transcriptional profiling. Probes for specific genes were generated by PCR amplification using chromosomal DNA from strain GC4468 as template and gene-specific primers (ORFmers) obtained from Sigma-Genosys. Typically, PCR amplifications were carried out in 30 cycles of annealing at 60°C (45 s), elongation at 72°C (1 min), and denaturation at 94°C (30 s). The PCR products were resolved by electrophoresis in 1.25% agarose gels, recovered by excision from the gel, and purified using Qiaquick DNA-binding microspin columns (Qiagen). The DNA fragments were labeled by nick translation using a Klenow DNA polymerase fragment, random hexamers (Gibco BRL), and [32P]dCTP (3,000 Ci/mmol) plus unlabeled dATP, dGTP, and dTTP. The labeled probe was purified by gel filtration in Sephadex G-25 columns (Pharmacia). For the Northern blot experiments, 2 µg of total RNA was run per lane in 1.25% agarose gels containing formaldehyde and was transferred to Nytran membranes using a Turboblotter setup (Schleicher & Schuell). The RNA was cross-linked to the membrane by UV irradiation, and the membranes were then hybridized at 65°C with radioactively labeled DNA fragments in cylindrical tubes using QuickHyb solution (Stratagene). The membranes were washed according to the instructions from the manufacturer. X-ray films were exposed to the membranes at -70° C and were developed using a Fuji automatic developer. The radioactive signals were measured using an Applied Biosystems phosphorimager.

RESULTS

A transcriptional profile of *E. coli* exposed to PQ. The genomic transcriptional profile of *E. coli* growing on Luria

TABLE 1. PQ-regulated genes^a

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Gene type	No.	Gene	Ratio	Description
PO-activated	b0463	acrA	2.0	AcrAB efflux system effects Mar multiple resistance
	b0605	ahnC	2.8	Alkyl hydroperoxide reductase small subunit
	b1415	aldA	2.3	Aldehyde dehydrogenase. NAD linked
	b0863	artI	1.9	Periplasmic binding protein of Arg transport system
	b0864	artP	19	Arg periplasmic transport system
	b0710	b0710	2.0	Function unknown
	b1378	b1378	17	Putative pyruvate-flavodoxin oxidoreductase
	b1452	b1452	1.7	Function unknown
	b2251	b2251	1.9	CPS 52 prophage: putative bectopropel glucocul transferrese
	b2062	b2062	1.7	Eurotion unknown
	02902 b4121	02902	2.4	Function unknown
	04131 b4122	cuuA	1.0	Demietery gene
	04155 h2109	cuae	2.4	Creach round a related
	02196 h0420	ccmD	1.7	Cytochrome c-related
	00429 50750	cyoD	1.7	Cytochionie o oxidase subunit 1 v
	02/52	cysD	1./	Suitate adenyiyiransierase
	D2414	CYSK	1.9	Cysteine synthase A
	b1190		1./	Alanine racemase
	64383	deoB	1.9	Deoxyribouratase, phosphopentomutase
	60184	dnaE	2.0	DNA polymerase III, alpha subunit
	60812	dps	1.7	Stress response DNA-binding protein
	<u>b0684</u>	fldA	4.7	Flavodoxin
	b3288	fmt	1.8	Methionyl-tRNA formyltransferase
	<u>b3924</u>	fpr	3.6	Ferredoxin NADP ⁺ reductase; anaerobic
	<u>b1611</u>	fumC	6.9	Fumarase C
	<u>b0683</u>	fur	2.2	Ferric iron uptake, negative regulatory gene
	b2094	gatA	2.9	Galactitol-specific enzyme IIA of PTS ^b
	b2093	gatB	3.7	Galactitol-specific enzyme IIB of PTS
	b2091	gatD	1.7	Galactitol-1-phosphate dehydrogenase
	b0450	glnK	1.8	Regulated through NRI/NRII two-component regulatory system
	b0720	gltA	3.1	Citrate synthase
	b2552	hmpA	1.8	Dihydropteridine reductase 2 and nitric oxide dioxygenase NAD/FAD activity
	b0440	hupB	1.7	Histone-like protein HU-alpha, HU-1
	b2237	inaA	2.9	Function unknown
	b4036	lamB	4.8	Maltose high-affinity uptake
	b0096	lnxC	2.0	Cell envelope and cell separation
	b4034	malE	2.1	Maltose-binding protein, periplasmic: transport and chemotaxis
	b4035	malK	19	Maltose transport complex ATP-hinding subunit
	b0168	man	1.5	Methionine aminopentidase
	b1531	marA	2.6	Transcription activator of multiple-antibiotic-resistance system
	b0086	murF	17	D_Alanyl:D_alanine_adding enzyme
	b0578	nfnR	2.1	Devistance to nitrofurantoin: a nitroreductase
	b2281	njnD nuol	2.1	NADH debydrogenose I subunit
	b2201	nuor	1.0	NADII dehydrogenase I subunit
	02279 b0112	nuok	1.9	NADH deliydiogenase i subulli
	00115	pank	1.9	Characterization of the second s
	D4025	pgi	2.1	Giucose prosphate isomerase
	D1101	ptsG	3.3	P15 family enzyme file, glucose-specific
	b1658	purR	1.9	Purine repressor
	63317	rplB	1.9	50S ribosomal subunit protein L2
	63319	rplD	2.5	50S ribosomal subunit protein L4
	63305	rplF	1.7	50S ribosomal subunit protein L6
	b3985	rplJ	1.7	50S ribosomal subunit protein L10
	b3318	rplW	1.8	50S ribosomal subunit protein L23
	b3312	rpmC	1.7	50S ribosomal subunit protein L29
	b3314	rpsC	1.7	30S ribosomal subunit protein S3
	b3321	rpsJ	2.0	30S ribosomal subunit protein S10
	b3316	rpsS	1.7	30S ribosomal subunit protein S19
	b0724	sdhB	1.8	Succinate dehydrogenase iron-sulfur protein
	<u>b390</u> 8	<i>sodA</i>	12.3	Superoxide dismutase, Mn
	b4062	soxS	2.3	Regulatory protein of <i>soxRS</i> regulon
	b0729	sucD	1.9	Succinyl-coenzyme A synthetase alpha subunit
	b3708	tnaA	2.4	Tryptophanase
	b0850	vhiC	17	Function unknown
	h2523	yfhI	1 9	Pentidase B: aminopentidase
	b3520	vhiR	3.4	Putative transcriptional regulator (LuxR/LlhnA family)
	h4217	vtfK	23	Function unknown
	h1852	yujix 7wif	2.5	Glucose-6-phosphate dehydrogenase
	01032	~wj	4.1	Shuesse o phosphate denyarogenase

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TIDLE I COMMINCI	TABLE	1—C	ontinued
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Gene type	No.	Gene	Ratio	Description
PQ-down-regulated	b3237	argR	0.6	Repressor of Arg regulon
	b4139	aspA	0.5	Aspartate ammonia-lyase (aspartase)
	b0218	<i>b0218</i>	0.3	Function unknown
	b0271	<i>b0271</i>	0.5	Function unknown
	b0938	<i>b0938</i>	0.6	Function unknown
	b1029	b1029	0.4	Function unknown
	b1567	b1567	0.6	Qin prophage
	b1903	b1903	0.5	Function unknown
	b2102	b2102	0.5	Function unknown
	b2355	b2355	0.5	Function unknown
	b2629	b2629	0.4	Function unknown
	b2768	b2768	0.6	Function unknown
	b0032	carA	0.5	Carbamoylphosphate synthase (glutamine-hydrolyzing) light subunit
	b0620	criR	0.5	Response regulator in two-component regulatory system with DpiB
	b1575	dicB	0.5	Control of cell division. Activates MinC
	b2369	evgA	0.6	Multicopy on plasmid in strain with a deletion of $envZ$ induces $ompC$ expression
	b2323	fabB	0.4	Beta-ketoacyl-acyl carrier protein synthase I
	b1925	fliS	0.5	Flagellar synthesis; flagellar regulon member
	b2025	hisF	0.5	Cyclase component of IGP synthase complex
	b3580	lvxK	0.5	L-Xylulose kinase, cryptic
	b0923	mukE	0.5	Involved in chromosome partitioning
	b1224	narG	0.3	Nitrate reductase alpha subunit
	b3480	nikE	0.6	Formate hydrogen-lyase activity
	b0929	ompF	0.2	Outer membrane protein, porin
	b4245	<i>pvrB</i>	0.3	Aspartate transcarbamylase, catalytic subunit
	b0945	pvrD	0.5	Dihydroorotate oxidase
	b4387	smp	0.6	Membrane protein
	b1656	sodB	0.5	Superoxide dismutase. Fe
	b1646	sodC	0.6	Superoxide dismutase, Cu, Zn
	b2497	uraA	0.4	Uracil concentration dependence of <i>pvr</i> mutants: Ura ABC transporter
	b0193	vaeF	0.4	Function unknown
	b0315	vahA	0.6	Putative transcriptional repressor (LuxR/UhpA family)
	b1347	vdaC	0.6	Rac prophage
	b2597	vfiA	0.5	Ribosome-associated factor, stabilizes ribosomes against dissociation
	b3087	vgiR	0.4	Putative NADP-binding dehydrogenase
	b3088	voiT	0.5	Putative transmembrane protein
	b3112	vhaQ	0.5	Anaerobic nathway I-serine deaminase I-serine dehydratase
	b3516	vhiX	0.5	Putative transcriptional regulator (AraC/XvlS family)
	b3582	viaR	0.5	Putative hexulose-6-nhosnhate isomerase
	b3879	vihR	0.5	Putative aldose-1-enimerase
	b3888	viiD	0.5	Putative addise i opinierase
	b4048	vibM	0.5	Function unknown
	h4333	viiK	0.5	Putative outer membrane protein
	b4337	viiO	0.0	Putative transport protein
	b4380	viiI	0.4	Function unknown
	b/20/		0.0	Function unknown
	04324	y]]A	0.4	

^a No., unique identifier. Boldface denotes genes modulated by either exposure to PQ or expression of SoxS. Underlining denotes previously characterized soxRS genes.

^b PTS, phosphotransferase system.

broth under superoxide stress was determined by comparison of cultures in which one sample was left untreated while the other was exposed to 250 μ M PQ for 45 min. This concentration of PQ induced the genes of the *soxRS* regulon (35) but failed to inhibit growth rate in any substantial way during the 45-min exposure. We expected that these exposure conditions would prevent the activation of "general stress" pathways that generally accompanies growth inhibition (22) and would thus maximize the chance to identify specific, oxidative stress-responsive genes. Figure 1 shows the growth of the untreated and PQ-treated cultures and demonstrates the lack of effect of the chosen PQ concentration on growth during the 45-min exposure.

Total RNA was extracted from treated and untreated cul-

tures and was used to synthesize cDNA, which was hybridized to gene arrays. The radioactive signal from each spot in the arrays served as a measure of the expression level of each gene and was used to calculate the expression ratio between the PQ-treated and untreated cultures for all genes in duplicate experiments (see Materials and Methods). Figure 2 shows the correlation between the treated and untreated samples of the averaged expression levels for the 4,290 genes and control spots represented in the arrays for one experiment. It is clear that the vast majority of the mRNAs did not vary significantly with exposure to PQ, an observation substantiated by a correlation coefficient of 0.987 between the expression values for the untreated and PQ-treated cells. Table 1 shows the genes that were activated or down-regulated significantly after exposure



FIG. 3. Comparison of expression ratios from transcriptional profiling and Northern blots. (A) Total RNA was extracted from untreated or PQ-treated cultures (250μ M for 45 min). Aliquots from these preparations were used as a template for cDNA synthesis and hybridization with gene arrays or were run in agarose gels, transferred to Nytran membranes, and probed with labeled gene-specific PCR fragments. The expression ratio of 21 genes is shown for Northern blotting (horizontal axis) or cDNA synthesis and hybridization to gene arrays (vertical axis). The genes tested were *cyoD*, *cysK*, *dnaE*, *gshB*, *inaA*, *lpxC*, *nadE*, *nfo*, *nupC*, *pdhR*, *ptsG*, *pyrB*, *rpsS*, *sodA*, *speE*, *uraA*, *yadJ*, *ybjC*, *yhiM*, and *zwf*. See Materials and Methods for detailed protocols. (B) Northern blots of the *nfo*, *yaiA*, *uraA*, *sodA*, *gshB*, and *ptsG* genes. –, absence of PQ; +, presence of PQ. A replicate gel was run and stained with ethidium bromide (EtBr), revealing the 16S and 23S rRNA, which serves as loading control.

of growing cells to PQ. The complete data set for the genomewide expression ratios is available online (http://www.hsph .harvard.edu/demplelab/genomics). In total, 112 genes were modulated by PQ beyond threshold levels, with 66 genes activated and 46 down-regulated. Of the 16 SoxS-activated genes represented in the array, 9 were detected. Of the remaining seven SoxS-activated genes, five (*nfo, rimK, tolC, fldB,* and *mdaA*) were activated with values below threshold while one (*ribA*) appeared slightly repressed. The *micF* gene codes for an untranslated RNA and therefore is not represented in the array. However, the down-regulation of *ompF*, the effect of *micF* induction, was registered (Table 1).

The *hmpA* gene, which encodes a hemoglobin-like protein and is induced by PQ in a *soxRS*-independent manner (32), was also detected by the gene array experiments. Only two OxyRregulated genes (*ahpC* and *dps*) were activated above the statistical threshold, indicating that the levels of hydrogen peroxide generated under our conditions were relatively low. Finally, 7 of the activated genes and 22 of the down-regulated genes have no function known at this time. The absence of induction of any heat shock genes or genes for stress-responsive sigma factors was consistent with the lack of growth inhibition by PQ. Thus, the observed transcriptional profile of the response to PQ bears most of the hallmarks of the known responses to superoxide stress while providing abundant new information on putative antioxidant functions.

Validation by Northern blotting of expression ratios from transcriptional profiling. In order to test independently the values for the expression ratios obtained from the gene arrays, we performed Northern blot analysis for 21 genes. The same RNA samples used as templates in one of the PO-treatment experiments were run on an agarose gel, transferred to nylon membranes, and hybridized with labeled gene probes (see Materials and Methods). The intensity of each signal was measured by phosphorimaging, and the expression ratio (treated/ untreated intensities) was calculated for each gene. Figure 3A shows the comparison of the expression ratios obtained from gene array experiments and conventional Northern blots. The 21 genes selected for the comparison included 11 genes that scored as activated in the gene array experiment, 7 genes that scored as unmodified (expression ratios between 0.5 and 2), and 3 genes that scored as down-regulated. In general, the results of the two methods were similar across at least 2 orders of magnitude. However, the correlation between the Northern blot and the array values was weaker for genes with basal (or down-regulated) expression levels that were close to background. Figure 3B shows three examples of genes (nfo, uraA, and yaiA) with comparatively large differences between the expression ratios obtained by transcriptional profiling and Northern blotting. In all three cases, the basal or down-regulated level of mRNA was extremely low as estimated by Northern blotting. In contrast, genes with detectable basal levels 10



FIG. 4. Growth of *E. coli* GC4468 exposed to NaSal. OD_{600} as a function of time for strain GC4468 was determined. The cultures were either left untreated (empty circles) or treated with 5 mM NaSal (filled circles). NaSal was added to log-phase cultures (empty arrow), and cells were harvested after 45 min (filled arrow). For detailed culture conditions, see Materials and Methods.

(*sodA*, *gshB*, and *ptsG*) show good correlation in their expression ratios measured by the two methods (Fig. 3A).

A search for novel SoxS-regulated genes. Although transcriptional profiling provides information about relative RNA levels, it does not establish regulatory hierarchies among genes. In an effort to begin dissecting the regulatory cascade within the response to PO, we expressed SoxS protein in the absence of oxidative stress. The plasmid pJP105 expresses the SoxS protein from an isopropyl-B-D-thiogalactopyranoside (IPTG)-regulated promoter and has been used to identify SoxS-regulated operon fusions (35). The activity of the SoxS protein is regulated exclusively by its intracellular concentration, and thus the artificial induction of soxS expression from pJP105 should be sufficient to modulate all genes of the soxRS regulon. The *E. coli* strain DJ901 ($\Delta soxRS$) was transformed to Apr with plasmid pJP105, and cultures were either left untreated or were treated with IPTG. The labeled cDNA from these cultures was hybridized to Panorama gene arrays, and the blots were analyzed using the same stringency conditions applied to the PQ experiment. Again, the vast majority of genes was unaffected, with only 95 genes modulated beyond the statistical threshold: 37 genes were activated and 58 genes were down-regulated. The activated genes included 11 out of the 16 known SoxS-activated genes represented in the gene array (data not shown). The indirect down-regulation of ompF was also registered. Of the 37 SoxS-activated genes revealed by transcriptional profiling, 14 were also registered in the PQ exposure experiments. The genes that were activated both by PQ and by expression of SoxS are indicated in Table 1 in boldface. The complete results from the SoxS-expression experiment can be obtained online (http://www.harvard.hsph.edu /demplelab/genomics).

A transcriptional profile of the *E. coli* response to NaSal. NaSal is a natural product with a role in signal transduction in the response to plant infection (8). In the millimolar concentration range, NaSal dissipates the proton gradient across the inner membrane, chelates iron, inhibits growth, and induces the heat shock and *marA* regulons (41), the latter by binding to the repressor of the *marRAB* operon (31, 39). In order to characterize the global response to NaSal and to identify novel regulatory overlaps with the response to PQ, the transcriptional profile of growing cultures of *E. coli* treated with NaSal was determined.

The concentration of NaSal used (5 mM) was chosen because it has been used experimentally to induce the *marA* regulon (30). Figure 4 shows that this concentration of NaSal inhibited growth; therefore, we expected to observe both a NaSal-specific and a "general stress" response.

Figure 5 depicts the correlation of averaged expression levels for the 4,290 genes and control spots between the untreated and NaSal-treated samples, which shows that the expression of most genes was unaffected by the treatment. Table 2 shows the genes that were significantly activated or down-regulated after the NaSal exposure. The complete data set for the genome-wide expression ratios is available online (http://www.hsph .harvard.edu/demplelab/genomics). In total, 144 genes were modulated beyond threshold levels in response to NaSal, with 84 genes activated and 60 down-regulated.

Of the 62 genes postulated to be activated by MarA (5), 19 were detected in our NaSal experiments and an additional 22 were modulated following the previously reported trend but below our statistical threshold. As expected from its inhibitory effect over growth and from previous observations (41), NaSal activated a set of genes associated with general cell stress and damage. These included genes coding for proteins involved in heat shock (*dnaK*), an inhibitor of cell division (*sulA*), adenylate cyclase (cyaA), and several rpoS-activated genes: the DNAbinding iron chelator (dps), two periplasmic proteins (hdeAB), and a catalase (katE). The genes encoding the global regulators σ^{S} (*rpoS*) and σ^{E} (*rpoE*) were also activated, albeit under threshold levels. Exposure to NaSal also produced a downregulation of genes coding for translation machinery elements (e.g., ribosomal proteins and elongation factors) and ATP synthase subunits. Thus, the response to NaSal exposure bears the hallmarks of the activation of marA-regulated genes, plus a substantial number of the characteristics of a growth-limited culture.

A search for MarA-regulated genes. To begin dissecting the regulatory cascade of the response to NaSal, we expressed MarA in the absence of exogenous toxic agents. The plasmid pMB102 harbors the marA gene under the control of an IPTGregulated promoter. As with SoxS, the activity of the MarA protein is regulated exclusively by its intracellular concentration (2). Thus, the artificial induction of marA from pMB102 should be sufficient to modulate all MarA target genes. Cultures of an E. coli ΔmarRAB strain containing plasmid pMB102 were grown and either left untreated or treated with IPTG. After 45 min, total RNA was extracted from both cultures and analyzed by hybridization to gene arrays. As for the previous experiments, background-corrected expression values were determined and used to calculate the expression ratios for each gene and the same significance thresholds were applied. In total, 88 genes were modulated by MarA expression; 67 genes were activated and 21 genes were down-regulated. The acti-



FIG. 5. Scatter plot of expression levels for the *E. coli* genome: untreated and NaSal-treated cells. The percent total intensity for each gene represented in the arrays is plotted on a log scale. A relatively small number of genes had associated signal intensities that were below average background levels. The subtraction of the background value from these signals resulted in a negative corrected value and therefore a negative percentage of total signal. These genes were given an arbitrary value of 0.000001% of total intensity.

vated genes include 21 of the 62 postulated MarA-regulated genes (5) (data not shown). An additional 19 genes had similar expression trends as reported but fell below our statistical threshold. Those genes activated both by exposure to NaSal and by expression of MarA, 20 in total, are indicated in bold-face in Table 2. The complete results from the MarA-expression experiment can be obtained online (http://www.hsph .harvard.edu/demplelab/genomics).

The overlap between the PQ and NaSal stimulons. Sixteen genes were modulated with the same trend by both PQ and NaSal (Table 3). Some genes were known from standard genetic studies to be regulatory targets for SoxS and MarA (fumC, inaA, marA, and sodA). In addition, the PQ- or SoxSresponsive genes gatABD, gltA, nfnB, and ybjC were recently shown to be activated by constitutive expression of MarA (5). The ybjC gene was also activated by expression of SoxS in our experiments (Table 1). This study identified five additional genes activated by both PQ and NaSal. These genes code for products involved in arginine transport (artP), cysteine synthesis (cysK), protection of DNA from iron-mediated oxidative damage (dps), and salvage of nucleotides (deoB). One other gene, activated by both PQ and NaSal, has no known function or extensive homology to any other gene of known function (b1452). Only one gene was down-regulated by both treatments: pyrB, which codes for aspartate transcarbamylase, involved in pyrimidine biosynthesis.

A second group of 10 genes was commonly regulated by exposure to PQ or NaSal but with opposite trends (Table 3). Eight of these genes code for ribosomal proteins, one codes for a ribosome-associated factor, and the last one codes for a putative member of the AraC/XylS family of transcriptional regulators.

DISCUSSION

We have used a functional genomics approach to identify novel genes that respond to oxidative stress. In all the experiments, our results not only bear the hallmarks of the cellular responses that we intended to evoke but also provide new insights in the physiology of oxidative stress. The resulting tally of the genes involved in these responses should be considered an underestimate for reasons that are inherent to the method used. First, commercially available gene arrays are a fixed platform that do not admit modifications. The arrays used excluded untranslated RNAs, which are clearly involved in responses to changing redox conditions (46-48). Second, transcriptional profiling reveals only comparative, steady-state levels of mRNAs, without any information about posttranscriptional processes or actual protein expression. Third, despite the almost complete coverage of the genome, transcriptional profiling experiments consistently fail to detect changes in genes known to be modulated by the stimuli of interest. For example, the use of gene arrays to analyze the heat shock response revealed only 23 of the 51 known genes (37). Finally, the results can vary significantly between transcriptional profiling experiments. We have tried to address this problem by averaging replicate experiments and by establishing statistical thresholds for the expression ratios beyond 99% confidence.

TABLE 2. NaSal-regulated genes^a

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b3908sodA2.3Member of soxRS regulon; superoxide dismutase, Mnb2703srlA_22.7PTS family, glucitol/sorbitol-specific enzyme IIB component		b3284	smg	2.1	Function unknown
b2703 srlA_2 2.7 PTS family, glucitol/sorbitol-specific enzyme IIB component		b3908	sodA	2.3	Member of soxRS regulon; superoxide dismutase, Mn
		b2703	$srlA_2$	2.7	PTS family, glucitol/sorbitol-specific enzyme IIB component

TABLE 2-Continued

w0938su4.2.9Inhibits cell division and <i>fu2</i> ring formationb1004wrled2.1Affects association between Try repressor and operators in stationary phaseb10707by642.1Function unknownb10850ybfC2.7Function unknownb10850ybfC2.7Function unknownb10850ycf2.6Function unknownb2379ycf2.8Function unknownb2387ysff2.9Putative transcriptional regulator (AraCXySf family)b35161ybfX2.9Putative transcriptional regulatorb35161ybfX2.9Putative transcriptional regulatorb4378yjfY2.2Putative transcriptional regulatorb4378yjfY2.2Putative transcriptional regulatorb4378yjfY2.2Putative transcriptional sequenceb35161ybfX3.9Ferric bydxoxanate transportb4373apf0.4Membrane-bound ATP synthase, F1 sector, epsilon subunitb3736apf0.3Membrane-bound ATP synthase, F1 sector, deta subunitb3737apf0.4Membrane-bound ATP synthase, F1 sector, deta subunitb3738apf0.2Turanive phydrolaseb3749apf0.4Membrane-bound ATP synthase, F1 sector, deta subunitb3739apf0.4Putative transcriptional service for KNA operonsb3340(isc40.4Ventrimenhour for KNA operonsb3341(isc40.4Putative transcriptional service	Gene type	No.	Gene	Ratio	Description
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b(707) $jkpd$ 2.1Function unknownb(703) $jkpd$ 2.2Putation minkownb(805) jkd 2.7Function unknownb(805) jkd 2.6Function unknownb(703) jkd 3.4Ribroome-associated factor, stabilizes ribosomes against disociationb(704) jkd 2.9Putative transcriptional regulatorb(704) jkd 2.9Putative transcriptional regulatorb(704) jkd 2.9Putative transcriptional regulatorb(705) jkd 2.8Putative transcriptional regulatorb(705) jkd 2.8Putative transcriptional regulatorb(705) jkd 2.8Putative transcriptional regulatorb(705) jkd 2.8Putative transcriptional science of the stability		b1004	wrbA	2.1	Affects association between Trp repressor and operators in stationary phase
b0719 $jkpD$ 2.2Putatice finabria-like proteinb0839 jkD 2.6Function unknownb1003 ycd 2.6Function unknownb2346 jfd 3.0Rtbosome associated factor, stabilizes ribosomes against dissociationb2346 jfd 3.0Rtbosome associated factor, stabilizes ribosomes against dissociationb2346 jfd 3.0Putative transcriptional regulator (AraCXyls family)b4357 $jjkS$ 3.9Perric hydrosumate transportb4367 $jjkS$ 3.9Perric hydrosumate transportb4378 $jglD$ 2.8Function unknownb4378 $gglD$ 0.4Membrane-bound ATP synthase, F1 sector, alpha subunitb4374 $ergC$ 0.4Membrane-bound ATP synthase, F1 sector, alpha subunitb3736 $ergP$ 0.3Membrane-bound ATP synthase, F1 sector, alpha subunitb3737 $ergP$ 0.3Membrane-bound ATP synthase, F1 sector, alpha subunitb3738 $ergP$ 0.3Membrane-bound ATP synthase, F1 sector, alpha subunitb3739 $ergP$ 0.3Membrane-bound ATP synthase, F1 sector, alpha subunitb3739 $ergP$ 0.3Membrane-bound ATP synthase, F1 sector, alpha subunitb3749 $ergP$ 0.4Membrane-bound ATP synthase, F1 sector, alpha subunitb3749 $ergP$ 0.4Membrane-bound ATP synthase, F1 sector, alpha subunitb3749 $ergP$ 0.4Membrane-bound ATP synthase, F1 sector, alpha subunitb3759 $ergP$ 0.4Membrane-bound ATP		b0707	ybgA	2.1	Function unknown
$ b0850 ptpC = 2.7 Function unknown \\ b1098 yrgC = 2.3 Function unknown \\ b2307 ytpA = 2.0 Function unknown \\ b2307 ytpA = 2.0 Function unknown \\ b2306 ytpB = 2.0 Function unknown \\ b2307 ytpG = 2.0 Function unknown \\ b2308 ytpD = 2.0 Function unknown \\ b2308 ytpD = 2.0 Function unknown \\ b2378 ytpV = 2.2 Futative transcriptional regulator (AraC/XytS fumily) \\ b4378 ytpV = 2.2 Futative transcriptional regulator (AraC/XytS fumily) \\ b4378 ytpV = 2.2 Futative transcriptional transport \\ b4378 aptA = 0.4 Membrane-bound ATP synthase, F1 sector, sloph a subunit \\ b3739 aptA = 0.4 Membrane-bound ATP synthases (F1 sector, sloph a subunit b3739 aptA = 0.4 Membrane-bound ATP synthases (F1 sector, sloph a subunit b3739 aptA = 0.4 Membrane-bound ATP synthases (F1 sector, sloph a subunit b3739 aptA = 0.4 Membrane-bound ATP synthases (F1 sector, sloph a subunit f1 sector, sloph a subunit f1 sector, sloph a subunit f1 f1 sector (F1 sector) ($		b0719	ybgD	2.2	Putative fimbria-like protein
		b0850	ybjC	2.7	Function unknown
h 1988 yegC 2.3 Function unknown h 2597 yfr.4 34 Ribosome-associated factor, stabilizes ribosomes against dissociation h 2546 yegV 20 Function unknown h 2555 yir.4G 3.3 Putative transcriptional regulator (AraCAXIS family) h 2555 yir.4G 3.3 Putative transcriptional regulator h 2576 yir.5 yir.4G 3.3 Putative transcriptional regulator h 2578 yir.4G 2.4 Putative transcriptional regulator h 2578 yir.4G 2.5 Putative transcriptional regulator h 2578 yir.4G 2.5 Putative transcriptional regulator h 2578 yir.4G 2.6 Putative transcriptional regulator h 2579 yir.4G 2.6 Putative transcriptional regulator h 2579 yir.4G 2.7 Transcriptional active for rRNA operoas h 2520 fibs 0.2 Putative transcriptional activator for rRNA operoas h 2520 fibs 0.2 Putative transcriptional protein, protease VII h 2520 pm/f 0.4 Primosomal protein N h 2521 fibs 0.2 Putative transcriptional unclosuption factor G h 2521 pm/f 0.4 Primosomal protein N h 2520 pm/f 0.3 Outer membrane protein, protease VII h 2610 pm/f 0.3 S05 ribosomal subunit protein 1.1 h 2630 pm/f 0.3 S05 ribosomal subunit protein 1.2 h 2630 pm/f 0.3 S05 ribosomal subunit protein 1.4 h 2630 pm/f 0.3 S05 ribosomal subunit protein 1.4 h 2630 pm/f 0.3 S05 ribosomal subunit protein 1.6 h 2631 pm/f 0.4 S05 ribosomal subunit protein 1.6 h 2631 pm/f 0.3 S05		b1003	yccJ	2.6	Function unknown
b2597 y/rA 3.4Rubosome-associated factor, stabilizes rubosomes against dissociationb2946 3884 20Function unknownb3160 $yhbW$ 29Pulative monocogenaseb3161 $yhbW$ 23Puritive transcriptional regulator (AraC/XylS family)b4376 $yhfS$ 39Perric hydroxanate transportb4376 $yhfS$ 22Pulative hydrolaseb4378 $yhfZ$ 22Pulative hydrolase, FI sector, apha subunitb5378 apf 0.4Membrane-bound ATP synthase, FI sector, aphan subunitb5378 apf 0.3Membrane-bound ATP synthase, FI sector, aphan subunitb5378 apf 0.4Membrane-bound ATP synthase, FI sector, domain to the transcriptional model of the transcription of the transc		b1198	ycgC	2.3	Function unknown
$ b2946 gggf 2.0 \\ b1306 ybbW 2.9 \\ b13516 ybX 2.2 \\ b13516 ybX 2.2 \\ b13556 ybX 2.2 \\ b13756 ybX 2.2 \\ b13756 ybW 2.3 \\ b13756 ybW 2.5 \\ b13756 ybW 2.5 \\ b13757 ybW 2.5 \\ b1375 ybW 2.5 \\ b1357 ybW 2.5 \\ b13510 fint A 2.5 \\ b13510 fi$		b2597	yfiA	3.4	Ribosome-associated factor, stabilizes ribosomes against dissociation
billof $phDP$ 2.3 Putative transcriptional regulator (AraCXylS family)bi355 yaC 3.3Pitative transcriptional regulatorbi450 yyT 2.2Pitative transcriptional regulatorbi373 apf 0.4Membran-bound ATP synthase. FI sector, alpha subunitbi373 apf 0.3Membran-bound ATP synthase. FI sector, delta subunitbi3735 apf 0.3Membran-bound ATP synthase subunit, FI-F0-type proton-ATPasebi0205bi22050.4Function unknowabi3739 apf 0.3Outer membrane protein, portanebi3739 apf 0.3Outer membrane protein, portanebi3739 apf 0.3Aspartate transcriptional sets of S0 subunitbi3205 pmR 0.3Aspartate transcriptional sets of S0 subunitbi320 pmR 0.3Aspartate transcriptional sets of S0 subunitbi3309 pmR 0.4S0 sithosomal subunit protein L3bi3309 pmR 0.3S0 sithosomal subunit protein L4bi3309 pmR 0.4S0 sithosomal subunit protein L6bi3308 pmR 0.4S0 sithosomal subunit protein L6bi3308 pmR 0.4S0 sithosomal subunit protein L16bi33		b2946	yggJ	2.0	Function unknown
bission product transcriptional regulation (ArEAA)s family) bission product transcriptional regulation bission product transcription product transcriptional regulation bission product transcription product transcription product transcription bission product transcription product transcription product transcription product transcription bission product transcription product transcription product transcription product transcription bission product transcription product transcription product transcription bission product transcription product transcription product transcription bission product transcription product		b3160	yhbW	2.9	Putative monooxygenase
bitsb		D3510	yniX wi-C	2.3	Putative transcriptional regulator (AraC/XyIS family)
bit $3/3^3$ $3/3^3$ 7^{11} 2.5 Funtice induction unknown NaSal-down-regulated b374 apA 0.4 Membrane-bound ATP synthase, F1 sector, alpha subunit b3731 apA 0.4 Membrane-bound ATP synthase, F1 sector, subunit b b3735 apA 0.4 Membrane-bound ATP synthase, F1 sector, subunit b b3735 apH 0.3 Membrane-bound ATP synthase, F1 sector, subunit b b3735 apH 0.4 Membrane-bound ATP synthase, F1 sector, subunit b b3735 apH 0.4 Membrane-bound ATP synthase, F1 sector, subunit b b3736 apF 0.3 Membrane-bound ATP synthase, F1 sector, subunit b b3201 <i>fis.</i> 0.2 Transcriptional activator for rRNA operons b3215 $ompC$ 0.5 Outer membrane protein, poria b1225 $ompT$ 0.3 Outer membrane protein, poria b1245 prH 0.4 Aspartate transcraburghase, catalytic subunit b3219 pfD 0.3 S05 ribosomal subunit protein L12 b3230 pfH		03333 b4267	ylaG	3.3 2.0	Futative transcriptional regulator
bit D_{11} D_{11} D_{11} NaSal-down-regulated bit bit T_{11} D_{11} NaSal-down-regulated bit bit T_{11} D_{11} D_{11} NaSal-down-regulated bit bit D_{11} D_{11} D_{11} NaSal-down-regulated bit D_{11} D_{11} D_{11} D_{11} NaSal-down-regulated bit D_{11} D_{11} D_{11} D_{11} bit D_{11} D_{11} D_{11} D_{11} D_{11} bit D_{11}		04307 b/278	yjj5 wii1/	3.9	Putativo hydroloso
Našal-down-regulated byg/J Los Function unknown Našal-down-regulated b3731 $atpC$ 0.4 Membrane-bound ATP synthase, F1 sector, alpha subunit b3735 $atpF$ 0.3 Membrane-bound ATP synthase, F1 sector, alpha subunit b3735 $atpF$ 0.3 Membrane-bound ATP synthase, F1 sector, alpha subunit b3735 $atpF$ 0.3 Membrane-bound ATP synthase, F1 sector, alpha subunit b3735 $atpF$ 0.4 Function unknown b3205 $btZ25$ 0.4 Function unknown b3215 $atpC$ 0.5 Outer membrane protein, portin b3230 $fut.4$ 0.4 Function unknown b3241 ptB 0.4 Aspartate transcrabarylase, catabylic subunit b3259 $ptmH$ 0.3 Outer membrane protein, protein modification b3259 $ptmH$ 0.3 S05 rhosomal subunit protein 1.2 b330 pfC 0.5 S05 rhosomal subunit protein 1.2 b3317 pfB 0.3 S05 rhosomal subunit protein 1.2 b3320		b3008	yjjv vgiD	2.2	Function unknown
NaSal-down-regulatedbi734 bi731 apA 0.4Membrane-bound ATP synthase, F1 sector, alpha subunit bi736 bi735 bi735 bi735 apH 0.3Membrane-bound ATP synthase, F1 sector, alpha subunit bi739 bi739 apH 0.3Membrane-bound ATP synthase, F1 sector, alpha subunit bi739 $bi730$ apH a		05090	уцµ	2.0	Function unknown
b)311 apL 0.3Membrane-bound ATP synthase, F0 sector, subunit bb)325 apH 0.3Membrane-bound ATP synthase, F0 sector, subunit bb)323 apH 0.4Membrane-bound ATP synthase, F0 sector, subunit bb)324 fis 0.2Function unknownb)325 fis 0.2Transcriptional activator for rRNA operonsb)3340 $fisA$ 0.4Fusidic acid resistance; protein chain elongation factor Gb)225 $onpC$ 0.3Outer membrane protein, porinb)340 $fisA$ 0.4Fusidic acid resistance; inclusion modificationb)225 $ompC$ 0.3Outer membrane protein, porinb)545 $ompC$ 0.3Outer membrane protein, porinb)545 $ompC$ 0.3Sof rbosomal subuint protein IL1b)547 puR 0.4Aspartate transcarbanghase, catalytic subunitb)5289 pmA 0.3Sof rbosomal subuint protein IL2b)3301 $pulD$ 0.3Sof rbosomal subunit protein IL3b)3319 $pulD$ 0.3Sof rbosomal subunit protein IL4b)3305 $pulE$ 0.3Sof rbosomal subunit protein IL6b)3305 $pulE$ 0.3Sof rbosomal subunit protein IL6b)3305 $pulE$ 0.3Sof rbosomal subunit protein IL7b)3385 $pulD$ 0.3Sof rbosomal subunit protein IL6b)3301 $pulD$ 0.3Sof rbosomal subunit protein IL6b)3302 $pulD$ 0.3Sof rbosomal subunit protein IL6b)3303 $pulD$ <td>NaSal-down-regulated</td> <td>b3734</td> <td>atpA</td> <td>0.4</td> <td>Membrane-bound ATP synthase, F1 sector, alpha subunit</td>	NaSal-down-regulated	b3734	atpA	0.4	Membrane-bound ATP synthase, F1 sector, alpha subunit
b) b		D3/31	atpC	0.4	Membrane-bound ATP synthese, F1 sector, epsilon subunit
b) 133 app 0.3 Membrane-bound ATP synthase, subunit, P1-Obype proton-ATPase b) 255 b) 255 0.4 Function unknown b) 2561 fis 0.2 Transcriptional activator for rRNA operons b) 340 fis. 0.4 Fusicic acid resistance; protein chain elongation factor G b) 251 and C 0.3 Outer membrane protein, porin b) 252 and C 0.3 Outer membrane protein, porin b) 252 and C 0.3 Outer membrane protein, protease VII b) 252 pmA 0.3 Methyltrans/erase for 50S subunit L11 protein modification b) 252 pmA 0.3 Signification activation protein N b) 252 pmA 0.3 Signification activation protein N b) 252 pmA 0.3 Signification activation activati		03/30 b2725	aipr atpH	0.3	Memorane-bound ATP synthese, F0 sector, subunit b
b):15:5 μ_{D} 0.4:7We intribute volume Art i syntase submit, if 2^{10} pipe problem Art is setb):25:5 b_{12} 0.2:7Transcriptional activator for rRNA operonsb):35:40fu:A0.4Fusicia cid resistance; protein chain elongation factor Gb):21:5 $ompC$ 0.5Outer membrane protein, protease VIIb):05:65 $ompT$ 0.3Outer membrane protein, protease VIIb):05:259 $prnA$ 0.3Methyltransferase for 50S subunit L11 protein modificationb):05:259 $prrA$ 0.3Soft inbosomal subunit protein L1b):05:261 prB 0.4Apartate transcarbamylase; catalydific subunitb):05:279 prB 0.4Apartate transcarbamylase; catalydific subunitb):05:05 prB 0.550S ribosomal subunit protein L2b):05:05 prB 0.350S ribosomal subunit protein L4b):05:05 prB 0.450S ribosomal subunit protein L6b):05:05 prB 0.350S ribosomal subunit protein L10b):05:08:07 prB 0.350S ribosomal subunit protein L11b):05:08:07 prB 0.350S ribosomal subunit protein L12b):05:08:07 prB 0.450S ribosomal subunit protein L14b):05:08:07 prB 0.450S ribosomal subunit protein L14b):05:08:07 prB 0.450S ribosomal subunit protein L14b):05:08:07 prB 0.450S ribosomal subunit protein L15b):05:08:07 prB 0.450S ribosomal subunit protein L14 </td <td></td> <td>b3733</td> <td>atp1</td> <td>0.5</td> <td>Memorane-bound ATP synthese subunit E1 E0 type proton ATPase</td>		b3733	atp1	0.5	Memorane-bound ATP synthese subunit E1 E0 type proton ATPase
b3251 $b3261$ $fits$ 0.2 Transcriptional activator for rRNA operonsb3340 $futA$ 0.4Fusidic acid resistance: protein chinal elongation factor Gb2215 $ompC$ 0.5Outer membrane protein, poriases VIIb4201 $priB$ 0.4Primosomal proteinb4245 pyB 0.4Primosomal proteinb4245 pyB 0.4Aspartate transcriptions VIIsb4245 pyB 0.4Aspartate transcriptionsb3306 rp/L 0.3505 ribosomal subunit protein L1b3317 rp/B 0.3505 ribosomal subunit protein L3b3319 rp/L 0.5505 ribosomal subunit protein L4b3308 rp/R 0.4505 ribosomal subunit protein L5b3305 ppH 0.3505 ribosomal subunit protein L6b4203 rpH 0.2505 ribosomal subunit protein L7b3985 rpH 0.3505 ribosomal subunit protein L11b3986 rpH 0.3505 ribosomal subunit protein L7b3986 rp/H 0.4505 ribosomal subunit protein L7b3310 rp/N 0.4505 ribosomal subunit protein L14b3311 rp/R 0.3505 ribosomal subunit protein L14b3312 rp/R 0.4505 ribosomal subunit protein L14b3313 rp/R 0.3505 ribosomal subunit protein L14b3314 rp/R 0.4505 ribosomal subunit protein L14b3315 rp/R 0.4505 ribosomal subunit protein L14b3316 </td <td></td> <td>b0205</td> <td>60205</td> <td>0.4</td> <td>Function unknown</td>		b0205	60205	0.4	Function unknown
basis for the second s		b3261	00295 fis	0.4	Transcriptional activator for rRNA operons
b215 $ongC$ 0.5 Outer membrane protein, portan to the order of the second seco		b3340	fus A	0.2	Fusidic acid resistance: protein chain elongation factor G
basis $onp T$ 0.3 Outer membrane protein proteinse VII b4201 $priB$ 0.4 Primosonal protein N b4201 $priB$ 0.4 Apartate transcarbamylase, catalytic subunit b4245 $pyrB$ 0.4 Apartate transcarbamylase, catalytic subunit b4245 $pyrB$ 0.4 Apartate transcarbamylase, catalytic subunit b4245 $pyrB$ 0.4 Apartate transcarbamylase, catalytic subunit b5317 ptB 0.3 50S ribosomal subunit protein L1 b5317 ptB 0.3 50S ribosomal subunit protein L3 b5319 ptD 0.3 50S ribosomal subunit protein L4 b53308 ptE 0.4 50S ribosomal subunit protein L5 b5305 ptF 0.3 50S ribosomal subunit protein L6 b5305 ptH 0.3 50S ribosomal subunit protein L6 b5305 ptH 0.3 50S ribosomal subunit protein L6 b5305 ptH 0.3 50S ribosomal subunit protein L10 b53983 ptH 0.3 50S ribosomal subunit protein L10 b53983 ptH 0.3 50S ribosomal subunit protein L11 b53986 ptH 0.3 50S ribosomal subunit protein L11 b53981 ptH 0.4 50S ribosomal subunit protein L11 b53910 ptH 0.2 50S ribosomal subunit protein L11 b53310 ptH 0.4 50S ribosomal subunit protein L11 b53310 ptH 0.4 50S ribosomal subunit protein L14 b53311 ptH 0.4 50S ribosomal subunit protein L14 b53311 ptH 0.4 50S ribosomal subunit protein L14 b53311 ptH 0.4 50S ribosomal subunit protein L14 b53313 ptH 0.3 50S ribosomal subunit protein L14 b53314 ptH 0.4 50S ribosomal subunit protein L12 b5315 ptW 0.1 50S ribosomal subunit protein L12 b5315 ptW 0.4 50S ribosomal subunit protein L21 b5315 ptW 0.4 50S ribosomal subunit protein L21 b5315 ptW 0.4 50S ribosomal subunit protein L21 b5315 ptW 0.4 50S ribosomal subunit protein L24 b5316 ptH 0.3 50S ribosomal subunit protein L24 b5317 ptH 0.4 50S ribosomal subunit protein L24 b5318 ptW 0.4 50S ribosomal subunit protein L24 b5319 ptH 0.3 50S ribosomal subunit protein L25 b5302 ptH 0.3 50S ribosomal subunit protein S3 b5309 ptH 0.3 50S ribosomal subunit protein S3 b5309 ptH 0.3 50S ribosomal subunit protein S3 b5309 ptH 0.3 30S ribosomal subunit protein S3 b5309 ptH 0.3 30S ribosomal subunit protein S3 b53		b2215	ompC	0.5	Outer membrane protein, porin
b4201prdb0.4Primosomal protein Nb4259 pmA 0.3Methyltransferase for 50S subunit L11 protein modificationb4245 $prdb$ Aspartate transcarbamylase, catalylic subunitb3984 $rplA$ 0.350S ribosomal subunit protein L2b3320 $rplC$ 0.550S ribosomal subunit protein L3b3320 $rplC$ 0.350S ribosomal subunit protein L4b3308 $rplE$ 0.450S ribosomal subunit protein L6b3305 $rplI$ 0.250S ribosomal subunit protein L6b4203 $rplI$ 0.250S ribosomal subunit protein L10b3985 $rplI$ 0.350S ribosomal subunit protein L7112b3985 $rplI$ 0.350S ribosomal subunit protein L7112b3983 $rplM$ 0.450S ribosomal subunit protein L7112b3231 $rplM$ 0.350S ribosomal subunit protein L7112b3231 $rplM$ 0.350S ribosomal subunit protein L13b3310 $rplN$ 0.350S ribosomal subunit protein L14b3311 $rplQ$ 0.350S ribosomal subunit protein L15b3312 $rplR$ 0.450S ribosomal subunit protein L15b3313 $rplR$ 0.450S ribosomal subunit protein L14b3304 $rplR$ 0.450S ribosomal subunit protein L15b3315 $rplR$ 0.450S ribosomal subunit protein L24b3316 $rplR$ 0.450S ribosomal subunit protein L24b3315 $rplR$ 0.450S ribosomal subunit protein L24<		b0565	ompT	0.3	Outer membrane protein, protease VII
b3259 pmA 0.3Methyltransferase for 500 subunit L11 protein modificationb4245 $pyrB$ 0.4Aspartate transcabamylase, catalytic subunitb3984 pHA 0.3505 ribosomal subunit protein L1b3317 pHB 0.3505 ribosomal subunit protein L2b3320 pHC 0.5505 ribosomal subunit protein L3b3319 pHD 0.3505 ribosomal subunit protein L4b3308 pHE 0.3505 ribosomal subunit protein L5b3305 pHE 0.3505 ribosomal subunit protein L9b3983 pHL 0.3505 ribosomal subunit proteinb3985 pHL 0.3505 ribosomal subunit proteinb3986 pHL 0.3505 ribosomal subunit proteinb3110 pHN 0.4505 ribosomal subunit proteinb3131 pHN 0.4505 ribosomal subunit proteinb3313 pHN 0.4505 ribosomal subunit proteinb3314 pHN 0.3505 ribosomal subunit proteinb3315 pHN 0.4505 ribosomal subunit proteinb3316 pHV 0.3505 ribosomal subunit proteinb3318 pHV 0.4505 ribosomal subunit proteinb3318 pHV 0.4505 ribosomal subunit proteinb3318 pHV 0.4505 ribosomal subunit proteinb3319 pHX 0.3505 ribosomal subunit proteinb3319 pHX 0.4505 ribosomal subunit proteinb3319 pHX 0.4505 ribosoma		b4201	priB	0.4	Primosomal protein N
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b3984 pA 0.350\$ rbosomal subunit protein L1b3317 pB 0.350\$ rbosomal subunit protein L2b3320 ppC 0.550\$ rbosomal subunit protein L3b3319 ppD 0.350\$ rbosomal subunit protein L4b3308 pFE 0.450\$ rbosomal subunit protein L5b3030 ppI 0.250\$ rbosomal subunit protein L9b4203 ppI 0.350\$ rbosomal subunit protein L10b3985 ppI 0.350\$ rbosomal subunit protein L11b3986 ppI 0.350\$ rbosomal subunit protein L11b3987 ppI 0.450\$ rbosomal subunit protein L11b3988 ppI 0.350\$ rbosomal subunit protein L14b3310 plO 0.450\$ rbosomal subunit protein L16b3311 ppO 0.450\$ rbosomal subunit protein L16b3313 $ppIQ$ 0.350\$ rbosomal subunit protein L16b3314 pPQ 0.350\$ rbosomal subunit protein L16b3315 pPV 0.150\$ rbosomal subunit protein L18b3315 ppW 0.350\$ rbosomal subunit protein L2b3315 pPV 0.150\$ rbosomal subunit protein L2b3315 pPW 0.350\$ rbosomal subunit protein L2b3315 pPW 0.450\$ rbosomal subunit protein L2b3315 pPW 0.450\$ rbosomal subunit protein L2b3315 pPW 0.450\$ rbosomal subunit protein L2b3315 pPM 0.450\$ rbosomal subunit p		b4245	pyrB	0.4	Aspartate transcarbamylase, catalytic subunit
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b3319 $rplD$ 0.350S ribosomal subunit protein L4b3308 $rplF$ 0.450S ribosomal subunit protein L5b4203 $rplI$ 0.250S ribosomal subunit protein L6b4203 $rplI$ 0.250S ribosomal subunit protein L10b3985 $rplK$ 0.450S ribosomal subunit protein L10b3986 $rplL$ 0.350S ribosomal subunit protein L7/L12b3231 $rplM$ 0.450S ribosomal subunit protein L14b3301 $rplN$ 0.350S ribosomal subunit protein L15b3313 $rplP$ 0.250S ribosomal subunit protein L16b3234 $rplQ$ 0.350S ribosomal subunit protein L16b3394 $rplQ$ 0.350S ribosomal subunit protein L18b3186 $rplW$ 0.450S ribosomal subunit protein L21b3318 $rplW$ 0.450S ribosomal subunit protein L23b3309 rpR 0.350S ribosomal subunit protein L24b3312 $rpmW$ 0.450S ribosomal subunit protein L24b3313 $rplW$ 0.450S ribosomal subunit protein L24b3314 $rplW$ 0.450S ribosomal subunit protein L24b3315 $rpmA$ 0.450S ribosomal subunit protein L26b3316 $rpmH$ 0.450S ribosomal subunit protein L27b3317 $rpmH$ 0.450S ribosomal subunit protein L28b3318 $rpmM$ 0.450S ribosomal subunit protein L29b3312 $rpmA$ 0.450S ribosomal subunit protein L29b3313<		b3320	rplC	0.5	50S ribosomal subunit protein L3
b5308 $pplE$ 0.4508 ribosomal subunit protein L5b3305 $rplI$ 0.2508 ribosomal subunit protein L9b3985 $rplI$ 0.3508 ribosomal subunit protein L10b3986 $rplL$ 0.3508 ribosomal subunit protein L11b3986 $rplL$ 0.3508 ribosomal subunit protein L11b3283 $rplM$ 0.4508 ribosomal subunit protein L13b3231 $rplM$ 0.4508 ribosomal subunit protein L14b3301 $rplO$ 0.4508 ribosomal subunit protein L16b3294 $rplQ$ 0.3508 ribosomal subunit protein L16b3294 $rplR$ 0.4508 ribosomal subunit protein L17b3304 $rplR$ 0.4508 ribosomal subunit protein L18b3185 $rplW$ 0.1508 ribosomal subunit protein L21b3318 $rplW$ 0.3508 ribosomal subunit protein L21b3318 $rplW$ 0.4508 ribosomal subunit protein L24b3312 $rpmA$ 0.4508 ribosomal subunit protein L24b3312 $rpmC$ 0.3508 ribosomal subunit protein L28b3312 $rpmC$ 0.3508 ribosomal subunit protein L30b3302 $rpmD$ 0.3508 ribosomal subunit protein A (L35)b3295 $rpoA$ 0.4808 ribosomal subunit protein S2b3314 $rpsC$ 0.4308 ribosomal subunit protein S2b3314 $rpsC$ 0.4308 ribosomal subunit protein S3b3295 $rpoA$ 0.4308 ribosomal subunit protein S4b3303 </td <td></td> <td>b3319</td> <td>rplD</td> <td>0.3</td> <td>50S ribosomal subunit protein L4</td>		b3319	rplD	0.3	50S ribosomal subunit protein L4
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b3985 rpl / 0.3 50S ribosomal subunit protein L10 b3986 rpl / 0.3 50S ribosomal subunit protein L11 b3986 rpl / 0.3 50S ribosomal subunit protein L12 b3231 rpl / 0.4 50S ribosomal subunit protein L14 b3301 rpl / 0.3 50S ribosomal subunit protein L14 b3301 rpl / 0.4 50S ribosomal subunit protein L16 b3313 rpl / 0.2 50S ribosomal subunit protein L16 b3304 rpl / 0.3 50S ribosomal subunit protein L17 b3304 rpl / 0.4 50S ribosomal subunit protein L17 b3304 rpl / 0.3 50S ribosomal subunit protein L17 b3304 rpl / 0.4 50S ribosomal subunit protein L18 b3186 rpl / 0.1 50S ribosomal subunit protein L21 b3318 rpl / 0.4 50S ribosomal subunit protein L22 b3318 rpl / 0.4 50S ribosomal subunit protein L22 b3318 rpl / 0.4 50S ribosomal subunit protein L24 b3318 rpl / 0.4 50S ribosomal subunit protein L24 b3318 rpm / 0.4 50S ribosomal subunit protein L27 b3637 rpm / 0.4 50S ribosomal subunit protein L28 b3312 rpm / 0.3 50S ribosomal subunit protein L28 b3312 rpm / 0.4 50S ribosomal subunit protein L30 b1717 rpm / 0.4 50S ribosomal subunit protein L30 b1717 rpm / 0.4 50S ribosomal subunit protein A (L35) b3299 rpn / 0.3 50S ribosomal subunit protein X (L36) b3295 rpo / 0.4 RNA polymerase, alpha subunit b169 rps // 0.4 30S ribosomal subunit protein S2 b3303 rpx // 0.4 30S ribosomal subunit protein S2 b3303 rpx // 0.3 30S ribosomal subunit protein S3 b3304 rpx // 0.3 30S ribosomal subunit protein S3 b3305 rpx // 0.4 30S ribosomal subunit protein S3 b3306 rpx // 0.3 30S ribosomal subunit protein S4 b3303 rpx // 0.3 30S ribosomal subunit protein S5 b3306 rpx // 0.3 30S ribosomal subunit protein S8 b3307 rpx // 0.3 30S ribosomal subunit protein S11 b3307 rpx // 0.3 30S ribosomal subunit protein S11 b3307 rpx // 0.3 30S ribosomal subunit protein S11 b3307 rpx // 0.3 30S ribosomal subunit protein S14 b2609 rpx // 0.3 30S ribosomal subunit protein S17		b4203	rplI	0.2	50S ribosomal subunit protein L9
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b2609 $rpsP$ 0.3 30S ribosomal subunit protein S14 b3311 $rpsQ$ 0.3 30S ribosomal subunit protein S16		b3307	rnsN	0.3	30S ribosomal subunit protein S11
b3311 $rpsQ$ 0.3 30S ribosomal subunit protein S17		b2609	rnsP	0.3	30S ribosomal subunit protein S16
cees you, on contrologian brown brown brown		b3311	rpsO	0.3	30S ribosomal subunit protein S17

Gene type	No.	Gene	Ratio	Description
	b3316	rpsS	0.2	30S ribosomal subunit protein S19
	b0023	rpsT	0.4	30S ribosomal subunit protein S20
	b0121	speE	0.4	Spermidine synthase
	b4240	treB	0.4	IITre, translocation system, Tre-specific PTS enzyme II
	b2607	trmD	0.3	tRNA (guanine-7)-methyltransferase
	b3384	trpS	0.5	Tryptophanyl-tRNA synthetase
	b0170	tsf	0.5	EF-Ts, elongation factor for transcription, stable
	b3339	tufA	0.5	Duplicate gene for EF-Tu subunit, elongation factor, unstable
	b2014	yeeF	0.4	Putative amino acid transport protein

TABLE 2—Continued

^a No., unique identifier. Boldface denotes genes modulated by either exposure to NaSal or MarA expression.

^b PTS, phosphotransferase system.

For those experiments involving induction of the SoxS and MarA transcription factors, we performed a single experiment. However, we included in our analysis only those genes that were also modulated in the duplicate experiment involving the corresponding global inducer.

PQ activates genes involved in pathways that reconstitute NADH and NADPH pools. PQ is reduced intracellularly at the expense of NADPH in a reaction catalyzed by at least three oxidoreductases (26). PQ reduced by one electron is oxidized by O_2 to form superoxide, resulting in a redox cycle that produces a flux of superoxide. Thus, the cell faces a double threat under exposure to PQ and to other redox-cycling agents: the deleterious effects of superoxide itself and the decreased level of NADPH that limits biosynthetic capabilities. Equilibration of NADPH with NADH would generalize this limitation of cellular reducing power.

Previous observations suggested that treatment of growing

cells with PQ induces pathways that replenish reducing power. First, PQ activates the expression of glucose-6-phosphate dehydrogenase, the first enzyme of the pentose phosphate pathway (19, 24). This pathway generates NADPH and is required for resistance to redox-cycling agents (17a). Second, PQ also activates the expression of two enzymes of the tricarboxylic acid cycle, fumarase C and aconitase. These enzymes contribute to the reduction of NAD⁺. The coordinated activation of G6PD, fumarase C, and aconitase by PQ occurs at the transcriptional level in a *soxRS*-dependent manner.

In our studies, exposure to PQ activated the expression of additional genes involved in pathways that contribute to replenish reducing power. These genes code for proteins involved in sugar transport (*ptsG*, *gatABD*, *malEK*, *lamB*), glycolysis (*pgi*), amino acid transport and degradation (*artIP*, *tnaA*, *dadX*), and the tricarboxylic acid cycle (*gltA*, *sdhB*, *sucD*). A similar redirection of carbon metabolism to pathways that

No.	Gene	PQ ratio	NaSal ratio	Description
b0864	artP	1.9	2.5	Arg periplasmic transport system
b1452	b1452	1.9	3.0	Function unknown
b2414	cysK	1.9	2.4	Cysteine synthase A
b4383	deoB	1.9	2.1	Deoxyribouratase, phosphopentomutase
b0812	dps	1.7	7.0	Stress response DNA-binding protein
b1611	fumC	6.9	8.4	Fumarase C, aerobic; member of soxRS regulon
b2094	gatA	2.9	5.3	Galactitol-specific enzyme IIA of PTS^b
b2093	gatB	3.7	5.2	Galactitol-specific enzyme IIB of PTS
b2091	gatD	1.7	3.8	Galactitol-1-phosphate dehydrogenase
b0720	gltA	3.1	2.6	Citrate synthase
b2237	inaA	2.9	3.9	Function unknown
b1531	marA	2.6	11.3	Transcription activator of multiple-antibiotic-resistance system
b0578	nfnB	2.1	3.4	Resistance to nitrofurantoin; a nitroreductase
b4245	pyrB	0.3	0.4	Aspartate transcarbamylase, catalytic subunit
b3908	sodA	12.3	2.3	Member of <i>soxRS</i> regulon; superoxide dismutase, Mn
b0850	ybjC	1.7	2.7	Function unknown
b3317	rplB	1.9	0.3	50S ribosomal subunit protein L2
b3319	rplD	2.5	0.3	50S ribosomal subunit protein L4
b3305	rplF	1.7	0.3	50S ribosomal subunit protein L6
b3318	rplW	1.8	0.4	50S ribosomal subunit protein L23
b3312	rpmC	1.7	0.3	50S ribosomal subunit protein L29
b3314	rpsC	1.7	0.4	30S ribosomal subunit protein S3
b3321	rpsJ	2.0	0.3	30S ribosomal subunit protein S10
b3316	rpsS	1.7	0.2	30S ribosomal subunit protein S19
b2597	<i>y</i> fiA	0.5	3.4	Ribosome-associated factor, stabilizes ribosomes against dissociation
b3516	yhiX	0.5	2.3	Putative transcriptional regulator (AraC/XylS family)

TABLE 3. List of genes^a

^a No., unique identifier. Underlining denotes previously characterized soxRS genes.

^b PTS, phosphotransferase system.

reconstitute NADPH was observed in *S. cerevisiae* after treatment with hydrogen peroxide and proteome analysis by twodimensional gels (17). Thus, regenerating NADPH may be a fundamental and general aspect of cellular responses to oxidative stress.

Evidence for adaptation and repair pathways under oxidative stress. Challenge of growing E. coli cells with PQ induces the genes coding for nine ribosomal proteins (Table 1). This increase in ribosomal building blocks was not predicted, in that the bacterial growth rate was not significantly affected during the 45-min treatment with PQ. Another gene coding for a translational regulator, fmt, is also induced by PQ. The product of this gene, methionyl-tRNA formyltransferase, is an important factor in translational initiation (21). One possibility is that increased translational capacity counterbalances a faster turnover of proteins due to oxidative damage and increased degradation. In this scenario, enhanced synthesis would be required to maintain the high growth rate. The possibility of an increased metabolic rate under superoxide stress is consistent with the activation of genes coding for products involved in crucial anabolic and catabolic pathways. These genes include nuol and nuoK coding for subunits of NADPH dehydrogenase, the first electron acceptor of the respiratory chain. Interestingly, 11 out of the 12 genes coding for NADPH dehydrogenase subunits showed some degree of activation in both PQ exposure experiments, albeit below the statistical threshold levels.

Recently, a direct regulatory connection between oxidative stress and iron metabolism was shown by Zheng et al., who demonstrated the transcriptional activation of fur by SoxS and OxyR (49). Our work confirmed the activation of fur by superoxide stress. In addition to the increase in fur expression, superoxide stress resulted in the down-regulation of sodB, a Fur-activated gene (13). Collectively, these changes in gene expression are consistent with a phenotypic iron deficiency in PQ-treated cells, but how this deficiency might be caused by oxidative stress is unknown. It has been suggested that the Fur-iron complex is sensitive to oxidative damage and that this damage leads to the eventual loss of repressor function (49). An alternative hypothesis is based on the observation that Fe^{3+} does not seem to function as corepressor. It is possible that under oxidative stress the Fe²⁺ associated with Fur is oxidized to Fe³⁺, which leads to the derepression of Furrepressed genes. While observing that fur is not activated by treatment with NaSal, it is important to note that modulation by Fur does not account for all the observed regulation of iron uptake.

The activation of the dadX and murF genes, coding for proteins involved in peptidoglycan synthesis, and of the lpxC gene, coding for an enzyme involved in lipopolysaccharide synthesis, suggests that the repair mechanisms triggered by oxidative stress extend to extracytoplasmic structures.

Common themes in the responses to PQ and NaSal. The list of genes activated by treatment of *E. coli* with PQ or NaSal (Table 3) is a first approximation to the common solutions to the physiological challenges posed by these two compounds. In addition to the common genes listed in Table 3, many other genes activated by the individual stresses have comparable functions. For example, the induction of genes involved in sugar transport occurs in both situations, albeit with specificity

for different sugars. Exposure to both PQ and NaSal results in activation of the galactitol (*gat*) operon, while exposure to PQ activates the additional glucose and maltose transport genes (Table 1) and exposure to NaSal activates genes for the transport of sorbitol and mannose (Table 2).

At first sight, our results might appear to be inconsistent with those recently published by Barbosa and Levy (5), who also employed gene arrays from the same supplier. Despite this similarity, we detect only about one-third of the MarA-regulated genes that they proposed (5), while identifying 67 others. The actual disagreement may be less dramatic, however. Firstly, and noted earlier, gene arrays can miss large fractions of a coregulated group, as in the case of the heat shock regulon (37). Moreover, two methodological differences might have contributed to the observed discrepancies. Barbosa and Levy based their genomic analysis on a strain that expresses MarA constitutively, as opposed to our inducible MarA expression system. The constitutive expression of a gene regulator might provoke both direct and indirect gene modulation, thereby producing a different set of modulated genes. The statistical treatment of the data also differed between the two studies at several levels. Barbosa and Levy used an expression level cutoff equal to twice the average background level, while we set the threshold at the mean background plus 3 standard deviations. Barbosa and Levy also chose to treat both replicate experiments separately, admitting genes with the arbitrary expression ratio of at least 2 in one experiment and the same trend (≥ 1.2) in the other. We have averaged our two replicates and included only genes above a statistical cutoff of 2.5 standard deviations from the mean of the log ratios. In spite of these differences, both studies coincide on many novel genes, providing independent evidence for novel regulatory connections between MarA and its target genes. Finally, this example of independent studies addressing similar questions underscores the need for the availability of complete genomic data sets that can be compared beyond the particular statistical treatment selected by the original researchers.

From statistical significance to biological relevance. Transcriptional profiling can measure changes in only the steadystate levels of mRNA, and the significance of these changes can be estimated by statistical analysis. However, the biological relevance of the detected variations in mRNA levels must be substantiated by genetic and biochemical analysis of the functions. We have constructed deletion mutants of the genes *cysK* and *b2962* and measured the sensitivity of these strains to PQ and other oxidants. Preliminary results show that both deletion mutants are hypersensitive to PQ but not to H_2O_2 or to *tert*butyl hydroperoxide (data not shown). These results suggest that even relatively small increases in gene expression, as in the cases of *cysK* and *b2962*, can point to genes with important roles in defense against oxidants.

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